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Evolutionary demography of a partial migrant shorebird species

Frédéric Touzalin

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THÈSE

En vue de l'obtention du

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Titre: Evolutionary demography of a partial migrant shorebird species

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"Writing life-history, fieldwork session around Europe"
Picture: P. Guibert

Chapter 1

General introduction

1.1 Partial migration

“The ultimate mechanisms that drive individual differences in migratory tendency remain controversial, and very little empirical work has considered the potential consequences of partial migration.”

Chapman *et al.* (2011)

The term “partial migration” comes from the ornithological literature (Lack, 1943). This phenomenon has long been identified as a widespread feature in migratory birds of the temperate zone (Berthold, 2003); it is shared by a wide range of species from many taxa (*e.g.*, invertebrates, fishes, birds, mammals) under most latitudes (except close to the poles), even in tropical birds (Boyle, 2008). Partial migration is defined as a within-population dimorphism in migratory behaviour; some individuals remain at the same place or in a territory of limited size all year round, whilst other individuals migrate to a different place for part of the year. While common, this phenomenon is poorly understood. Numerous theoretical and empirical studies have tried to elucidate the ecological and evolutionary processes explaining the emergence and persistence of partial migration and several hypotheses have been put forward (reviewed in Chapman *et al.*, 2011). The empirical support for these hypotheses remains limited and controversial, and some fundamental questions remain unanswered: why are there different migratory phenotypes within a population? How can these phenotypes persist over time? What are the evolutionary consequences of the persistence of these phenotypes?

In the current context of threats to biodiversity due to climate change and anthropogenic damages to habitats (Sutherland *et al.*, 2012), it becomes urgent to answer these questions, especially to understand how species face these rapid changes. Several processes have already been identified as responses to recent climate warming, mainly alterations of the migratory behaviour, range shift toward higher latitude or higher elevations (Chen *et al.*, 2011) and population redistribution (Maclean *et al.*, 2008). Other important phenomena are the phenological changes, especially in the patterns of date of migration (Miles *et al.*, 2017) and the shortening of migration distance (Visser *et al.*, 2009). Recent experiments, aimed at testing

hypotheses about evolutionary responses to recent climate change; they predict a shift in migration strategy toward residency (Pulido & Berthold, 2010). Partial migration offers the opportunity to study the effect of global change on phenotypes at different geographic and seasonal scales. It is reasonable to hypothesize that each migratory phenotype can be differently affected by environmental changes, which can have important consequences on the population dynamics. Indeed, recent studies have provided evidence of differences in vital rates (reproductive success) in partial migrants strategies (Grist *et al.*, 2017), or among individuals migrating over different distances (Lok *et al.*, 2017). A fundamental step to investigate differences between partial migrant phenotypes is to estimate their demographic rates and fitness.

From an evolutionary viewpoint, the question of the persistence of partial migration, *i.e.* the persistence of a polymorphism in a population, can be tackled in the framework of life history evolution theory. Indeed, each phenotype can be characterized by a combinations of life-history traits which can be subject to natural selection. The context of selection can be complex and involves behavioural (*e.g.*, mating system, dispersal), physiology (*e.g.*, senescence, somatic maintenance, immune response) or genetics (*e.g.*, mutations, heritability of traits, drift). Regardless of the processes involved in the evolution of migratory traits, estimating the overall fitness, or at least fitness components of individuals exhibiting different life-history traits remains a key point to draw inferences about the evolution of strategies by natural selection (Stearns, 1976) From this perspective, we need to characterise the main demographic rates that are responsible for the frequency distribution of the migratory strategies in the population, and their fluctuations.

Theoretical work on partial migration has previously explained its persistence by a frequency-dependent evolutionary stable state (ESS), where the point at equilibrium corresponds to equal fitness (Lundberg, 1987). In this framework, a change in a demographic rate such as survival must be compensated by a change in another demographic rate such as reproduction for maintaining equal overall fitness and allowing the persistence of a polymorphism in the population. However, recent development showed that the question of the evolution of partial migration can also be answered by density-dependant selection (Lund-

berg, 2013). However, very few empirical studies have been able to test these hypotheses, especially because most theoretical studies assume homogeneity in demographic rates in populations, or because data well suited for testing such hypotheses are difficult to collect. The persistence of the polymorphism could also involve a frequency-dependent process relying on a “conditional strategy” (Lundberg, 1988). Under this hypothesis, the individual migratory strategy is depends on intrinsic (*e.g.*, body condition, disease) and extrinsic factors (*e.g.*, climate, intra-specific competition). There are more empirical support for this hypothesis (Sanz-Aguilar *et al.*, 2012). Different migratory strategies are potentially associated with different vital rates, and different trade-offs between these rates. In this particular framework, a deeper understanding of the ecological and evolutionary processes modelling migration strategies requires. The assessment of the demographic rates characterizing each strategy.

Trade-offs are central to life-history theory (Williams, 1966; Kirkwood, 1977); individuals have to allocate their finite resources between functions. Typically, according to this “principle of allocation”, investment in current reproduction is assumed, to be traded-off against investment in future reproduction or survival (Williams, 1966; van Noordwijk & de Jong, 1986). In the context of migration, empirical studies have provided evidence that the migration carries costs on survival and reproduction; these costs depend on migration distance (Lok *et al.*, 2017). Differences in mating and breeding success have been shown in partial migrants, with a higher success in residents (Adriaensen & Dhondt, 1990). Long-lived species are considered as “survivor species” (Saether & Bakke, 2000), which suggests that migration costs are more likely to concern reproduction than survival. In addition, variability in survival is considered disadvantageous (Gaillard & Yoccoz, 2003). Consequently, we expect reproduction to be more affected than survival by migration and to exhibit more temporal variability (Saether & Bakke, 2000; Gaillard & Yoccoz, 2003). This would be consistent with a recent experimental study, in a long-live species that provided evidence that survival and offspring quality can be maintained through condition-dependant reproductive allocation (Griesser *et al.*, 2017). Reproductive traits that can be concerned by migration costs are recruitment age, brood size, cumulative investment in reproduction or

Lifetime Reproductive Success (LRS). Among them, reproductive efforts had received a particular attention (Stearns, 1992). However, detecting reproductive cost using observational data is known to be particularly difficult, and some experimental studies have been criticized (Reznick, Bryga & Endler, 1990). Recent approaches, based on phenotypic manipulations of brood size *in natura* have shown that there are direct and delayed costs of reproduction (Hanssen *et al.*, 2005). In the latter study, direct costs of incubating large clutches were a higher mass loss and a decrease in the immune function, while delayed cost was a reduction in fecundity the following year. Moreover, a number of long-term empirical studies have documented a positive correlation between survival and reproduction in different taxa (Cam *et al.*, 2002; Beauplet *et al.*, 2006; Weladji *et al.*, 2008; Hamel *et al.*, 2009; Cam *et al.*, 2013). These results do not refute the hypothesis of costs, but they highlight the need for carefully designed analyses that allow addressing costs within homogeneous classes of individuals (van Noordwijk & de Jong, 1986). Assessing potential costs of migration on reproduction and costs of reproduction over time requires a demographic approach to estimate strategy-dependant reproductive performances, while accounting for the effect of age and reproductive states (where “state” is assumed to correspond to different levels of investment, such as breeding failure versus successful reproduction).

Another important life-history phenomenon whose evolution is assumed to involve trade-offs among traits is senescence. Senescence is characterized by a decrease in reproductive performances or in survival probability with age, and is widespread in wildlife (reviewed in Nussey *et al.*, 2013; Jones *et al.*, 2014). Costs of reproduction are the basis of one of the hypotheses put forward to explain variation in the onset of senescence in populations; if migration carries costs on reproduction, the migration strategy can also be associated with variation in the onset of senescence. Assessing the onset of senescence in vital rates according to reproductive or migratory strategy is an important way of characterising life-histories specificities. There are at least three theories of ageing. The “mutation accumulation” theory is based on the idea of accumulation of germ-line deleterious mutations whose effects appear late in life, and that are not “selected against” because detrimental effects appear when selection pressures are weak (Medawar, 1952; Edney & Gill, 1968). As the efficiency

of natural selection to eliminate these alleles is poor, we can expect a high heterogeneity in these deleterious alleles among individuals. This suggests that it is important to account for individual heterogeneity in demographic parameters to address senescence (Aubry *et al.*, 2011). The second theory, “antagonistic pleiotropy” involves pleiotropic genes, which have a positive effect on the phenotype at early life, and a negative effect at later age (Williams, 1957). This results in a life-history trade-off between early advantages and costs later in life. The third theory, the “disposable soma” is also based on a trade-off, but specifically between resources allocation for somatic maintenance and reproductive functions. This theory predicts that early investment in reproduction will carry costs expressed by an earlier onset of senescence (Kirkwood, 1977; Kirkwood & Austad, 2000). The two latter lead to similar expected pattern of variation in reproductive performance over reproductive life, but the former rests on genetic mechanisms, while the latter rests on trade-off between energy allocation to maintenance and repair mechanisms. The hypotheses that migration can affect reproductive success (Adriaensen & Dhondt, 1990) and that migration strategies are associated with different reproductive costs suggest that these strategies can be associated with different aging patterns. This pleads for the assessment of age-dependant demographic rates. There are increasing evidences of the effect of early investment in reproduction and earlier ageing in life (Charmantier *et al.*, 2006).

The estimation of demographic rates and ultimately of the individual fitness remains the key for understanding the evolution of partial migration. The description of migration strategies involves determining whether individuals always adopt the same strategy during their life, which can be achieved by estimating transition probabilities between yearly “states”, where state is the wintering destination (either in the vicinity of breeding grounds, or not). Such an approach is also useful to address temporal changes in the frequency of strategies in populations. Estimated demographic parameters (age-specific breeding and survival probabilities) are required to understand the dynamics of each migratory strategy. Migratory phenotypes can be characterised by their main vital rates: survival, fecundity, recruitment age or composite measures such as LRS. These demographic rates can also help to disentangle the trade-offs between early and late performances (*e.g.*, growth, somatic maintenance,

survival, reproduction).

1.2 The case of Pied Avocet

The Pied Avocet is a long-lived shorebird that has been relatively little studied but that is on the forefront of species facing environmental changes due to both climate changes and direct anthropogenic effects (Sutherland *et al.*, 2012). The species indeed use of natural or man-made wetland areas during both winter and breeding seasons. After a sharp decline since the 19th century, the number of Pied Avocet is increasing since the second half of the 20th century and colonized France mainly in the late 70's. Shorebirds are amongst the first species to respond to environmental changes, through processes such as population redistribution (Maclean *et al.*, 2008).

1.2.1 General description

The Pied Avocet (*Recurvirostra avosetta*) is a wader with a completely white and black plumage, weighting between 220 and 400 g. This slender bird is characterised by long blue legs and especially by a thin long and upcurved black bill (7 - 9 cm). The sexual dimorphism is weak, the females having a slightly more strongly curved bill than males, but this is nearly impossible to detect in the field. Distinction between sexes in the field can thus only be achieved by the observation of the mating ritual, but this event occurs only during a short period in spring.

There is no subspecies and the distribution covers a wide range in the Palaearctic and in Africa from Ethiopia to South Africa, but is very patchy everywhere. On the Eastern part, Pied Avocets are inland birds breeding from central Europe and Turkey to China (Fig. 1.1). By contrast, in the Western part of the Palaearctic Pied Avocets are mainly a coastal waders. They distribute from Lithuania to South of Spain during the breeding season and from South-West of Netherlands to West Africa (Senegal and Guinea-Conakry) in winter, but a few thousands of Pied Avocet can stay in the Wadden sea region during mild winters. In the Western Palaearctic, Delany *et al* (2009) separate two populations: birds

breeding on the coasts of Western Europe and birds breeding around the Mediterranean Sea and in South-east Europe. Here we focused on the population of Western Europe estimated at 73,000 individuals on the basis of midwinter counts in the 90s, and 26,600 pairs (Hötker & West, 2005).

Pied Avocet is semi-colonial during the breeding season and gregarious during the rest of the year. The habitat used for feeding by this semi-colonial bird is linked to the particular shape of its bill and its very special way of feeding. Indeed, Pied Avocets feed on soft, fluid sediments from which they extract benthic animals, by sweeping or scything movements of the head (Pierce, Kirwan & Boesman, 2017). During the breeding season, avocets mainly use saltmarshes on the coasts of the North Sea and the Baltic Sea, and more locally lagoons and embankments with fresh or brackish water (Hötker & West, 2005). Saltpans and fishponds are by far the main habitats on the Atlantic coasts of France and Spain (Gélinaud, 2005; Arroyo & Hortas, 2005). Outside breeding season, Avocets frequent mainly tidal mudflats in bays and estuaries in North-west Europe and Portugal, saltpans and fishponds on the Atlantic coast of Spain (Hötker & Dodman, 2009).

The food of Pied Avocet is mainly composed of aquatic and benthic invertebrates. In winter, the diet in Portugal consisted mostly of several species of worms (Moreira, 1995a,b,c). During the breeding season, it feeds primarily on insects, small crustaceans et some polychaetes worms (Cramp & Simmons, 1983).

1.2.2 Population dynamics

The Pied Avocet population was at a very low level at the end of the 19th century, mainly centred along the North Sea (Wadden Sea and Elbe delta). While poorly described, this situation was mainly explained by shooting, habitat destruction and eggs collecting. As a testimony, Harting (1874) considered the Pied Avocet as a rare species in England and claimed that "It was formerly a regular summer visitant to England; but the general cultivation of waste lands, and the drainage of extensive pieces of water (the natural consequence of an increasing population and an improved system of agriculture), have gradually banished it from its former haunts". He also reported observations in the Netherlands and pointed

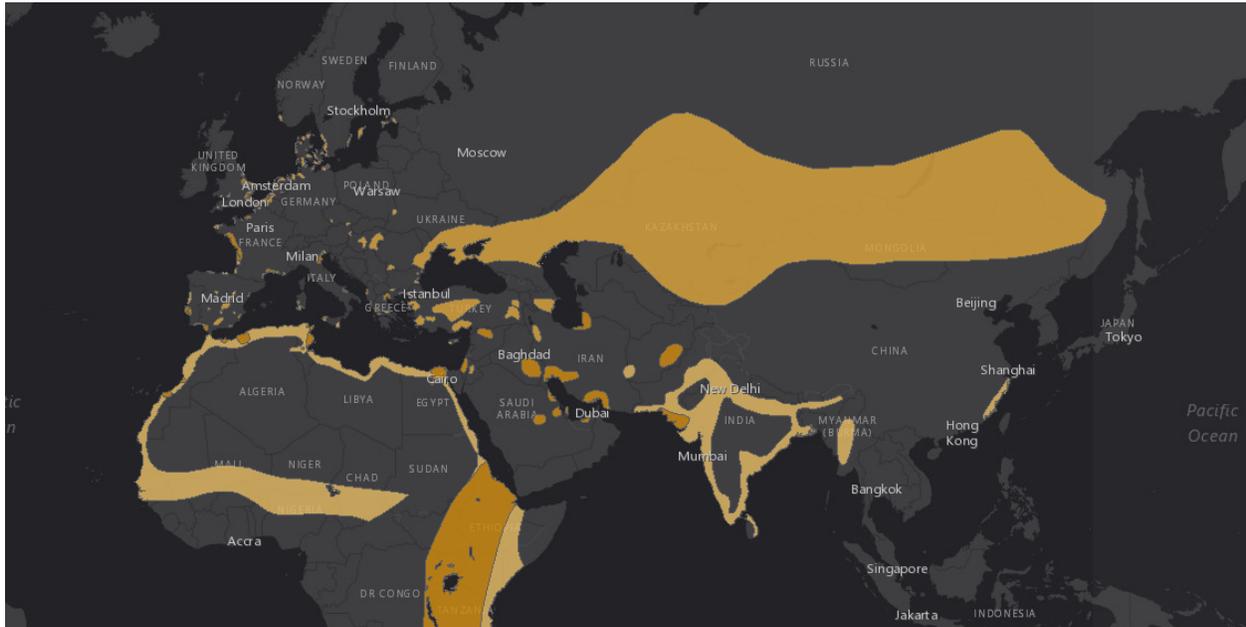


Figure 1.1: **Palaeartic distribution of the Pied Avocet.** Data from the IUCN Red List of Threatened Species: *Recurvirostra avocetta*, published in 2016 (<http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22693712A86539838.en>).

out that "the veto which is placed upon shooting during the nesting season in that country enables it to rear its young in many places with more or less freedom from molestation". This article probably summarized the main damages done to this species, which are all anthropogenic.

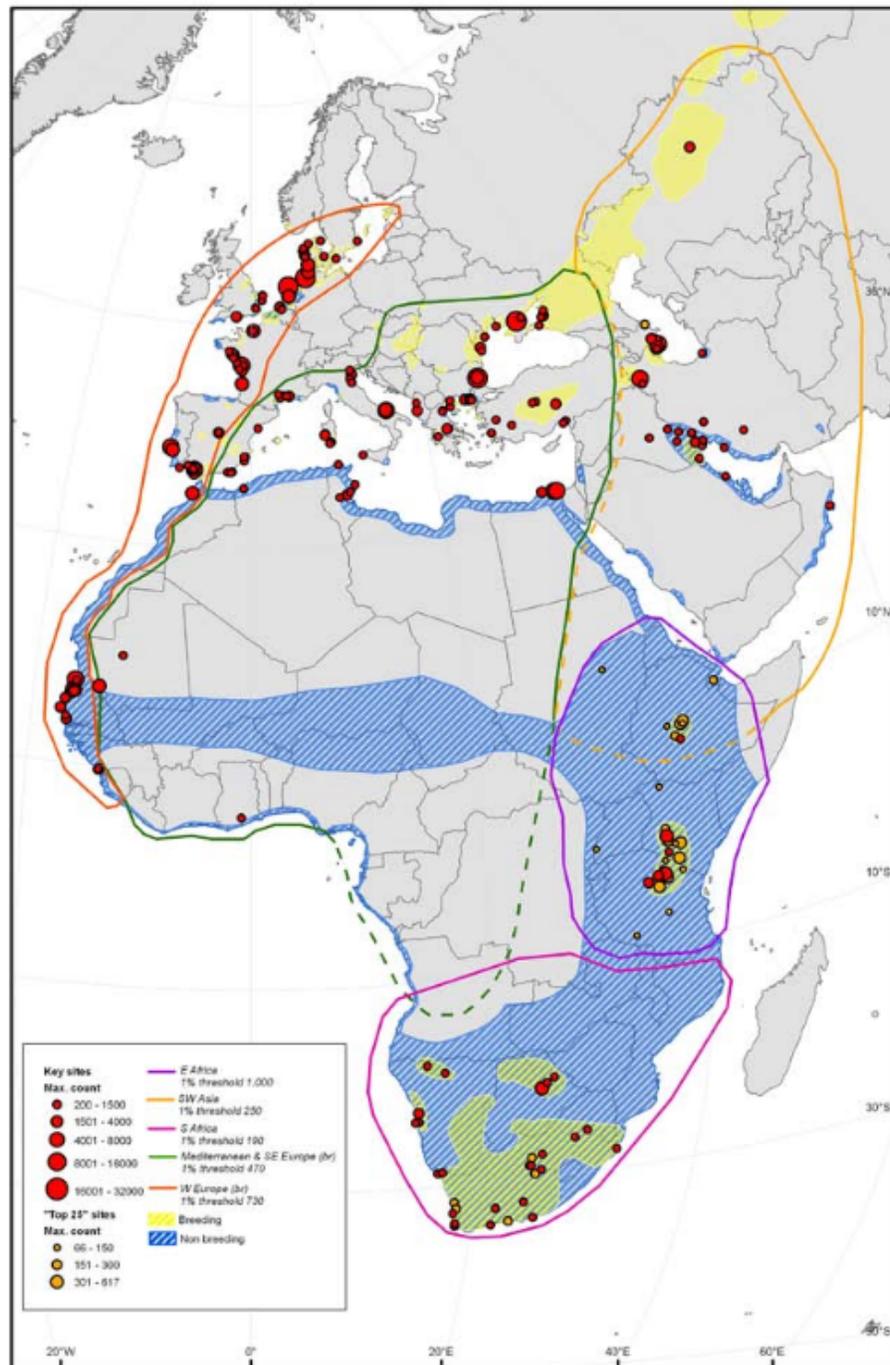


Figure 1.2: **Distribution and flyways of the European population of Pied Avocet.** Figure from Hötcker & Dodman (2009).

The population growth started probably during the first half of 20th century in the

core area, the Wadden sea are, where the species never went extinct, and probably reached the carrying capacity there in the late 80s. The expansion began in the early 20th century in Sweden (1927) but mostly took place in the second half of the century (Hötker & West, 2005). Hence, the recolonization of the breeding population successively concerned Italy (1940), England (1947) and France (1952). At this time and until the late 1980s the growth of the population was exponential, with an annual rate of increase of 26% in France during the 1970s for example (Gélineaud, 2005). At the present time, the estimates of the European population are 58 400 - 74 300 pairs, corresponding to 117 000-149 000 mature individuals (Birdlife-International, 2015), but these numbers are subject to caution. More than 17 000 pairs (Piersma, Ens & Zwarts, 2004) breed along the west coast of Europe, from Spain to Lithuania (Fig. 1.2); this corresponds to the Western European population. There are some evidences from resightings of birds colour-ringed in the Wadden sea or in Spain that dispersed to newly colonized areas, but these data are too scarce to determine whether these areas served as sources during expansion (Hötker & West, 2005). These authors discuss several hypotheses that may explain the changes in abundance and distribution during the 20th century in Western Europe, first of all the decrease in hunting and eggs collecting, and the establishment of reserves in breeding and wintering areas. The increase is also probably linked to some large scale coastal engineering project, particularly along the North Sea and the Wadden Sea (Hötker & West, 2005). The long-term climate change may also have played a role in the population dynamic in Western Europe. Pied Avocet has also probably benefited from dedicated habitats management on breeding sites (Cadbury & Olney, 1978; Girard & Yésou, 1989; Castro Nogueira *et al.*, 1996).

1.2.3 Population from Brittany

Apart from the wintering period, Avocet were absent from France in the 19th century and in the first half of the 20th century (Gélineaud, 2005). The first breeding record dates back to 1952 in the Marais d'Olonne in Vendée. The colonization of new French sites mainly began during the 70s (Fig. 1.3) and the species first bred in Brittany in 1980.

Contrary to the birds of the North of Europe, which use mainly salt marshes for breeding,

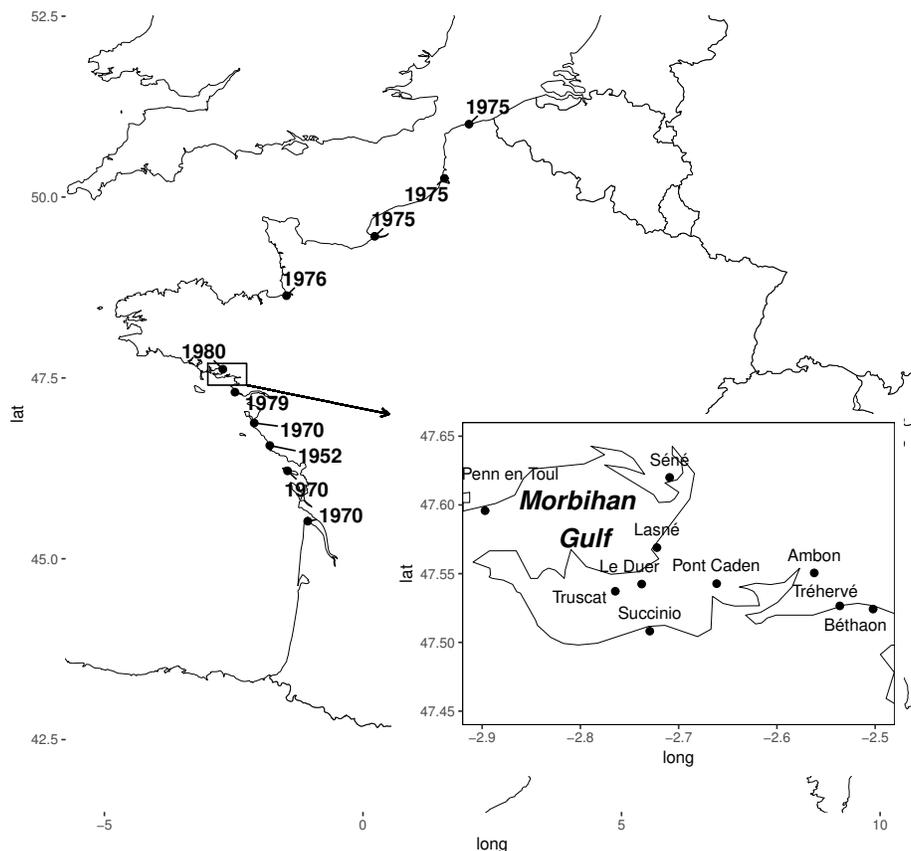


Figure 1.3: **Colonization of the French coast.** Date are indicated closely to the sites. The zoom (boxed) corresponds to the breeding colonies in Brittany, studied hereafter. The main colony is Séhé, all others are accessory and temporary colonies.

Pied Avocets from Brittany and, most of the breeders of the French Atlantic coast, breed in salt ponds (used or disused), *i.e.* man-made wetlands. All the birds considered in this study were born in South Brittany (see zoom in Fig. 1.3), *i.e.* around Morbihan gulf, mainly in the natural reserve of marais de Séhé. Among the 10 sites in Fig. 1.3, Séhé is the first colonized and supports most of the breeding birds. It is a protected area as are Penn en Toul, Lasné and Le Duer. All the other sites in Fig. 1.3 are temporary or recently colonized sites (due to management changes for conservation purpose). They are all disused salt ponds. Pied Avocets use dykes and small muddy islands in these ponds to lay eggs. They generally lay 4 eggs per nest, but can attempt to breed two or three times per breeding season in case of predation, which is common in all these sites. Both parents share incubation duties for

the length of the incubation period (23 ± 2 days) (Hötker, 1998b; Lengyel, Kiss & Tracy, 2009; Chokri & Selmi, 2011). They use shallow salt water ponds or lagoons to feed and raise their chicks. Chicks are precocial and can feed by themselves just after hatching. Parental care is thus restricted to keeping them warm and dry in the early stages, to protect them against any threats, and defend a feeding territory, generally until fledging. After fledging parents and progeny generally separate, it is usual to see post-breeding flocks with groups of juveniles together with the adults.

After the breeding season, Pied Avocets leave their breeding sites to gather in large flocks for moulting in bays and estuaries like the Loire estuary in France (generally in August and September). After this period they slowly begin to join their wintering areas. During Winter, Pied Avocets from Brittany distribute along a wide coastal range, from England to Senegal.

1.2.4 Monitoring program

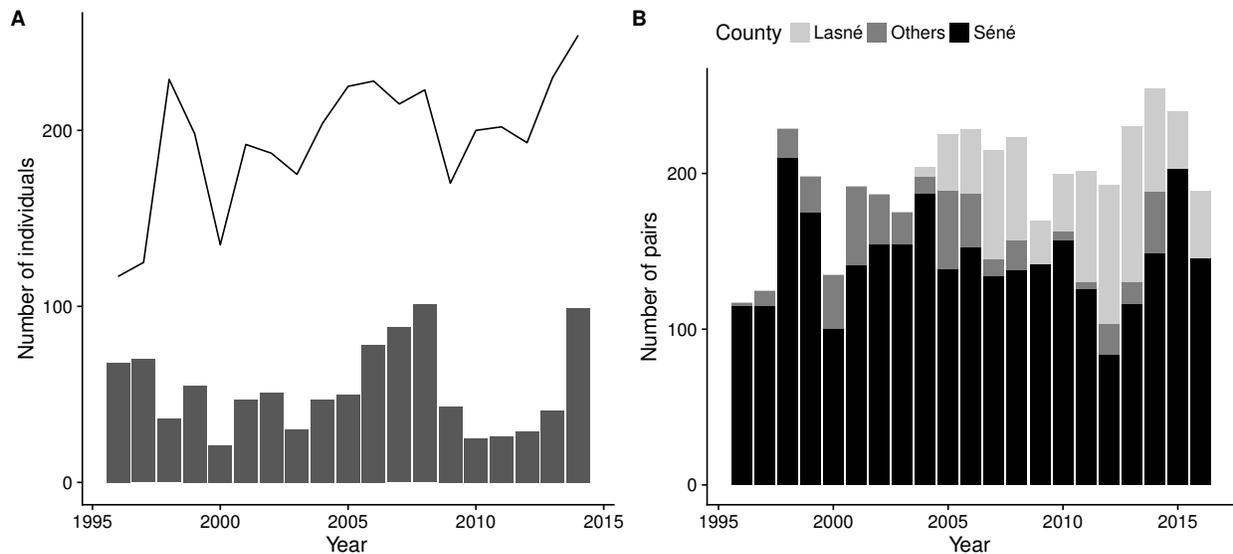


Figure 1.4: **Number of pairs and juveniles (counts)**. Panel A: bars: annual number of juveniles produced in Brittany; solid line: total number of pairs (counts). Panel B: annual number of pairs in the two main colonies (Séné and Lasné) and the sum of all other colonies.

In 1996, Guillaume Gélinaud, the current director of the nature reserve of Séné, began a long-term monitoring program of Pied Avocets breeding locally, based on individual colour

marks; and extended rapidly to the Morbihan Gulf. Chicks were marked just before fledging with a unique combination of plastic coloured bands, flags or engraved rings. More than 550 individuals have been ringed since the beginning of the program (Appendix A.3.1, p. 144), among which 420 in the nature reserve of marais de Séné. At least weekly during the breeding season, the colony is visited looking for colour-ringed birds: presence, reproductive behaviour and reproductive success of ringed individuals were recorded, from April to July (Fig. 1.4). The number of active nests is also recorded weekly and the overall number of breeding pairs is estimated from counts during the week of laying peak. The number of fledgings was also recorded yearly. Specific surveys also took place during pre- and post-breeding gatherings and during winter. The number of colonies in Brittany (Fig. 1.3) has been fluctuating during the study, with a core colony, the nature reserve of marais de Séné (Fig. 1.4B), from which individuals dispersed and created new breeding colonies. A second colony appeared (Lasné) in year 2004, due to the colonization of new managed breeding areas (Fig. 1.4B).

The main wintering sites were surveyed from December to February on the Atlantic coast of France, but the main wintering sites of migratory birds in Portugal and Andalusia were also monitored thanks to multiple sampling sessions (13) in the Iberian Peninsula. In addition, a vast network of volunteers across the range of the Western European population of Pied Avocets collected capture-recapture (CR) data from ringed birds.

1.3 Objectives of the dissertation

This dissertation is inspired by G. Gélinaud's hypothesis based on data from wintering Pied Avocets: the number of Pied Avocets marked in Brittany, and wintering in the Iberian Peninsula had been decreasing over time since 1997. This pattern based on raw data could be misleading because of detectability issues (Williams, Nichols & Conroy, 2002): there was no guarantee that the birds wintering in the Iberian Peninsula and the others had the same probability of being detected by observers, neither in the wintering area nor in the breeding area. However, several studies had provided evidence that migration strategies are currently changing in other species (destination, distance, frequency of migrants in partial migrant

species), and that such changes are concomitant with global change (climate change and changes in habitat availability caused by anthropogenic activities). The starting point of this dissertation was twofold; question 1: was the proportion of partial migrants declining after correcting for detectability issues, and question 2: did the two strategies differ in terms of demographic rates (survival, breeding performance)? The core focus of this dissertation is on the life-history of individuals adopting a different migration strategy (*i.e.* wintering in the South, or nearby the breeding ground in Brittany). Obviously, the aforementioned questions are also intrinsically linked to the question of the evolution of partial migration: my goal is also to provide initial answers concerning the persistence of this life history phenomenon. First, I will describe the wintering strategies in Pied Avocets and their dynamics. I will compare the demographic rates of the two main phenotypes in order to assess migration costs on survival and reproductive rates. Last, I will assess the demographic trend of the population born in Brittany and calculate the fitness of the migratory strategies. The dissertation is based on a 19-year monitoring dataset (CR data) and is composed of three articles which use three different modelling approaches.

In the first paper we collected the available data concerning the wintering range distribution (Western European) of this species since 1990. We used the international mid-January counts of waterbirds from the six concerned European countries to assess the temporal trend at the country level and we also assessed trends in the North (France, England, Belgium, the Netherlands) and the South of Europe (Portugal and Andalusia). These geographic limits correspond to a natural discontinuity in the wintering distribution of the Pied Avocets, between the Gironde estuary, in France, and Aveiro, in Portugal. In order to account for the temporal autocorrelation in these counts, we developed an autoregressive model for count data. Understanding the temporal changes in the wintering distribution at the European scale requires investigating the wintering behaviour and the inter-annual movement of the individuals inside the range. For this purpose, we used CR data of individually marked juveniles Pied Avocets born in breeding colonies in Brittany to investigate the wintering strategies of Pied Avocets and the dynamics of the two strategies. We used a multi-state approach for open populations and data augmentation to account for unmarked individu-

als entering in the population. We estimated inter-annual wintering transition probability between North and South areas, in order to characterise wintering strategies. We also estimated the annual number of individuals in each wintering area. We used model selection to draw inferences on several biological hypotheses about, the factors affecting survival such as migration strategies, age, time and latent individual heterogeneity (Aubry *et al.*, 2011). We also address the effect of various environmental and biological factors (*e.g.*, hatching date, winter harshness) on the choice of wintering strategy.

In the second paper, we addressed the demographic consequences of wintering strategies on reproductive performances. We used a multi-season multi-event model, which allowed estimation of transition probabilities between seasonal states while accounting for uncertainty in breeding state assignment. We defined three breeding states (non-breeder, unsuccessful breeder, *i.e.* breeders which did not succeed to breed juveniles until fledging, and successful breeder) for philopatric and emigrant individuals and two wintering states (resident and migrant). This seasonal approach also allowed us to estimate seasonal survival probabilities. We discussed the effect of wintering strategy on recruitment age, and on breeding performance. As a measure of breeding investment we used the annual cumulative number of breeding attempts (cumulative reproductive investment at age a : CRI). As different recruitment strategies (early or delayed) could lead to divergent long-life reproductive trajectories (sequences of breeding states) and different senescence patterns, we compared the seasonal survival rates and CRI at different recruitment ages. We then investigate slope of CRI for different recruitment ages and according to wintering strategy. The onset of senescence was also investigated on the light of the recruitment ages and the wintering strategies.

In the third paper we addressed the question whether the overall fitness values of the two wintering strategies differed. We used an integrated population model (IPM), which is designed to estimate a typically unobservable quantity: immigration probability (in most study systems, immigrants are not marked and cannot be identified as such in the breeding area). We also assessed emigration (breeding dispersal) by modelling CR data in a multistate way, whose transitions corresponded to inter-annual probability of breeding inside or outside Brittany. Indeed, to assess the dynamics of each strategy using temporal changes in the

proportions of individuals adopting one or the other, we need to account for unobservable components directly affecting the abundance of each strategy, such as immigration. This approach allowed us to assess the “true” temporal population size and trend by estimating three joint likelihoods from three data types: annual pair counts, annual productivity and CR data. We used this approach to obtain robust estimates of fundamental annual demographic rates such as juvenile survival, fecundity, juvenile age-specific recruitment probability, emigration and immigration probabilities. We estimated the individual overall fitness using the population or sub-population growth rate (Charlesworth, 1994) and we addressed the effect of immigration and emigration on fitness. Last, we addressed the regulation processes of the population and the persistence of partial migration by assessing *post-hoc* correlations between population growth rate or population size and the distributions of the demographic parameters.



"Wintering life in Iberia"
Picture: P. Guibert

Chapter 2

The demography of wintering distribution changes in a partial migrant

Frédéric Touzalin, José A. Alves, Guillaume Gélinaud, Matthieu Authier, Étienne Sirot and
Emmanuelle Cam

2.1 Abstract

Recent changes observed in range or frequency distribution in wintering populations of migratory bird species are generally attributed to global changes (milder winters) but they are still poorly understood. Studying life history traits of partially migrant species is central to understand underlying processes that drive distributional changes.

Identifying demographic dynamics specific to different wintering strategies in a population, and their environmental causes, requires the analysis of changes in phenotype frequencies. The individual scale is the finest and most relevant. The West Palaearctic population of Pied Avocet (*Recurvirostra avosetta*) is a suitable model that currently experiences a dramatic decrease in the South of its wintering area in Europe and an increase northward. As most shorebirds, this species is exposed to substantial and rapid environmental changes.

We used an open-population capture-mark-recapture model and simultaneously estimated survival, transition probabilities between wintering sites, fidelity to wintering area and population dynamics parameters for two phenotypes: North versus South wintering birds. We analysed 19 years of data from a French breeding population marked in Brittany and resighted all range wide.

The estimated proportion of birds migrating South in their first winter was higher at the beginning of the study, then dropped at a very low level in the XXIth century. Pied Avocets remained faithful to their first winter quarter during subsequent years. We did not find evidence of a difference in survival between South and North wintering birds but the dynamics of the population is now mainly driven by the North wintering sub-population, that dramatically increased until 2010 and nearly stabilized afterwards.

From an evolutionary perspective, the selection of phenotypes may be under control of cold spells; migrating South may be advantageous if conditions are harsh in the North. The lack of cold winters the last 2 decades may explain why the resident phenotype became dominant. Finally, ecological and/or social canalisation may explain winter quarter fidelity and the rare shifts observed in migratory behaviour (migrants becoming residents) may concern birds sensitive to environmental factors such as heavy rainfall events in the Iberian

Peninsula.

2.2 Introduction

Partial migration is the most widespread migration system in birds (ca. 70% of the species in the Western Palaearctic are partial migrants Berthold, 2003), and deeply affects the spatial distribution of the population, at both seasonal and annual scales. In addition, spatio-temporal variation in the distribution frequencies can also stem from differences in fitness among phenotypes (Palacin *et al.*, 2017). These combined phenomena result in complex demographic processes driven by environmental conditions and lead to local extinction or colonisation events, especially at the range borders (Bell, 2000; Griswold, Taylor & Norris, 2011; Pulido, 2011).

Under temperate climates, many bird species are currently experiencing important changes both in local abundances and overall distribution, often with a shift of their range northward (Hickling *et al.*, 2006; La Sorte & Thompson, 2007; Maclean *et al.*, 2008; Chen *et al.*, 2011). In the framework of the wintering ecology of partial migratory birds, this shift involves an increase in density at higher latitudes, generally accompanied by colonisation of new areas northward, and a decrease in density southward with desertion of the southernmost historical sites (Berthold, 1999, 2003; Lehikoinen & Virkkala, 2016). In the southern part of the range, changes in numbers only result from the dynamics of wintering migrants, but northward there is a mixture of phenotypes (migrants and residents share the same breeding and wintering areas) and the observed changes in abundance result from more complex demographic processes. Disentangling these processes is important for understanding both how they affect overall and local population dynamics and which evolutionary processes may be taking place. However, demographic processes underlying these changes have seldom been studied (Nevoux, Barbraud & Barbraud, 2008; van de Pol *et al.*, 2010).

The theory of partial migration, which aims to explain the maintenance and the evolution of the two phenotypes in a same population, can be essentially partitioned in two categories: (i) a theoretical approach, generally based on evolutionary stable state (ESS)

models (*e.g.* Kaitala, Kaitala & Lundberg, 1993), relying on frequency-dependant selection, either density-dependent demographic or behavioural switching. (ii) by contrast, the environmental threshold model of migration has more empirical and experimental support (Pulido, Berthold & vanNoordwijk, 1996; Pulido, 2011) and pleads for an extrinsic threshold from which individual intrinsic state determines the propensity to migrate (a conditional strategy). As a consequence, two non exclusive mechanisms can determine the frequency of the two phenotypes: (i) demographic processes: *e.g.* a decrease in fitness of the South migratory population generating a decline in the proportion of migratory individuals (Adriaensen & Dhondt, 1990; Berthold, 1999, 2003). (ii) Behavioural processes: a change in migratory movement, *e.g.* a decrease in migratory distance, or a switch to the sedentary strategy, corresponding to individuals skipping migration (Visser *et al.*, 2009; Smallegange *et al.*, 2010; Eggeman *et al.*, 2016) that also lead to the decrease of the proportion of migrants. Both processes are intimately linked to individual life history. Processes operating during the non-breeding season (wintering strategy and its corollary, wintering site selection) indeed have major consequences on individual fitness (Gunnarsson *et al.*, 2005; Harrison *et al.*, 2011; Alves *et al.*, 2013) and can explain partial migratory population dynamics (Perez-Tris & Telleria, 2002; Lok *et al.*, 2011; Sanz-Aguilar *et al.*, 2012).

In partial migrants the first winter is critical and from an evolutionary viewpoint, a cost-benefit analysis can help to understand the decision of staying in the breeding area in winter, or leaving. Migratory individuals endure specific risks along the journey such as predation, parasitism, illness, and they have to face the costs associated with the journey (Alerstam, Hedenstrom & Akesson, 2003; Hegemann, Marra & Tieleman, 2015; Sillett & Holmes, 2002; Ydenberg *et al.*, 2004). Conversely, staying in the vicinity of the birth site in winter can expose individuals to lethal weather conditions such as cold spells and possible starvation (Goss-Custard, 1996; Johnson, Green & Hirons, 1991). Numerous hypotheses have been put forward to explain the decision making process, but empirical support is still insufficient, and the underlying mechanisms remain poorly understood despite decades of research (see Chapman *et al.*, 2011, for a review). Nevertheless, the existing evidence favours a conditional strategy where the fitness gain associated with each strategy depends

on the phenotype of each individuals (Adriaensen & Dhondt, 1990). These later authors agreed with the environmental threshold model of migration (Berthold, 1999; Pulido, 2011), arguing that over the genetic control of migration, environmental and behavioural factors are relevant. This provides a useful departure point to investigate the causes of the choice of the first winter location and the consequences for individuals and populations.

Once an individual has chosen its first wintering site several options are possible for the following years. In particular, this strategy can be fixed (individuals exhibit fidelity) or flexible (individuals change strategy between years). In case of fidelity to the wintering site the choice of the first wintering site determines individual life history for the entire life. This pattern is common in birds and has the advantage of promoting “site familiarity”, *i.e.* improvement of habitat use (for food acquisition or predation avoidance) especially by use of “public information” (Greenwood, 1980; Németh & Moore, 2014; Palacin *et al.*, 2017; Piper, 2011). Conversely, changing wintering site leads to a variety of phenotypes, depending on the age at which changes occur and the number of times the individual changed between wintering site. Empirical evidence suggests that the decision to remain faithful to the initial wintering site, or not, is a conditional process that depends on age, experience, body condition and environmental conditions, with possible interactions between these factors (Lok *et al.*, 2011; Palacin *et al.*, 2017; Sanz-Aguilar *et al.*, 2012). Furthermore, the co-existence of different wintering strategies within populations can generate complex dynamics in case of unbalanced fitness among phenotypes.

The foregoing suggests that demographic models incorporating a precise description of individual behaviour are necessary to address the individual and population consequences of wintering strategies, while many studies essentially focused on the environmental factors associated with changes in population size (Jorgensen *et al.*, 2016; Lehikoinen *et al.*, 2013). Comparing the demographic traits of migrant and sedentary birds is necessary to understand changes in the proportion of each strategy, and ultimately the processes responsible for a shift in the overall population distribution. Indeed, observed changes in distribution per se can hardly be interpreted without additional information because they result from the combination of dynamics of multiple strata in populations (e.g. age, environmental condi-

tions in different locations), often with delayed effects (Duriez *et al.*, 2012; Lok, Overdijk & Piersma, 2013). Long-term studies of individual life history traits and environmental factors influencing individual behaviour are required to assess both changes in demographic parameters at population level and to explore the evolutionary determinism of wintering strategies (Pulido, 2011). Here we addressed the life history consequences (namely, mortality) of migration strategies in a coastal shorebird, the Pied Avocet (*Recurvirostra avosetta*), and the relationships between the frequency of migratory strategies, population dynamics and wintering distribution. This species has recently experienced substantial local changes in abundance, with a dramatic increase in winter in England and a decrease in Portugal (Mendez 2017). Furthermore, as other migratory shorebirds, the Pied Avocet mostly uses wetland areas during both winter and breeding season and is thus on the forefront of environmental change (Sutherland *et al.*, 2012). Paradoxically, most shorebirds exhibit a high level of site fidelity and behavioural consistency, as many seabirds and raptors (Alerstam, Hake & Kjellen, 2006; Gill *et al.*, 2014; Phillips *et al.*, 2005). If behavioural processes are not driving changes in their distribution, demographic ones could thus be the key processes driving these changes.

The habitat of Pied Avocet is limited to salt or brackish wetlands such as estuaries and shallow lakes and has dramatically shrunk over the past decades (polderized and drained) or has been deeply transformed by human activities and is nowadays mostly artificial (*e.g.* salt-pans and fish farms). The population of the West Palaearctic flyway has a vast range from Lithuania to the Iberian Peninsula, with core breeding areas located in western Europe, along the Atlantic coast. Members of northern populations are strictly migrants, while those of the population situated southern to Germany are partial migrants (Hötker & Dodman, 2009). Wintering range covers a coastal band from Guinea to the Netherlands (Hötker & Dodman, 2009). The distribution of wintering individuals is nearly continuous on coasts from the Netherlands to South-west of France. A gap of nearly 750km (great circle distance) of poorly suited habitats separates wintering quarters mainly from north Portugal to Andalusia (Smith & Piersma, 1989). We focused on a long-term monitoring programme from individually marked birds in a breeding colony in western France. Birds from this colony are partial

migrants, with some individuals wintering in the vicinity of the colony and along the West Atlantic French coast, and others in the Iberian Peninsula and southern (West Africa). We addressed the temporal changes in wintering strategies in this particular colony from 1996 to 2015, and assessed population changes at the wintering sites.

We used both the coordinated mid-January counts (Wetlands International) and capture-recapture data ; our goals were the following ones: (i) Estimating the size for the population wintering in the North (the Netherlands, Belgium, Great Britain and France) and the South (Iberia, restricted to Portugal and Andalusia), their trend and their growth rates. We also addressed temporal variations in the number of individuals wintering in each area. (ii) Estimating the survival rate according to wintering 'state' (South or North) and testing for the effect of age, year and climatic covariates on survival (North Atlantic Oscillation - NAO, and winter severity). (iii) Estimating the proportion of individuals choosing a specific area (North, South) in their first winter and its annual variation. We also tested for the effects of year, birth date, NAO and winter severity on this parameter. (iv) Evaluating fidelity to wintering strategies over time and testing for the influence of climatic covariates (NAO, and winter severity) and year on fidelity. (v) Addressing the dynamics of the breeding colony, *i.e.* temporal variation in the total population and in state-dependant sub-populations. We used a multi-state model for open populations in a hierarchical framework (Schofield & Barker, 2011) which allowed estimating population dynamics metrics and all relevant demographic parameters, *i.e.* survival rate, the probability of an individual choosing a wintering area during the first winter of life, and fidelity to the previous wintering site in subsequent years. Determining the major life history patterns also allowed us to address the question of the evolutionary causes of the maintenance of partial migration in this colony.

2.3 Methods

2.3.1 Range-wide monitoring of wintering population size

Monitoring of water birds in the Western Palaearctic was initially established by Wetlands International in the early 1970s and yielded estimates of range-wide population size (Hötker

& Dodman, 2009; Stroud *et al.*, 2004). Since then, many countries have refined their monitoring schemes to different degrees, but the initial mid-January count remains the most relevant indicator of wintering population size. We compiled the January counts in all European countries (or regions when possible) that encompass the winter range of the Western population of Avocets; we focused on the last two decades, a period of high monitoring coverage (1990-2015). These data were provided by distinct entities and monitoring programmes: WeBS (United Kingdom), SOVON (the Netherlands), LPO/WI (France), ICNF (Portugal), Junta de Andalucia (Andalusia/Spain) and Wetlands International (2017) IWC Online database (URL: <http://iwc.wetlands.org>).

Although core winter sites have been monitored every year, a few small sites were not covered in some years, especially some Iberian wintering sites. Moreover, counts are sometimes subject to observation error (missing data, over or underestimation). We therefore developed a simple population model for count data (Kéry & Schaub, 2012) to estimate numbers of birds likely to be present during counts and to assess Pied Avocet population trends over Europe. We used a hierarchical formulation which allows accounting for: (i) observation errors by assuming that counts are log-normally distributed with a mean equal to the true, but unknown, population size and a variance parameter corresponding to uncertainty in the observation process; (ii) spatio-temporal correlations in counts by modelling true population size as an autoregressive (markovian) process and by adding a year \times country correlated random effect (see Appendix A.1.1, p. 116). We obtained abundance estimates for each European Country. Finally, we compared the trends between North and South wintering populations by grouping data from France, United-Kingdom, Belgium and Netherlands for the North, and from the Iberian Peninsula (Portugal and Andalusia) for the South.

2.3.2 Data from individually marked birds

Individual-level data were obtained from resightings of 540 individuals captured as juveniles and marked with a combination of leg bands in South Brittany, France (47°37'N , 2°42'W; Morbihan Gulf), from summer 1996 to summer 2014. During the nonbreeding season, resightings of marked individuals are reported by a vast network of volunteers across the winter

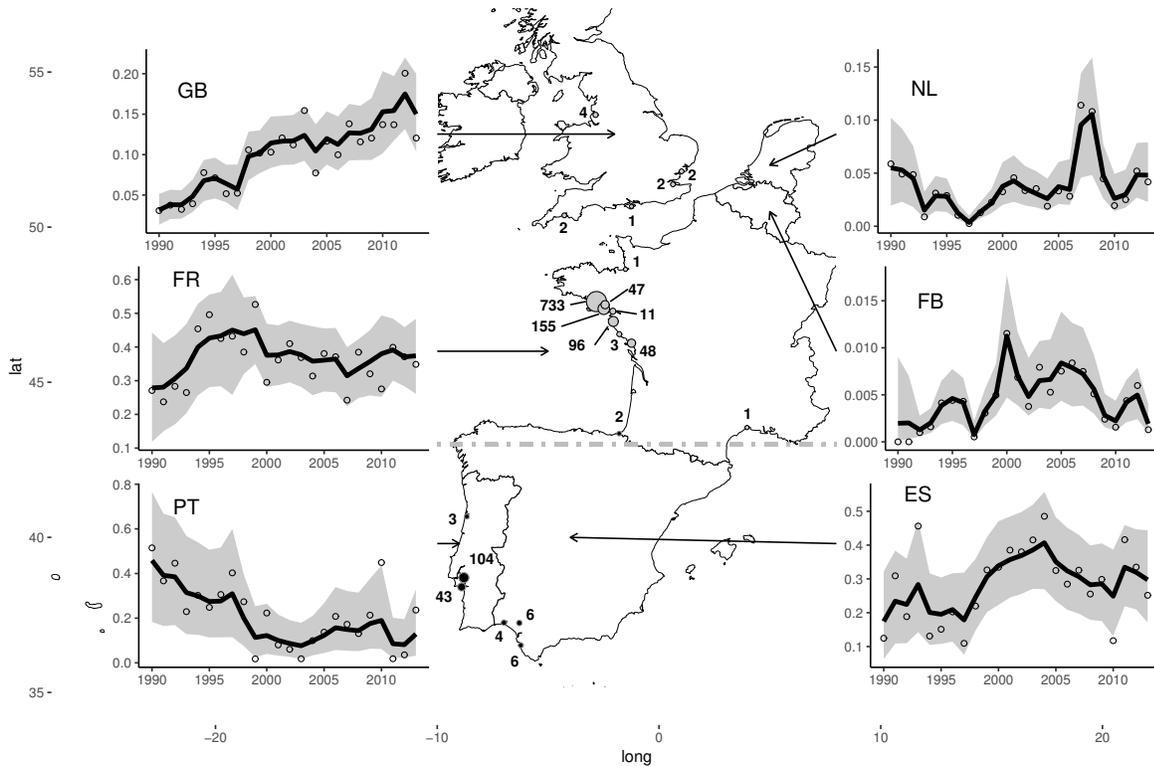


Figure 2.1: **Estimated proportion of wintering Pied Avocet in different areas in Europe.** Graphics: temporal variations in the mean proportion of Pied Avocet (black line) and confidence intervals (shaded area) from 1990 to 2013. Open circle: observed proportion from counts. Map: the grey dots show the wintering sites in the North area and black dots in the South area (Iberian Peninsula). Dot size is proportional to the number of resightings indicated beside. GB: Great Britain; FR: France; PT: Portugal; NL: Netherlands; FB: Belgium; ES: Spain.

range. In addition, regular surveys of key wintering areas have been conducted each winter in France since the beginning of the ringing programme (between December and March), and in Iberia (in February or March) from 1997 to 1999, and from 2006 to 2015. This allowed establishing individual wintering location, which was considered as the individual 'state'. Yet, we only considered 'state' as certain when an individual was observed in France during a specific time window, from December 20 to February 25, corresponding to the last observed departure date to the South and first return date of migratory birds. For birds resighted outside France we extended this window from late October to March in order to account for early arrival and late departure of migrants not resighted during the wintering

session. We restricted inference to individuals that were resighted at least once in winter during the study period because birds never observed in winter cannot be assigned to any wintering area at any time and can then not inform the model.

The data used included capture-recapture (CR) histories of 221 birds resighted in winter along the Atlantic coast and the Channel, from England to Spain, over 19 years (see Appendix A.4, p. 144). This corresponds to 1274 resightings distributed along the west European coast from South England to Andalusia (Fig.2.1). One individual was recorded once on the French Mediterranean coast, but recorded on the Atlantic coast during 4 winters and was considered as belonging to the northern wintering population, with state 'North wintering bird'. Among the 221 birds, 51 were seen at least once in the Iberian Peninsula during winter. Among them, birds observed in Andalusia were too few to be assigned to a separate state ($n=14$). We thus grouped them with 'South wintering birds'. Similarly, 3 birds observed in England were grouped with birds resighted in France in winter and thus assigned to the 'North wintering birds' group.

It is important to note that all the birds retained for analyses survived at least until their first winter: all the CR histories of birds dying before being resighted or never observed in winter but known to be alive later have been discarded. Furthermore, observations considered here only occurred in winter: this analysis does thus not allow for a comprehensive study of survival in the population.

2.3.3 Modelling

We used a variant of multistate CMR models to estimate demographic parameters (Schofield & Barker, 2011). Data consist in CR histories incorporating information about winter resighting locations. We defined two individual states corresponding to wintering areas, respectively North and South. Not all the individuals are detected by observers, thus models incorporate a state- and time-specific detection probability to account for the missing data process. If individuals survive, they can change state among years according to a transition (or movement) probability that depends on year, the state of departure and the destination state.

Classical multistate models use the likelihood based on observed data (ODL); missing data are integrated out of the likelihood (Arnason, 1973; Schwarz, Schweigert & Arnason, 1993). An alternative approach based on the complete data likelihood (CDL) incorporates all missing data. Schofield & Barker (2008) and Schofield, Barker & MacKenzie (2009) proposed a flexible approach based on data augmentation that generalises the use of the CDL thanks to well developed Markov chain Monte Carlo (MCMC) methods. This approach allows estimation of population-level demographic rates (growth, number of births and deaths per sampling occasion, or lifespan) for each state in situations where the life history of individuals is only partially observed (Dupuis & Schwarz, 2007).

Here we used a formulation which separates two main classes of processes in a hierarchical way (Schofield & Barker, 2011): the observation process corresponding to the detection of birds, and the biological processes corresponding to population dynamics (*e.g.*, population growth rates, survival, and movement probability). The detection process was considered as a Bernoulli process conditional on the availability of the individual, *i.e.* his presence in the population (recruited and alive). In the most general formulation of the model, detection probability p depended on individual state as well as a random time effect, which differed according to state: *i.e.*, a state-dependant intercept and a random state \times time effect, (see Appendix A.2.1 for details and prior distributions, p. 128). This specification was motivated by the difference in observation pressure between North (regular sampling occasions) and South (punctual and short sampling occasions) and among years. From winter 1999-2000 to winter 2004-2005, the Iberian Peninsula has not been well monitored: we then set the corresponding detection probability to 0.

Survival probability between t and $t-1$ is estimated through the mortality process, where death can only occur if the individual was born and still alive at $t-1$. We chose the robit link function to formulate the relationship between survival probability and “explanatory” variables, The robit link is the inverse of the cumulative distribution function of the Student- t distribution. It is known to be less sensitive to outlying data than alternatives like the logit or probit links for regression on binary responses (Liu, 2004). We set the parameters of the Student- t distribution to 7 degrees of freedom and the scale parameter to 1.5484, which

offers a good approximation to the logit link (Liu, 2004).

Individual state was not observed during all sampling occasions and was integrated in the CDL as a categorical individual-specific time-varying covariate. When not observed, state is assumed to be missing at random: missingness is assumed to be mainly due to non-detection, not to some systematic bias or to temporal emigration, as most of the range was covered. We modelled individual state as the outcome of a categorical process, We distinguished the probability of choosing a wintering strategy in the first winter (*i.e.* the first transition probability from the birth location to the first wintering site) and transition probabilities in subsequent years. This allowed testing biological hypotheses focussing on the choice of the first wintering area or subsequent decisions regarding migration strategy.

We used data augmentation to estimate parameters for which no explicit data were available, *i.e.* the number of unmarked birds belonging to the breeding population (Tanner & Wong, 1987; Schofield & Barker, 2011), for a complete description see Appendix A.2.1 (p.128). Estimates of demographic processes like birth, death and population size are derived from the estimated life histories of all the individuals entering the population (including pseudo-individuals used for data augmentation).

2.3.4 Covariate selection

We used several covariates to test hypotheses about the three main processes of interest: survival, choice of first winter site and subsequent transitions between sites. For survival probability, we tested the effect of climatic covariates: NAO and a winter severity index (Appendix A.2.1, p.128). Since the choice of the wintering area in year t occurs before winter, we used winter severity and NAO indexes in year $t-1$ as predictors of the first wintering strategy and of subsequent transitions between wintering sites. Indeed, we expected a carry-over effect of climatic covariates on these probabilities. We also considered hatching date as a predictor of the choice of the first winter quarter, in agreement with (Chambon *et al.*, 2017) who showed that early hatching birds are more prone to migrate than later ones. In particular, we addressed whether the choice of the first wintering area can be predicted by the mean annual hatching date of each state, or by the interaction between previous

winter severity and hatching date. We also tested for an effect of year and age on transition probabilities using factors, linear or quadratic form for the covariates. Moreover, individual heterogeneity was pointed out to be an important parameter to deal with in modelling of life-history traits when variations between individuals are suspected and because it can disentangle hidden patterns in estimated parameters (Aubry *et al.*, 2009; Péron *et al.*, 2010; Chambert *et al.*, 2013).

For computational reason it was not possible to compare all possible models using information criteria: the total number of combinations was too large. Consequently, we used a shrinkage prior (Hooten & Hobbs, 2015), that allows the detection of sparse signal: the horseshoe prior (Carvalho, Polson & Scott, 2010). This is a weakly informative, heavy tailed prior with a point mass at zero, which shrinks model coefficients toward zero unless there is strong signal in the data (Appendix A.2.1, p.128)). We used a sequential approach to select the predictors for the processes of interest. First, we ran models using the horseshoe prior on all candidate covariates for survival probability. We then ran four models containing a year and an age effect either treated as factor or a continuous variable with a quadratic function. At this step, year was treated as a factor for the first winter transition probability and subsequent transition probabilities were fixed constant over time. We selected covariates whose parameters had a 80% Bayesian confidence interval excluding zero. Then, keeping the selected covariates for survival, we ran four new models using the horseshoe prior with all candidate covariates for the choice of first wintering area and subsequent transition probabilities between years. The difference between the models concerned year effect, which was treated as factor or as quadratic for the first winter transition and the subsequent ones. In the last step we ran a set of models (12), which are combinations of the covariates previously selected, we used the deviance information criterion (DIC) in order to identify that best accounted for the data-generating process.

2.3.5 Estimation et posterior predictive check

We used a Bayesian approach with the software programme JAGS 4.0 (Plummer 2003) called from R 3.3.3 (R Core Team, 2016) through the package jagsUI 1.4.4 (Kellner, 2016). JAGS

code is available in Appendix A.2.3 (p.136). Concerning the model for count data we used three Markov chains, starting at random initial values in the range of parameter space. The total length of each chain was 200000 but we excluded 100000 samples from the initial convergence phase. We thinned Markov chains with a factor of 4, which led to a final number of samples of 75000. We used the Brooks-Gelman-Rubin criterion (Gelman & Rubin, 1992; Brooks & Gelman, 1998) to evaluate convergence (all $R_{hat} < 1.08$). The goodness-of-fit of the model was assessed using the Bayesian p-value for each country estimates and by checking graphically the sum of squared residuals for the data plotted against the sum of squared residuals for simulated data. For the CR model, we first ran models until convergence to select covariates, which led to 900000 iterations. For selection of the final model, we used three Markov chains starting at random initial values, a total of 300000 iterations and a burn-in period of 100000 iterations to obtain convergence. Starting from these values we re-ran the models (300000 iterations with a thinning factor of 9) to get more accurate estimates of posterior probabilities, and combined the samples, which led to a total sample of size 100000. We then compared DIC weights and chose the model with the largest one. Following Gelman *et al.* (2003) and Zheng *et al.* (2007) we conducted posterior predictive checks by comparing observed to simulated data using the parameter estimates of the best fitted model. 10000 data sets were simulated using 10000 draws from the joint posterior distribution of all parameters to account for uncertainty. The individual random effects were directly drawn from the posterior distribution. Individual states were estimated for the first winter and the subsequent states were conditioned on the previous one using estimated transition probabilities. Individual life histories were simulated by taking estimated detection probabilities into account.

2.4 Results

Pied Avocets wintering in Western Europe are currently experiencing considerable changes in numbers across their winter range. Since the late 1980s, the proportion of individuals wintering in Western Europe has been increasing, except in Portugal (Fig. 2.1). When pooling

countries according to geographical continuity *i.e.* North Europe versus Iberia, the number of individuals wintering in the North dramatically increased (Fig. A.5, Appendix A.2.1, p. 127). The geometric mean growth rate of the wintering European population was significantly > 1 for Spain, England and France (Fig. A.6, Appendix A.2.1, p. 127). The growth rate of the European population was nearly stable 1 (0.98, 1.03: 95% confidence interval - CI hereafter). However, annual growth rate in the northern countries was equal to 3.1% (CI: 2, 4.2) versus -1% (CI: -5, 3) in the Iberian Peninsula.

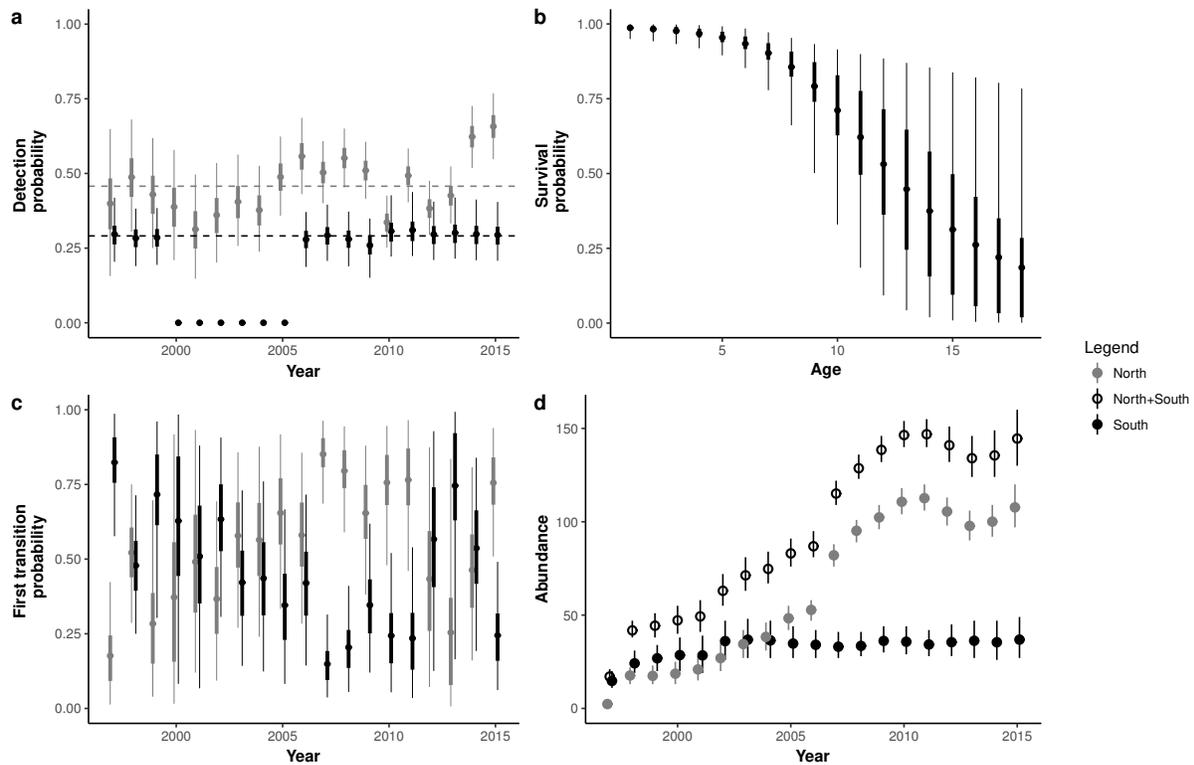


Figure 2.2: **Model parameters estimations.** A: Estimated detection probability according to year and survey area. Dotted lines: mean detection probability in each area. The South was not monitored between 2000 and 2005 (detect. prob.=0). B: Age effect on survival probability of Pied Avocet. C: Probability of choosing a specific first wintering area. D: Population dynamics; dots indicate mean values and vertical lines the 95% CI. A,B and C: thick vertical lines indicate the 50% CI and thin lines the 95% CI.

For survival probability, the model selection allow us to retain as significant a linear trend age effect and a frailty term (individual- and state-dependant heterogeneity parameters). We did not find evidence of a relationship between covariates and transition probabilities

between consecutive winters. Consequently, we considered these transitions to be constant. Concerning the first transition from birth site to the wintering area, we found evidence of a small signal for three covariates, a factor year effect, a linear time effect and the effect of winter severity index. Finally, the most parsimonious model (see Table A.2 and model code Appendix A.2.2) had a weight of 0.99 and included a linear age effect on survival probability and a factor year effect on the choice of the first wintering area.

Posterior predictive checks indicated a good fit (Fig. A.10 and A.11, Appendix A.3.2, p. 146), with the exception of survival probability that was underestimated in 1998 and 2014, and overestimated in 2000 and 2001. Detection probability was globally low in winter and lower in the South than in the North (main effect respectively $pS=0.29[0.2, 0.4]$ and $pN=0.46[0.23, 0.69]$), with substantial variations among years in the North but relatively constant in the South (Fig. 2.2.a). We did not find evidence of a difference in survival between individuals wintering in the South or in the North. Nevertheless, the most supported model included a negative linear age effect on survival on the robit scale which corresponds on the $[0, 1]$ scale to a slight linear decrease until the age of eight years followed by an steep decrease (Fig. 2.2.a). But the interpretation of the strength of the decrease in survival is obscured by the increase of the 95% confidence interval.

State-specific individual heterogeneity levels in survival probability are different from zero ($5[2,9]$ in the North and $6.2[2.4,9.8]$ in the South), and the variance ratio showed that they have similar distributions (Fig. A.13, Appendix A.3.4, p. 147). The distribution of this ratio was right skewed and the mean equal 0.87 indicated that heterogeneity among individuals in survival probability is slightly larger in the South. We also addressed whether individual survival heterogeneity within each state differed between local wintering areas (country sub-areas). We did not find any relationship between individual-specific survival heterogeneity and wintering area (Appendix A.3.4, p. A.3.4).

At the beginning of the study (1997), the probability of wintering in the South during the first winter was higher than the probability of wintering in the North. The reverse was true in 2015 (Fig. 2.2.c). The dominating wintering strategy thus changed during the study. Years with significant differences between strategies were 1997, 2007, 2008 and 2015. Years

when the probability of wintering in the North or the South had large CIs corresponded to years with small numbers of marked chicks retained for analyses and very few resightings (Fig. A.9 and Table A.4, Appendix A.3.1, p. 144). Fidelity to the initial wintering area was very high in the North 0.99[0.98,1] and slightly lower in the South 0.93[0.89,0.96]. Since 2011, only five birds that used to migrate to the South were observed wintering at least once in the North.

The overall population size increased substantially until 2010 then stabilized (Fig. 2.2.d). This situation resulted from two different tendencies affecting the main phenotypes: when the North wintering population was experiencing a major growth, the South wintering population stayed stable (Fig. 2.2.d). The annual growth rate of the total population over the study period was 1.16[0.93,2.5], with 1.48[0.88,8] for the North wintering population and 1.07[0.83,1.69] for the South wintering one (Fig. A.12.a, Appendix A.3.3, p. A.12). North wintering birds became more abundant than their Southern con-specifics around 2005. Other summaries of population dynamics (deaths, births) are reported in Appendix A.12 (p. A.12).

2.5 Discussion

We have shown that the demography of Pied Avocet from Brittany is the result of contrasting dynamics from two different sub-populations. Interestingly, the South wintering sub-population remained stable, while the North wintering sub-population has substantially increased during the past decades. The persistence of the South wintering population revives the old debate concerning the conditions that may promote the persistence of partial migration.

2.5.1 Demographic consequences of wintering strategies frequencies

We found that the overall dynamics of Pied Avocets breeding in Brittany results from the interplay of the specific dynamics of each wintering strategy. The North wintering sub-population has experienced a strong increase since the early 2000s and is now stable, since

2010 (Fig. 2.2.D). The total population trend characterized by an increase in density northward is now driven by the dynamics of the North wintering sub-population (Fig. 2.2.D). Changes in the demography of sub-populations are related to the temporal variations in the frequency of the first winter area selection (Fig. 2.2.C). These results at the Brittany population scale are in accordance with our first analysis at the European scale. More generally, they are also consistent with recent observations in Europe, which show a decrease in the migrant sub-population of partial migrant bird populations (Pulido & Berthold, 2010). During the past decades, the proportion of Pied Avocet in the North wintering area increased while it decreased in the Iberian Peninsula. Additionally, the fact that a few Pied Avocets observed have been wintering in England indicates a shift in the winter range of the Brittany population to the North (La Sorte & Thompson, 2007; Chen *et al.*, 2011). The European Population range of Pied Avocet has not experienced a shift northward, but part of the population from Brittany now winters Northern than its breeding ground. This is consistent with the theoretical corpus on migration determinism that attributes changes in distribution to a change in phenotypic proportion (more residency and Northern shift) as a response to environmental changes, especially global warming (Berthold, 1999, 2003).

The stability of the South wintering population (Fig. 2.2.D) results in a mechanistic decrease in the proportion of this strategy in the overall population. Empirical studies have shown that the non-breeding period is generally associated to a higher mortality rate, which shapes population demography (Barbraud & Weimerskirch, 2003; Leyrer *et al.*, 2013). Here, we found no difference in survival rate between the two phenotypes. This lack of difference has two major implications. First, it may partially explain the long persistence of the South migration strategy. Second, it highlights the contribution of other life-history traits to the decrease in frequency of this phenotype. Indeed, the Pied Avocet has a long life expectancy, as illustrated by the EURING database longevity record (27.8 years, Fransson *et al.*, 2010) and this study (19 year old birds still alive). Such long lifetime can compensate for a possible reproductive inferiority of South wintering individuals or a delay in age at recruitment of this sub-population. This might postpone the demographic decrease in the South wintering phenotype, especially as long as a small proportion of fledglings still decides to migrate to

the South.

Here, survival rate varied with age and exhibited individual heterogeneity. Senescence had been receiving a growing interest in the last decade: it is widely spread in nature and variation among individuals in ageing age can suggest a trade-off between life-history traits (Orell & Belda, 2002; Jones *et al.*, 2008). The decrease in survival with age was identical for the two phenotypes. However, this decrease difficult to assess accurately after eight years of age because of the sparsity of the data at the beginning of the study (*i.e.* before winter 2006; Fig. 2.2b). The distribution of individual effects on survival, however, differed between the phenotypes and the variance ratio suggested a larger degree of variation among individuals in the South wintering phenotype. Birds encountering very different environmental conditions in their migration route might endure different costs of migration: we might have expected a variation of greater magnitude in migrants, if any. This hypothesis was not supported. Individual heterogeneity in survival is governed by other factors that remain to be identified.

We did not find any support for a relationship between climatic covariates and the yearly probability of selecting a specific wintering area in the first winter. Resighting data showed that individuals gather in fall before wintering in large flocks in a few estuaries, such as the Loire estuary (middle west coast of France), during post-nuptial moult, as German Pied Avocets do (Hötker & Frederiksen, 2001; Hötker & Dodman, 2009), before joining their wintering grounds. Social interactions taking place within these groups could influence individual wintering strategies. In any case, the fact that individuals attending the same post-breeding flocks choose opposite wintering strategies suggests that this choice is not determined by climatic conditions exclusively. However, carry-over effects of weather conditions and especially wintering conditions cannot be totally excluded. In the past two decades in France, the last severe winters occurred during the 90s (90/91, 91/92, 92/93, and 96/97), essentially out of our study period. Hötker (1998a) has shown that these weather conditions were partially responsible for winter site selection of the strictly migrant German population of Pied Avocet. Indeed, the proportion of German birds wintering in France decreased during severe winters: individuals chose to migrate further South. Based on data from winter 1997 (the

only severe winter during this study) we cannot corroborate this hypothesis in our population. We suspect a delayed effect of repeated unfavourable winters, which may explain the higher proportion of birds migrating South at the beginning of the study.

After the choice of the first wintering area, the estimated probability of changing wintering area is low : $< 7\%$ from South to North, and close to zero in the other direction ($< 1\%$). Individuals are very faithful to their wintering strategy, which is commonly observed in birds (Blackburn & Cresswell, 2016; Lourenco *et al.*, 2016). A small number of individuals change their migration strategy. According to the threshold model of migration (Pulido, 2011), the ability of an individual to modify its migratory programme from migratory to sedentary behaviour and vice-versa is suspected to be influenced by environment. It was empirically shown that this behavioural flexibility can drive the maintenance of partial migration (Eggeman *et al.*, 2016). However, this strategy is under-represented in the population. We observed changes in only 5 birds during the entire study period: 9.6% of the studied South wintering individuals. Changes have been observed only recently (since 2011) and concerned too few individuals to draw conclusions about their causes and consequences; they could be rare stochastic events. However, this shows that the two populations are not genetically isolated but more probably that strong underlying canalisation processes exist (Pulido, 2011) and maintain the predominance of mainly two phenotypes among all possible ones. In this context, with high winter area fidelity, the temporal variations of first winter transition probability may entirely explain the sub-population dynamics if their breeding success is equal (*i.e.* globally equal fitness).

To summarise, this partial migration system is relatively simple: the winter strategy is mainly determined for life before first winter. The long lifespan, the variations in first winter transition probabilities associated to the high fidelity to wintering strategy are the main drivers of the observed demographic patterns (Fig. 2.2), especially of the persistence of South migration. Local wintering conditions may affect the frequency distribution of the phenotypes via carry-over effects.

2.5.2 Partial migration and evolutionary change

The demographic disconnection between North and South wintering populations also questions the evolutionary bases of the phenomenon. Partial migration theory can shed light on results, based on the comparison of life history traits between individuals wintering in two distinct geographical areas. To do so, we take apart the 2 birds observed in England and one observation on the Mediterranean coast of France; we can define the sub-population wintering on the Atlantic coast of France as 'sedentary' and the Iberian one as 'migrant'. Numerous hypotheses have been developed to explain the causes and the evolutionary stability of partial migration (see Chapman *et al.*, 2011, for a review).

(i) The dominance hypothesis (Gauthreaux Jr., 1982) invokes competition for food and predicts that dominant (typically older) individuals are able to stay around breeding grounds while subordinates (juveniles) have to migrate under dominance pressure. This hypothesis can be ruled out in the Pied Avocet. First, the dramatic increase of sedentary birds during the first winter contradicts the expected exclusion of these birds from their breeding grounds in winter. Second, the small transition probability ($< 7\%$) from migrant to sedentary strategy is inconsistent with the expected increase in competitiveness linked to experience. Last, the lack of difference in survival between states and the growth rate of the sub-population of sedentary individuals suggest that there is no negative density-dependent effect at least in the North wintering range (Taylor & Norris, 2007).

(ii) The familiarity hypothesis predict high site fidelity in sites where wintering conditions are predictable or stable over time (Greenwood, 1980; Piper, 2011). In gregarious species, site faithfulness and social familiarity can favour cooperative traits and reinforce social cohesion among individuals. For example, this can be advantageous for 'newcomers' such as juveniles that can benefit of knowledge from older (faithful) birds at wintering site (*e.g.* for food supplies or predation avoidance). Benefits due to site familiarity may however decrease dispersal with age and even prevent birds from moving to other sites of higher quality. Then cost and benefit balance to site fidelity can lead to important heterogeneity in fitness component between groups of individuals other than survival. Indeed, carry-over effects of

migration strategy, the ‘seasonal matching’, can generate long-term consequences on fitness by affecting a diversity of traits such as productivity (Gunnarsson *et al.*, 2005; Harrison *et al.*, 2011; Alves *et al.*, 2013). This is consistent with the wintering strategies developed by Pied Avocet: after choosing the first wintering area, most individuals remained faithful to this area during their entire life.

(iii) The frequency-dependant hypothesis, can work as a frequency dependent ESS, with equality in the fitness of the two strategies at the equilibrium point strategy (Lundberg, 1987). At population level the ESS depend on a genetic dimorphism the frequency of the phenotype is maintained irrespective to time or environmental conditions. The evolution of phenotypes frequency with time here rule out this hypotheses. At the individual level, the ESS do not depend on genetic but the maintain of the two strategies is condition on the homogeneity between individual (but see Griswold, Taylor & Norris, 2010), which is rejected here. The frequency-dependant hypothesis can also work as a “conditional strategy” which depend both on individual state and environmental variations (Lundberg, 1987, 1988). If the previous scenario (ii) relies on habitat predictability and the advantages of site fidelity, winter environment of Pied Avocet can also be unstable (e.g drying or flooding of shallow lagoon, winter storm entirely depleting mudflats) or environmental conditions can deteriorate (*e.g.* deleterious climate changes, increase of predation risk or density-dependence effects). For example, sedentary individuals are exposed to cold spells that can lead to deadly starvation (Sanz-Aguilar *et al.*, 2012). These extreme events are rare but even weaker changes can promote the coexistence and maintenance of several phenotypes with different fitness and dynamics within the same population (Brodersen *et al.*, 2008), the strategy with lower fitness making “the best of a bad job” (Lundberg, 1987, 1988). In our case, major and repeated cold spells ended at the early beginning of the study (96/97) followed by persistent mild winters, which coincides with the shift of individual probability of migrating (Fig. 2.2.C). We then suspect that this influenced the choice of the first winter quarter, in a conditional manner, and promoted migration just before and at the early beginning of the study.

(iv) The ‘environmental threshold model of partial migration’ (Pulido, 2011) states that at the individual level migratory behaviour is a quantitative genetic trait with a threshold

defined by environmental factors (ecological, social or intrinsic). This threshold separating low and high migration liability (residents versus migrants). The transition between phenotypes is a process under environmental control; the expression of the trait depends on individual migratory restlessness distance to the threshold. Individuals close to the threshold will quickly adapt their migratory behaviour to environmental changes, while individuals far from the environmental threshold are prevented from expressing phenotypic plasticity due to canalization (Flatt, 2005). Under this model, the environmental threshold delimiting partial migratory phenotypes (first winter dispersal area) in Pied Avocet could be partly determined by carry-over effects of cold spells (*e.g.* lower productivity) or social interactions on pre-migratory grounds. The high fidelity that follows wintering area choice could be explained by canalization inhibiting phenotypic plasticity. The rare individuals previously observed as migrants that return to residency are consistent with this phenomenon. The absence of cold spell since winter 96/97 could have led to an evolutionary change in the population toward a residency population. Additional data will be necessary to determine whether this process is transitory or can reverse in case of new cold spells occurring in Northern Europe, or if the migrant phenotype disappears.

(v) The 'arrival time hypothesis' (Kokko, 1999) finally predict that mature birds winter closer to their breeding ground in order to benefit of an earlier settlement, *i.e.* less competition for the best sites, and increase breeding success. Hötter (2002) showed that wintering distance to reproductive areas is negatively correlated to the breeding success in the German population of Pied Avocets, in accordance with this hypothesis. However, the breeding success of the population of Brittany was not on the scope of this study but on future work. We then cannot make inferences on this hypothesis here.

Several non exclusive hypotheses may explain the persistence of the South wintering phenotype in the corpus of the partial migration theory. Despite the absence of genetic data that limit our understanding of the entire evolutionary mechanisms, demographic changes in this population may underlie a conditional strategy under strong canalization processes which can be promoted by site familiarity. The scope of this study regarding fitness is limited by the fact that only the contribution of survival and some wintering life-history traits

were estimated for this population. Interestingly, there is equality in survival between the phenotypes. Estimating fitness will *in fine* confirm the relative importance of first wintering choice in the individual life-history. If the two phenotypes experience equal fitness (*i.e.* equal reproductive success) this trait determine the demographic dynamics of the sub-populations. If fitness differ, demography is under control of phenotype-specific reproductive success and the phenotype with lower fitness make the 'best of a bad job', *i.e.* fitness optimisation is conditional to the environment. To fully assess the fitness consequences of wintering strategies, breeding success should also be evaluated, which is beyond the scope of this paper.



"The beginning of life-history"
Picture: F. Touzalin

Chapter 3

Demographic consequences of life-history strategies in a partial migrant

Frédéric Touzalin, Guillaume Gélinaud, Étienne Sirot and Emmanuelle Cam

3.1 Abstract

Inter-individual heterogeneity in life-history or behavioural strategies can have substantial effects on population dynamics. However, it is often challenging to measure these effects. Partial migration, where only a part of the population is seasonally migrant, offers the opportunity to investigate the evolutionary consequences of among-individuals variations in life-history traits. Surprisingly, few empirical studies have addressed the estimation of strategy-specific reproductive performances or survival probabilities.

Using capture-recapture data from a long-term study of a partial migrant population of Pied Avocet (*Recurvirostra avosetta*) in Brittany, we estimated for each phenotype (residents and migrants) the seasonal survival, the reproductive investment (recruitment age, breeding probability and cumulative number of breeding attempts). We also addressed senescence in survival and reproduction for each phenotype, and as a function of recruitment age.

Per time unit survival differed between seasons (it was lower in spring than in fall), but we did not find evidence of a difference between residents and migrants. An important delay in recruitment age was highlighted in migrants, as well as a lower cumulative reproductive investment for individuals recruited after the age of one year. We found evidence of both survival and reproductive senescence, but the onset of senescence did not differ between the two migratory phenotypes. However, senescence in the cumulative reproductive investment varied with recruitment age, with individuals recruited at the age of one year exhibiting no senescence, and the others showing an onset of senescence around the age of 14 years.

This study thus demonstrated substantial differences in key aspects of the reproductive investment between migrants and residents, in a partial migrant population. The reproductive patterns described suggest that the resident strategy was the most advantageous strategy, which illustrates the complex demographic mechanisms that drive the selection of migratory phenotypes and the dynamics of such mixed populations.

3.2 Introduction

Identifying and quantifying the causes and the consequences of life-history strategies is a key to understanding both variations in population dynamics and life-history evolution. Partial migrant species provide an opportunity to study variations in life-history traits within a population and to quantify both the demographic rates and the fitness associated with each life-history strategy (Hegemann, Marra & Tieleman, 2015; Grist *et al.*, 2017). Partial migration is probably the most common expression of migratory behaviour (Berthold, 1999) and the debate over its origin and its persistence is still active (Chapman *et al.*, 2011). The fact that within the same population, some individuals seasonally migrate while the others remain on the breeding grounds, potentially generates differences in the life cycle, and in vital rates, *e.g.* survival or reproductive performances among individuals. Each strategy faces indeed different potential costs: migrants encounter more pathogens and predators in addition to the energetic cost of flight while resident experience potential starvation or harsh climatic events. However, accurate measures of variations in performance are rare, because studies often suffer from too short time series, or use proxies to establish life-history strategies (Hegemann, Marra & Tieleman, 2015; Grist *et al.*, 2017). Long-term studies based on marked individuals are thus required to explore the links between migrating behaviour, life history, and demography. assess the demographics of migration strategies and individual reproductive performance. Such studies should monitor the population on both breeding and wintering grounds.

Members of partial migrant populations coexist during the breeding season, but experience different environmental conditions during the non-breeding season (usually half of their annual cycle), because some individuals remain in the vicinity of their breeding area all year-round, while other migrate to separate locations during the non-breeding season (Gauthreaux Jr., 1982). Several hypotheses have been put forward to explain why the migratory and sedentary strategies persist and coexist in populations. (i) A fix dimorphism, *i.e.* a fully genetic determinism, can persist if the alternative strategies have equal fitness (Gauthreaux Jr., 1982; Lundberg, 1987, 1988). Under this hypothesis, survival and reproductive

rates of both migrants and residents should be equal, or if not, any difference in one rate must be balanced by the other rate. (ii) Partial migration could also be a conditional strategy: individuals will then choose one or the other behaviour according to intrinsic or extrinsic factors (*e.i.* environmental conditions, individual state). Under this hypothesis the persistence of partial migration does not require equal fitnesses of the two strategies (Lundberg, 1987), and individual behaviour may change over time. The strategy itself, this individual level of plasticity, involves the possibility to be either migrant or resident according to individual and environmental states and could be heritable. In addition, the strategy choice is assumed to be frequency dependent. Several empirical studies have shown that residents have a higher reproductive success than migrants, and that the latter tend to have a higher propensity to switch to residency than residents to switch to migration (Adriaensen & Dhondt, 1990; Sanz-Aguilar *et al.*, 2012). Because migrants have a lower fitness, they are supposed to "make the best of a bad job" (Lundberg, 1987, 1988; Adriaensen & Dhondt, 1990). In any case, exploring this question requires estimating strategy-specific demographic parameters, including survival rate. Differences in survival between migratory strategies can affect lifetime fitness, lead to temporal variation in the frequencies of the alternative strategies, and affect population structure (Gillis *et al.*, 2008).

In populations partially migratory, only migrants can be affected by migration costs, if any. Among commonly mentioned costs is late arrival to the breeding ground, access to lower-quality breeding territories, and lower reproductive output in migrants, related to migration distance (Forslund & Part, 1995; Hötter, 2002; Grist *et al.*, 2017; Lok *et al.*, 2017). In territorial bird species, it is reasonable to hypothesize that migration can lead to a delay in the age of first breeding; because young individuals could incur higher costs during the journey and difficulties in meeting the physiological or social conditions to breed when they return to breeding grounds (Rushing, Marra & Dudash, 2016; Lozano, Perreault & Lemon, 1996). If this holds, migration strategies could be associated with different individual reproductive "tactics" (*sensu* Stearns, 1976; *i.e.* a set of traits designed by natural selection, which defines a complex adaptation). Among these traits, the age at recruitment is a key parameter which can deeply influence both the individual fitness and population growth rate (Stearns,

1976; McGraw & Caswell, 1996; Acker *et al.*, 2014). Indeed, two individuals with the same longevity but different ages of first breeding will differ in terms of lifetime fitness (assuming equal probabilities of breeding successfully). In addition, a fundamental assumption of life history theory is that there are trade-offs between fitness components (Williams, 1966; Stearns, 1992; Harshman & Zera, 2007). In this framework, the decision to breed is assumed to be governed by correlations between, for example, the age of recruitment and the onset of survival senescence (Kirkwood, 1977; Kirkwood & Austad, 2000). Age of first breeding is considered as an important choice that possibly conditions the entire reproductive career, *i.e.* if reproduction carries costs on survival, age of first breeding might have consequences on the number of subsequent breeding opportunities. If migration strategies are associated with differences in age of first breeding, this could then have consequences on the entire reproductive trajectory and the longevity of individuals. Early recruitment could indeed be associated with higher reproductive costs during the first breeding attempt than late recruitment (Forslund & Part, 1995). Understanding the relationship between migration strategies and the lifetime longitudinal trajectory of individuals inevitably leads to consider hypotheses put forward to explain age-specific patterns of variation in reproduction and survival, including hypotheses about the evolution of senescence (Nussey *et al.*, 2008, 2013), which is widespread in the wild (Austad, 1993; Jones *et al.*, 2008; Péron *et al.*, 2016). Under the hypothesis of cumulative costs of reproduction, the larger the cumulated reproductive output up to age a , the smaller the probability of a large breeding output at this age. This could result in a progressive decrease in breeding output prospect as individuals age. Cumulative reproductive costs have also been invoked to explain the evolution of senescence. In this framework, we expect a negative correlation between early reproduction and late-life reproductive output: early recruits should exhibit an earlier onset of senescence than late ones (Orell & Belda, 2002).

In this paper we used long-term individual-based data on Pied Avocets (1996-2015) to investigate the variations of lifetime longitudinal trajectories among individuals in the context of partial migration. We previously provided evidence of the existence of two demographic processes in the population breeding in Brittany (Chapter II). Sedentary birds (individuals

wintering mainly on the West Atlantic coast of France) experienced a substantial increase from 1996 to 2010, while the migrant part of the population (wintering mainly in the Iberian Peninsula) remained stable. Migrants used to form the largest proportion of the population at the beginning of the study, but this is no longer true. We did not find evidence of a difference in survival probability between the two phenotypes, but we showed that the first winter destination mostly determined individual wintering strategy for the entire life.

Our main objective was to address the demographic processes that are responsible for the different dynamics of the two wintering phenotypes. Our goal was also to provide insight into the mechanism responsible for migration persistence. To investigate the relationship between wintering strategy and reproduction, we used a seasonal sampling scheme: sampling periods corresponded to the wintering and breeding seasons. Time interval between sampling correspond to transition period between post-nuptial gathering and winter quarter in autumn (80 days), and between winter quarter and breeding ground in spring (33 days).

First, we compared age at recruitment in the two categories of individuals, i.e. probability of making a transition between the pre-breeding state and the breeding state for the first time at the age of one, two or three years. Second, we assessed the cumulative reproductive output over life and the effect of age at recruitment on seasonal survival probabilities. Third, we investigated late life reproductive output. To address changes in vital rates throughout life, we took individual heterogeneity in survival into account. Indeed, previous work on the demography of migrating birds provided evidence of heterogeneity in mortality risk (see Chapter I). To avoid the well-known biases of approaches aggregating individuals with different baseline mortality risks (*e.g.*, Vaupel & Yashin, 1985; Zens & Peart, 2003) to draw inferences about changes in vital rates at the individual level, we considered models with random individual effects on survival probability. We also considered individual effects on reproductive rates. Indeed, one of the conditions for migration strategies to be directly affected by natural selection is that they affect fitness components, i.e. reproductive performance or survival rate. Indirect selection might operate when two fitness-related traits are correlated: selection on one trait may have consequences on the other. Our goal was not to disentangle direct and indirect selection processes, but to consider the possibility that

survival and breeding rates are correlated at the individual level. In this case, accurate evaluation of longitudinal reproductive trajectories at the individual level requires incorporating the correlation between breeding and survival rates into models (Cam *et al.*, 2013). Importantly, we used multi-event models to estimate demographic rates while taking uncertainty in reproductive state determination into account.

3.3 Method

3.3.1 Study population and data collection

We selected data from juvenile birds captured and marked on the breeding ground in a small number of colonies in South Brittany, France (47°37'N , 2°42'W; Morbihan Gulf), from summer 1996 to summer 2014. As the aim of this study is to estimate and compare vital rates between two wintering phenotypes we selected individuals observed at least once during winter in their life; for more details see sect. 1.2.3 and 2.3.2 (p. 11, 26). Resightings came both from regular surveys of key wintering and breeding areas in France and in the Iberian Peninsula and from a vast network of volunteers across the distribution range, from Denmark to Andalusia (see Fig. 3.1). Monitoring during winter in France consisted in sampling occasions taking place between December 20 and February 25 in the main wintering sites. In the Iberian Peninsula only one session per year took place in February, from 1997 to 1999 and from 2006 to 2015. We extended this period from November 1 to March 31 for individuals observed outside France, where detection probability was smaller. During the breeding season, monitoring consisted in weekly surveys at the breeding sites (Brittany) but also in other key sites along the Atlantic French coast. The breeding period encompassed the period from April 1 (first laying date) to September 30, which corresponds to the period when most members of the population share similar environments along the French Atlantic coast (this period includes both the breeding season and the moulting period characterized by post-nuptial gathering).

We used a total of 16144 observations to build the capture-recapture (CR) histories of 221 individuals in a multi-seasonal scheme over 19 years. These data were mostly collected

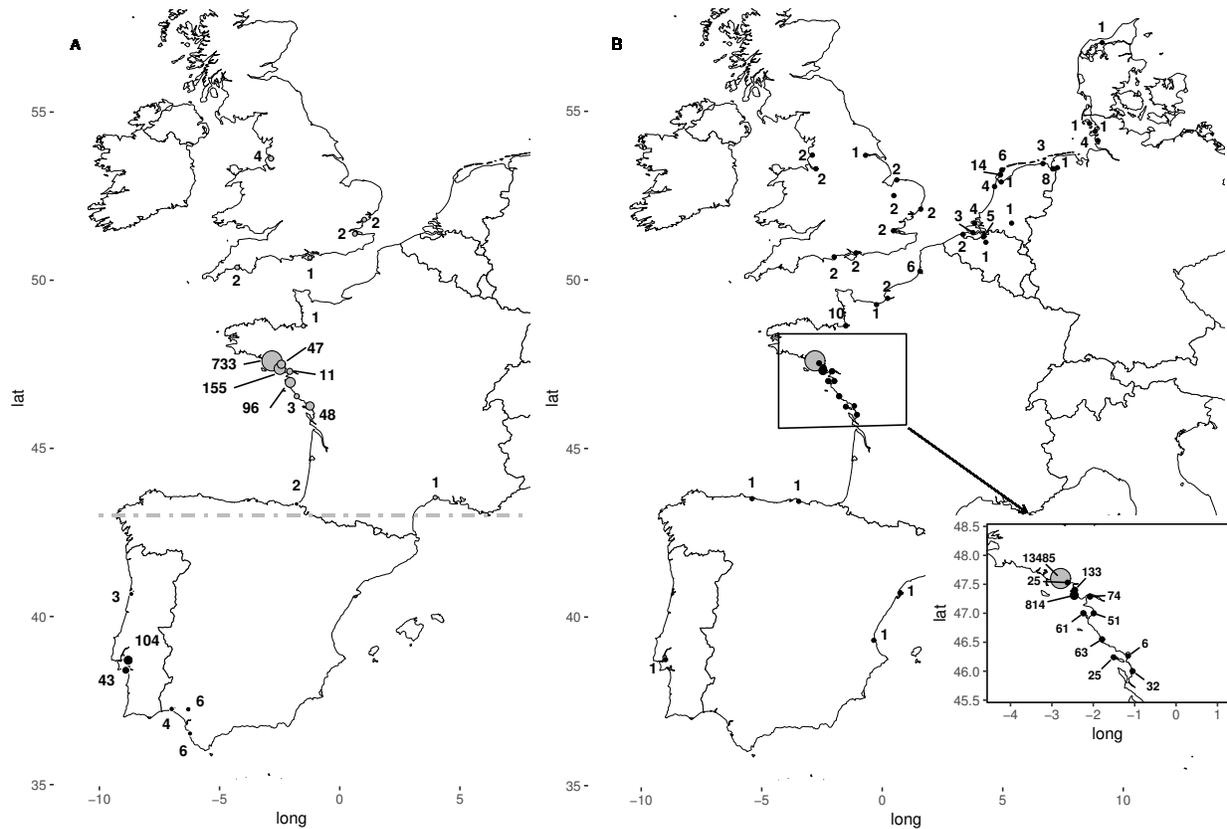


Figure 3.1: A: Distribution of resightings during winter. Grey dots: North wintering sites; black dots: South wintering sites. B: Distribution of resightings during the breeding period. Grey dots: ringing sites; black dots: dispersal during the breeding period and post-breeding migration. Dot size is proportional to the number of resightings at the site.

in France but also to a large extent on the North and West coast of Europe (from Denmark to Spain). In winter most resightings came from France and the Iberian Peninsula, and marginally from England. Three uncommon records concerned two observations in the North of Spain, made at a stopover region during fall migration (late October), and a bird wintering only once on the Mediterranean coast of France but seen in Brittany during other winters (Fig. 3.1.A). Concerning the breeding season (Fig. 3.1.B), the five observations in the Iberian Peninsula corresponded to early arrivals or late departures of migrant adults and two first year individuals that stayed in Iberia during the breeding season following birth. There was no evidence that these birds actually bred in Iberia, while observations in the North of Europe (from England to Denmark) can be attributed to northward breeding dispersal.

3.3.2 Observed events and state transition

We assessed individual states in winter by direct observations of birds at their wintering location. The "North" state corresponds to individuals resighted in France and in England (hereafter residents), the "South" state to individuals resighted in Portugal or Spain (hereafter migrants). These two states correspond to the two main wintering strategies of the Pied Avocet from Brittany (see chapter II). During the breeding season, we considered three states (non-breeder, unsuccessful breeder and successful breeder) and we drew a distinction between philopatric and other individuals (*i.e.* if the individuals were present in Brittany during the breeding season, or outside). Direct determination of the reproductive state from observation is problematic: it was indeed not possible to assign the non-reproductive state to individuals, except to juveniles and to pre-breeder or mature birds in a retrospectively manner because most of the time reproductive state is hidden. Indeed, breeding individuals do not devote their time budget to reproductive behaviour. Data collected thus consist in a set of behaviours, which can provide information on whether individuals are attempting to breed, or not (see Appendix B.1, p. 152). In order to take into account uncertainty in breeding state determination, we used the observed behaviours to define five event classes: (1) ascertained non-breeder, (2) possible breeder, (3) suspected breeder (4) ascertained breeder and (5) successful breeder (see Table B.1, p. 153). We used one event class, the highest observed, to characterise the individual state for the entire breeding season. "Ascertained non-breeder" was assigned to the juveniles, *i.e.* to individuals in their birth year, and to a few pre- or mature individuals in first or subsequent occasions (see Appendix B.1, p. 152). At the other end, the "successful breeder" state corresponds to the event with the highest possible rank. It is a special case of the fourth event class. Between these extremes we used different behaviours to assign individuals to two event classes corresponding to uncertain breeding state: they reflect the maximum level of information we were able to collect on the reproductive state of these individuals.

The possible transitions are illustrated in Fig 3.2, which includes only the first five occasions in the life of an individual, starting at birth (ringing). To summarize, after ringing,

i.e. the breeding season of his birth, an individual (in state N_B_i) has only two possibilities, wintering in the North or in the South. After the first winter, if it survived, this individual can make transitions to one of the six possible states defined during the breeding season, and so on. As selected individuals have at least survived until the first winter, death could only occur after that time; in this case no other transition was possible (death is an absorbing state). Consequently, this model only accounts for the longitudinal state trajectory of the individuals that survived up to the first winter and were observed at least once in winter. This means that the survival probability of the juveniles from birth to the first winter is set equal to one.

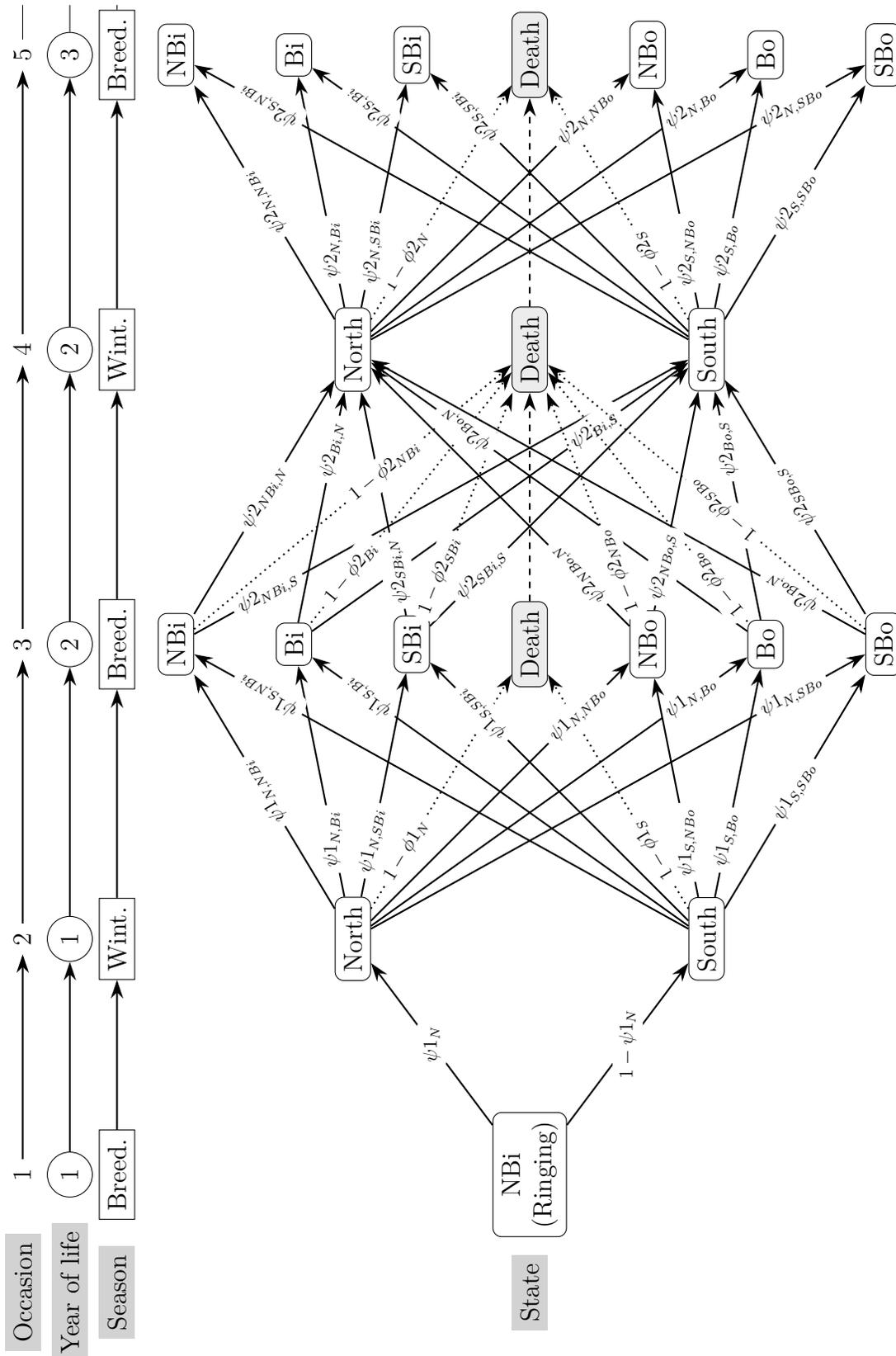


Figure 3.2: **Diagram of state transitions.** Breed.: breeding season; Wint.: wintering season; NBi: non-breeder in the birth colony, Bi: breeder in the birth colony; SBi: successful breeder in the birth colony; NBo: non-breeder outside the birth colony, Bo: breeder outside the birth colony; SBo: successful breeder outside the birth colony. All individuals selected survived until the first winter, death can occur only after first winter. Transition probabilities $\psi_{a,r,s}$: probability that an individual is in state r at age a and in state s at age $a+1$.

3.3.3 Modelling Approach

We used a multievent (Pradel, 2005) multi-season CR model to investigate fitness consequences (on survival and reproduction) of wintering strategies in Pied Avocet. We used a variant of the multievent model (Pradel, 2005) based on the complete data likelihood (CDL) (Gimenez *et al.*, 2007; Schofield, Barker & MacKenzie, 2009; Schofield & Barker, 2011) to estimate vital rates. Within this modelling framework, wintering and reproductive states are treated as categorical individual time-varying covariates. This model is analogous to a multistate models for wintering states for which there is no uncertainty if individuals are resighted (see 2.3.3 and Appendix A.1.1, p. 116). The multi-event framework was necessary to account for uncertainty in breeding state determination during the breeding season (Appendix B.2, p. 154). Here, we considered unknown states as missing completely at random (MCAR), *i.e.* the true individual state does not affect the ability of an observer to assign the individual to this state.

The hierarchical formulation of the model (for details see Appendix B.2, p. 154) allowed the estimation of transition probabilities between states conditionally on survival. Transitions to wintering areas were modelled in the same way as in chapter II, *i.e.* a year effect on the first transition and subsequent transition probabilities were considered constant over time. We estimated the effects of age on the transitions toward a particular breeding site, conditionally to wintering state. The importance of individual heterogeneity was highlighted in chapter II, especially for survival. Consequently we considered models accounting for heterogeneity in survival via random individual effects, with two possible levels of heterogeneity depending on the wintering area. We also addressed individual heterogeneity in survival during breeding periods, using an inclusion variable (Appendix B.2.1, p. B.2.1). Last, we added a random individual effect on transitions probabilities toward breeding states. We estimated the correlation between traits directly related to fitness (survival and reproduction).

Moreover, we assessed age related changes in cumulative breeding performance. As successful breeding is rare in our sample: less than 10% of the population is marked, predation is high at all chicks stages and determination of individual productivity is difficult; we then

cannot assess lifetime reproductive success (LRS) accurately. Consequently, we focused on the annual breeding attempts as a proxy for breeding performance. More precisely, we estimated the age-related cumulative number of breeding attempts and compared this variable between individuals wintering in the North and in the South area. We also compared individuals recruited at different ages. In the same way, we addressed the relationship between age at first breeding and survival probability. Last, we estimated the proportion of breeding attempts during the reproductive lifespan and the ratio of reproductive lifespan relative to the total lifespan. These ratios are proxies for the intensity of the reproductive investment during life. The closer to 1 is the ratio, the higher is the investment.

3.4 Results

The posterior predictive checks showed a good fit of the multivented model (Appendix B.4.2, p. 176). The mean of the posterior distribution of the inclusion parameter was equal to 0.72: this provides evidence that models should include parameters accounting for individual heterogeneity in survival from the breeding season to winter. Hereafter, posterior distributions of estimated parameters will be summarized by their mean and their 95% Bayesian credible interval (BCI).

3.4.1 Survival and observation processes

During winter, as shown in chapter II, the mean detection probability was lower for birds wintering in the South than for birds wintering in the North (Appendix B.4.1, Fig. B.2C, p. 175). This parameter was also less variable in the South than in the North. Within breeding seasons, results were contrasted too. In Brittany, on the ringing colonies, philopatric birds had a detection probability very close to one, with a higher mean probability of detection for successful breeders than for unsuccessful breeders (Appendix B.4.1, Fig. B.2B, p. 175). As non-breeders are mainly juveniles that were just marked, their detection probability was virtually equal to one. Outside Brittany (Appendix B.4.1, Fig. B.2A, p. 175), successful breeders (0.94, BCI: 0.7, 1) and unsuccessful breeders (0.81, BCI: 0.52, 1) had a high detec-

tion probability compared to non-breeders (0.14, BCI: 0.04, 0.28). The assignment probabilities illustrated the difficulty to assign individuals to the right state (Fig. 3.3.A). Multi-event framework accounted for important bias in state determination. Indeed, in Brittany, only non-breeders and successful breeders were correctly assigned with a high probability. As we automatically assigned the juveniles to the non-breeders class (immature birds) and that the assignment of non-breeders to event 2 and 3 is close to zero, there seemed to be virtually no marked adult non-breeders in Brittany. The probability of properly assigning individuals to the state of unsuccessful breeders is only 0.52 (BCI: 0.49, 0.56; event 4), the probability of assigning them to event 3 was 0.28 (BCI: 0.25, 0.31) and the probability to assign them to event 2 equal to 0.19 (BCI: 0.17, 0.22). Outside Brittany, the proper assignment for successful breeders was likely, but confidence interval were larger, in relation to the few occasions observed. As a consequence, the unsuccessful breeders were properly assigned with a rate of 0.5 (BCI: 0.4, 0.61), assigned with a rate of 0.38 (BCI: 0.26, 0.48) to event 2 and 0.12 (BCI: 0.07, 0.19) to event 3. Misclassification of non-breeders outside Brittany was high. Most of them were indeed classified in event 2 (0.77, BCI: 0.62, 0.89), against a rate of 0.05 (BCI: 0.01, 0.12) properly classified and the rest in event 3 (0.18 BCI: 0.07, 0.32), indicating that non-breeders can in fact have breeding behaviour.

Seasonal survival was high but was calculated over short periods, *i.e.* 33 days for spring and 80 days for autumn. For comparison purpose, we rescaled estimates on a 30 days period (Fig. 3.3.B). There was a strong age effect on survival with a decrease of -0.85 (BCI: -1.4, -0.4) on the robit scale, which is consistent with the hypothesis of senescence in survival rate. On average, the survival rate in spring is lower than in autumn with larger differences after the age of nine years old. However, estimates are imprecise after the age of 14 years old.

First autumn transitions probabilities toward wintering areas (North and South, Appendix B.4.1, Fig. B.2D, p. 175) were similar to those presented in chapter II, *i.e.* the migration tendency decreased and residents became the dominant strategy in the population breeding in Brittany. Estimates of subsequent transitions can be found in Table. 3.1. Probability to be non-breeder in Brittany (NBi) when previously resident or migrant are equal (0.5) but they actually are not identifiable, due to the lack of data, which supports the

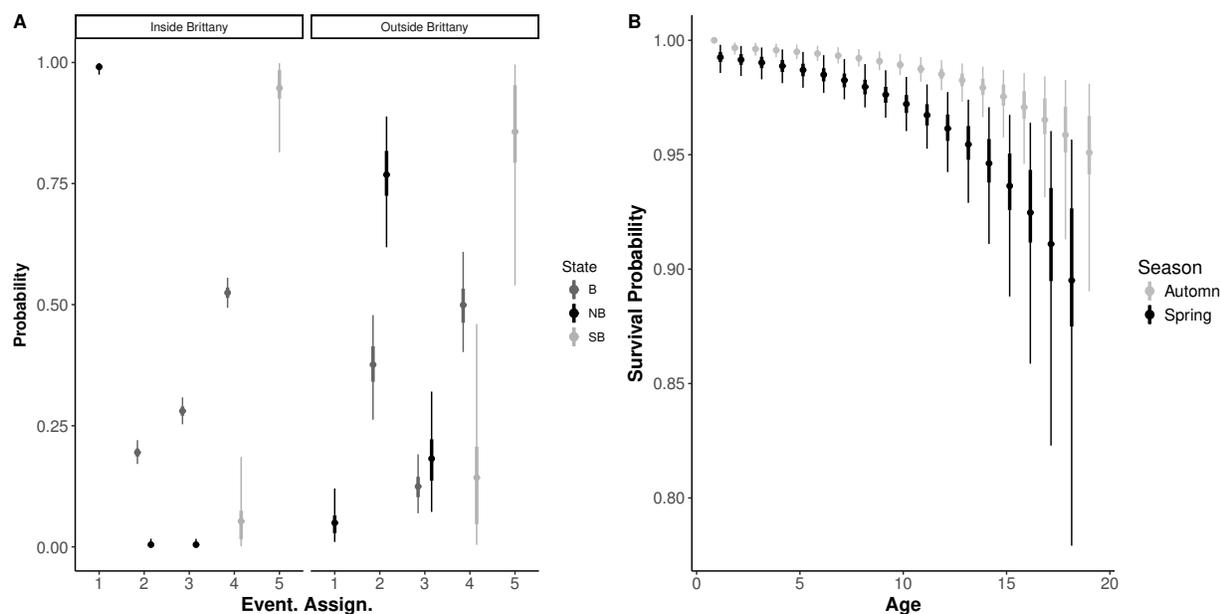


Figure 3.3: **State assignment and survival probability.** Panel A, state assignment probability, inside and outside Brittany. Panel B, survival probability according to season. NB: non-breeders; B: unsuccessful breeders; SB: successful breeder.

hypothesis that none or very few marked individuals were actual non-breeders in Brittany. Probabilities to be breeder (irrespective to the success) was higher in Brittany than outside (Table. 3.1).

Transitions from winter state to breeding state according to age class showed few differences considering winter state (Fig. B.3, p. 176), except for age classes two and three: probability to be a non-breeder outside Brittany was higher for migrants in age class two and three; probability to be an unsuccessful breeder outside Brittany was higher for residents in age class two and three; probability to be non-breeder in Brittany was higher for residents in age class two. Mean probability to be unsuccessful breeder is higher in Brittany, whatever the wintering state. Mean probability to be a non-breeder was higher outside Brittany, whatever the wintering state.

3.4.2 Breeding investment

Pied Avocets can attempt to breed when they are one year old, but the probability of such early breeding was largely higher for individuals spending their first winter in the North

	North			South			
	mean	2.5%	97.5%	mean	2.5%	97.5%	
NBi	0.50	0.03	0.98	NBi	0.50	0.03	0.97
Bi	0.56	0.49	0.65	Bi	0.44	0.35	0.51
SBi	0.62	0.37	0.86	SBi	0.38	0.14	0.63
NBo	0.37	0.25	0.50	NBo	0.63	0.50	0.75
Bo	0.71	0.58	0.83	Bo	0.29	0.17	0.42
SBo	0.86	0.55	1	SBo	0.14	0	0.45

Table 3.1: **Autumn transitions.** Left table, transition probabilities from reproductive state to North wintering area (residents). Right table, transition from reproductive state to South wintering area (migrants). These transitions were constant after first winter of life (Fig. 3.3.A). Mean and BCI are displayed. Reproductive states: NBi: non-breeder in Brittany, Bi: unsuccessful breeder in Brittany, SBi: successful breeder in Brittany, NBo: non-breeder outside Brittany, Bo: unsuccessful breeder outside Brittany, SBo: successful breeder outside Brittany.

(0.57, BCI: 0.04, 0.95) than for those wintering in the South (0.1, BCI: 0.01, 0.3; Fig. 3.4A). For birds attempting to breed for their first time when two and three years old, there was no difference in breeding probability between the two wintering strategies, (see Fig. 3.4B and Fig. 3.4C, respectively), when four years old, all individuals have virtually attempted to breed at least once (Fig. 3.4D). The number of four-year-old first breeders is negligible (≈ 0 , BCI: 0, 0.02). Consequently, we only report results of three ages of first breeding: one, two and three years, respectively.

Reproductive investment (RI) is the cumulative number of breeding attempts at age a , independently of breeding success (see Methods). If an individual attempts to breed at each breeding occasion, its investment is 100% and its performance (cumulative number of breeding attempts) is the bisecting line (Fig. 3.5A and B). North wintering individuals exhibited a higher investment than South wintering ones (Fig. 3.5A). Before age 6, the RI of the former ones is higher ($p(RI_{North} > RI_{South}) = 1$). No strategy reached full investment (bisecting line) and they both showed a change point around the age of 14 years, with a positive linear trend before that age and a plateau after. The estimated slope of the regression (before the age of 14 years), using ordinary least squares, was 0.8 for South wintering birds and 0.7 for North wintering birds. The two lines intersect around the age of

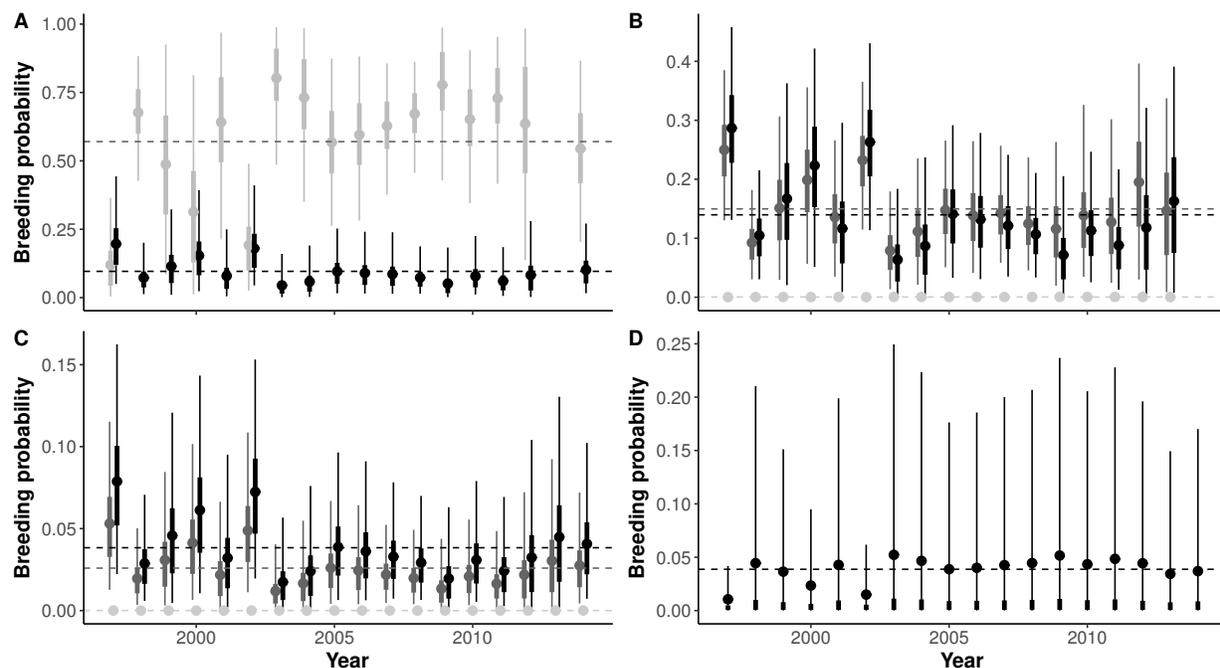


Figure 3.4: **Probability of first reproduction.** Panel A, breeding probability when one year old according to wintering state. Panel B, breeding probability when two years old according to wintering state. Panel C, breeding probability when three years old according to wintering state. Panel D, probability of never attempting breeding before age of four. light grey: individuals faithful to North (residents); black: individuals faithful to South (migrants); dark grey: individuals switching wintering strategy. Dashed lines indicate mean value.

seven years (Fig. 3.5A).

Considering age of first breeding, interestingly, individuals that began to reproduce when one year old exhibited a higher investment than those beginning later (Fig. 3.5B). Their cumulative investment remained higher than that of birds recruiting later, and the rate of increase of CRI with age decelerated only slightly at old ages. Individuals recruited when two years old exhibited a smaller investment than the two older classes, and seemed to stop their reproductive career around 15 years of age. The cumulative investment of individuals beginning to breed when three year old was the lowest, but converges towards the one of birds recruiting at the age of two, after the age of eight years. It is impossible to tell whether there is evidence of senescence in this last strategy because of identifiability issues, due to small the sample size after after age of 13 years. We did not find evidence of an effect of the

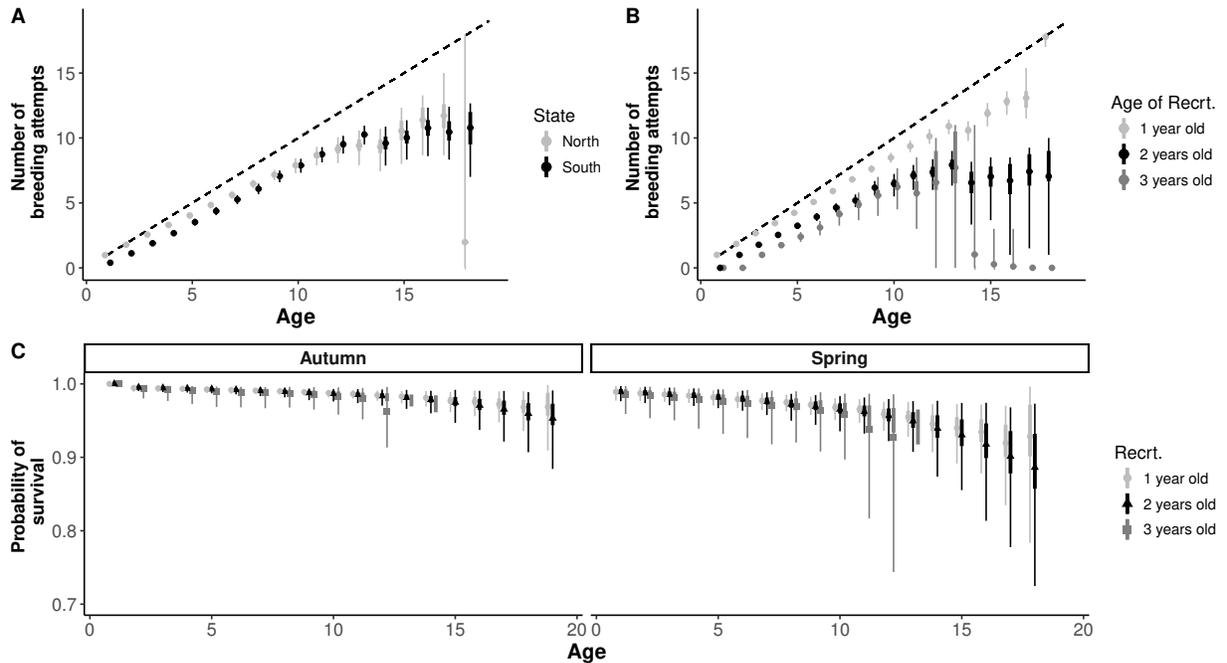


Figure 3.5: **Effects of wintering strategy and age of recruitment on reproduction investment and survival rates.** Panel A, number of breeding attempts according to wintering strategies. Panel B, number of breeding attempts according to age at first reproduction. Panel C, autumn and spring survival rates according to age at first reproduction. Dashed line correspond to line 1:1, indicating investment in reproduction every year of life. Survival rate for first breeders at three years old were not identifiable since 13 years old due to lack of data.

age at first reproduction on seasonal survival (Fig. 3.5C).

The estimated mean reproductive lifespan was equal to 0.77 (BCI: 0, 1). During this reproductive period, individuals would breed on 86% of the breeding occasions (BCI: 0, 1). Thus, individuals rarely skip breeding occasions, and the reproductive period encompasses more than three-quarters of Pied Avocets lifetime. However, these results must be considered with caution because many birds involved in this study were still alive during the last sampling occasion: their entire trajectory is not known yet. The estimated correlations of the variance-covariance matrix of individual random effects for survival and breeding rates provided slight evidence of a positive relationship between these two parameters (Appendix B.4.1, Fig. B.4 and Table B.2, p. 176). At the individual scale, a higher survival probability was associated with a higher breeding probability (regardless of the season and

the wintering strategy).

3.5 Discussion

In this study we explored the life-history traits involved in the contrasted demographic dynamics of migratory strategies in a population of partial migrant birds. Our main question was whether individuals with different migratory strategies exhibited different reproductive tactics. More precisely, we addressed the differences in cumulative reproductive investment with age, and in age at recruitment, and the differences of age at first breeding on age-related changes in cumulative investment. We knew from previous work (see chapter II) that the residents experienced a demographic increase from the 90s onwards, while the sub-population of migrants remained stable; we also know that the survival rates associated to the two strategies did not differ. Here, we provided evidence that autumn survival is higher than spring survival probability, but we still did not find evidence of a difference between the two migratory phenotypes. By contrast, results concerning reproductive investment revealed important differences. From a modelling point of view, we showed that it is important to take uncertainty in breeding state assignment into account. Indeed, miss-classification would lead to major biases: nearly 50% of the breeders were correctly classified and only 5% of the non breeders outside Brittany. Sources of errors were twofold: breeding behaviours is rarely observed when individuals are detected by investigators, and non-breeders are usually observed with ambiguous behaviour (partial sequences of breeding behaviours). Interestingly, non-breeders mainly dispersed outside Brittany and they were overrepresented among migrants younger than three years old.

One major difference in life-history traits between the migration strategies is the age at recruitment. While this parameter varies in time, nearly 60% of the residents attempts to breed when one year old *versus* 10% of the migrants. Such differences in the onset of reproductive investment could influence the sub-populations growth rates (Stearns, 1976; McGraw & Caswell, 1996; Acker *et al.*, 2014) and partly explain the contrasted dynamics of the migratory strategies. In addition migration can entail extra costs (Grist *et al.*, 2017); we

did not find evidence of survival costs, but migration could make reproduction more difficult for young individuals.

The age-related cumulative reproductive investment is higher in residents at least during their first six years of life, but the differences disappears afterwards. This can be interpreted as evidence of a higher early breeding investment in residents. Regardless of the strategy, we found evidence of a decline in reproductive abilities with age (reproductive senescence), starting at around 14-15 years of age. This phenomenon is common in wild vertebrates (Nussey *et al.*, 2008; Marzolin, Charmantier & Gimenez, 2011; Hammers *et al.*, 2013; Nussey *et al.*, 2013; Pardo, Barbraud & Weimerskirch, 2014). Several non-exclusive hypotheses have been developed to explain senescence. The “disposable soma” hypothesis suggests that selection pressures on somatic maintenance and repair favour early investment in reproduction to keep the organism in the best conditions as long as it can survive in the wild (Kirkwood, 1977; Kirkwood & Austad, 2000). The cost of a high performance in early life (reproduction and survival) is then balanced by higher somatic damages in later age, *i.e.* an accelerated senescence, a decrease in survival or reproductive performance or both (Kirkwood & Austad, 2000). According to this hypothesis, this decrease is cumulative with age (Orell & Belda, 2002). The “antagonistic pleiotropy” hypothesis proposed by Williams (1957) postulates that gene selection that favours early life performance, “youthful vigor”, confers disadvantage later on, “declining vigor”, due to a simultaneous diminishing selection against late-acting deleterious genes that accelerate senescence. These two theories clearly point to a trade-off between early life investment and late-life performance, which led to optimality theories of ageing, with mutation of genes (or alleles) with pleiotropic effects in the “antagonistic pleiotropy” hypothesis, and different possible resource allocation strategies in the “disposable soma” hypothesis (Partridge & Barton, 1993). While it is not possible to disentangle these mechanisms in this study, such mechanisms are consistent with the pattern described in Pied Avocets. Indeed, the convergence of age-related cumulative reproduction investment curves between the two migratory phenotypes, around the age of seven years, is consistent with the hypothesis of an extra cost of higher investment in early life in residents compared to migrants.

The “mutation accumulation” hypothesis suggests that senescence is mainly due to deleterious genes caused by mutation and genetic drift; these genes impede somatic maintenance and reparation at old age (Medawar, 1952; Edney & Gill, 1968). According to this hypothesis we can expect that senescence affects both reproduction and survival in all individuals. The “terminal investment” hypothesis stipulates that individuals facing decreasing performances allocate the rest of their resources in reproduction at the expense of survival, since survival is anyway, compromised (Williams, 1966). In such case we would observe no or weak decrease in reproductive investment before death (in breeding probability and cumulative reproduction with age, Isaac & Johnson, 2005). We observed this pattern only in individuals that recruited early. On the contrary, the senescence hypothesis predicts a decline in performance at old age (McNamara *et al.*, 2009; Weladji *et al.*, 2010). In accordance with this theory, we found evidence of decrease in performances (reproduction and survival).

We did not find evidence of differences in survival rate according to age of first breeding or of a decline in survival with age, neither in spring nor in fall. However, there was a substantial effect of the age of recruitment on cumulative age-specific reproductive investment. Interestingly, individuals recruiting when one year old showed the highest reproductive investment and nearly no decline in investment with age, which contrasts with individuals recruiting later. However, the cumulative investment of individuals recruiting at the age of three years became equal to the cumulative investment of those recruiting at age two around the age of seven years. These results are consistent with the “individual heterogeneity” hypothesis, or the “individual quality” hypothesis *sensu* Curio (1983). The conceptual difficulties raised by the “quality hypothesis” (i.e., a circular logic; Wilson & Nussey 2010; Bergeron *et al.* 2011) do not detract the fact that heterogeneous populations can be composed of individuals with both higher survival probability and breeding rates than others (Cam *et al.*, 2002, 2013). Under the heterogeneity hypothesis some individuals should be able to breed earlier and to exhibit higher reproductive and survival rates than others (van Noordwijk & de Jong, 1986). Such a positive correlation between life-history traits has been empirically demonstrated several times (Cam *et al.*, 2002; Beauplet *et al.*, 2006; Weladji *et al.*, 2008; Hamel *et al.*, 2009; Cam *et al.*, 2013). One of the hypotheses put forward to explain heterogeneity relies

on the idea that reproduction costs affect individuals differently (van Noordwijk & de Jong, 1986). In our study systems, some individuals recruited early, their cumulative reproductive trajectory was higher than that of others, and we did not find evidence of senescence in these individuals. These were mainly residents. In contrast, individuals exhibiting lower performances *sensu lato* (age of first breeding, age-related cumulative reproductive investment, late-life decline in reproductive investment), were mainly migrants. Similar results have been found in long-lived seabirds (Nol & Smith, 1987; Beauplet *et al.*, 2006; Aubry *et al.*, 2009). Our results primarily support the heterogeneity hypothesis because we found evidence that the models including individual random effects on both survival and reproductive transition probabilities had higher posterior probabilities than other models using an inclusion variable. We also found evidence of positive correlations between individual effects on fitness components.

However, the causes of fitness differences between migration phenotypes are unclear at this stage, *i.e.* we cannot conclude if there was direct or indirect selection on these traits. Indeed, other factors could explain why residents "do better" than migrants. Temporary environmental conditions during the study period (especially mild winters) could favour one phenotype (residents) against the other and explain the contrasted demographic dynamics of the two strategies over the study period. In contrast, harsh conditions in winter (wintering cold spell) could partially alter the relative advantages of both strategies. In other words, death by starvation or by cold can favour the migrant phenotype. This climatic pattern could explain the decline of the migrating population observed since the beginning of the study (see chapter II); thus over a period of time characterized by mild winters, especially compared to the previous period. In this context, the persistence of partial migration, where migrants have lower breeding performances could be explained by a conditional strategy in which migrants made "the best of a bad job" (Lundberg, 1987, 1988; Adriaensen & Dhondt, 1990).

Here, we found additional evidence of higher fitness in residents than in migrants, but we only assessed fitness components, not lifetime fitness. Generally, there is no unique response to selection in the wild and opposite responses of phenotypes can result in the same

lifetime fitness level. We thus need to evaluate several other age-related traits to qualify individuals or categories of individuals (Shuster & Wade, 1991). Consequently, further work will be required to estimate the part of the growth rates of the sub-populations explained by selection, and to fully address the fitness of each phenotype.



"Breeding in Brittany"
Picture: F. Touzalin

Chapter 4

Estimating fitness of life history strategies: when demographic movements are of prime interest

Frédéric Touzalin, Guillaume Gélinaud, Emmanuelle Cam and Étienne Sirot

4.1 Abstract

In the context of global warming, it is fundamental to understand observed changes in population size of mobile species, but assessing the demographic rates of open populations is still challenging. Few empirical studies allowed to quantify immigration and emigration over time, because immigration is generally not observable and emigration can only be estimated using capture-recapture (CR) data at a large spatial scale. Moreover, little is known on how life-history polymorphism could be associated with variations in population dynamics, *i.e.*, on strategy-dependent fitness.

We used a long-term data set (19 years) from a breeding population of Pied Avocet (*Recurvirostra avosetta*), a long-lived partial migrant shorebird, in Brittany. We addressed the temporal variations in population size and in the representation of both migratory phenotypes in the population. We developed an integrated population model (IPM) that allowed us to assess immigration rate without specific data. Because individuals of different ages are expected to have different contribution to population fluctuations, we modelled the population structure with fifteen age classes, on the basis of previous analyses that showed that survival was age-dependent. We assessed the fitness of both migratory phenotypes and addressed the question of their persistence in the population.

We found that the breeding population in Brittany was stable at the scale of Brittany, but was in fact declining if emigration was taken into account. The population was thus mainly sustained by immigration, productivity being too low. The fitness of the migrant phenotype (0.92) was substantially lower than that of the resident phenotype (1.0), which resulted in a decrease in the frequency of the migrant phenotype. We demonstrated that the overall dynamics of this population mainly depends on a metapopulation system with complex flux (immigration and emigration) with other populations, fluctuating over time in relation with the dynamics of the migrant and resident sub-populations.

This study highlights the importance of accounting for emigration and immigration when assessing local population size variations. These findings underscore the importance of long-term CR studies at large scale for understanding the drivers of open population dynamics.

This is the price for improving and evaluating conservation policies.

4.2 Introduction

Temporal fluctuations of population size have long been an important research area in ecology and evolution. Which are the key demographic rates responsible of such fluctuations, why some disappear and others persist (*i.e.* if and how regulation takes place), are yet under debate (Hixon, Pacala & Sandin, 2002). Understanding the mechanisms underlying population dynamics, not only concerning changes in number, but also in structure (age- or stage-structure) is of vital importance, especially in the context of increasing anthropological impacts on ecosystems and climate changes. However, estimating the size and structure of populations of free ranging animals, their variations over time and the corresponding variations in fitness for individuals, remains a challenge.

The dynamics of local populations result from the expression of individual life history strategies, which can be affected by all kinds of environmental conditions, including abiotic factors and inter-individual relationships, both within and between populations (Oro *et al.*, 2010; Pardo *et al.*, 2017). In addition, population dynamics is subject to stochastic events. First, a population can experience stochastic variations in size due to random realisation of a given demographic strategy: *i.e.* “demographic stochasticity” (Kendall, 1949; Roughgarden, 1975). Second, fluctuations in the environment due to unpredictable events, for example affecting climate (Goss-Custard, 1996; Johnson, Green & Hirons, 1991), can deeply influence individual success and hence lead to population changes, *i.e.* “environmental stochasticity” (Roughgarden, 1975). This complexity makes it challenging to identify the drivers of population variations, and to find evidence of regulation processes in empirical studies. Regulation relies on three basic phenomena (Murdoch, 1994): (i) persistence (long-term succession of generations), (ii) boundedness (existence of lower and upper limits of population size variations), (iii) return tendency (feedback mechanisms constraining population fluctuations to vary around a mean). Density-dependence is recognized as an essential mechanism generating regulation (Hixon, Pacala & Sandin, 2002), but the mechanisms involved can be

diverse (*e.g.*, competition, predation).

Furthermore, the different strata composing a population (*e.g.*, sex- or age-classes, developmental or physiologic stages) may react to their environment in different ways, which can strongly influence the overall dynamics of the population (Oro *et al.*, 2010; Saether *et al.*, 2013; Pardo *et al.*, 2017). The strength and form of the relationship between demographic parameters and environmental factors may indeed vary across the different strata of the population. For example, density dependence in the different age classes of the population has been demonstrated to differentially affect survival (Lok *et al.*, 2013). The "critical age group", defined theoretically by Charlesworth, 1972, denotes the age class or the group of age classes that most strongly contributes to density-dependent regulation. As an illustration, recent empirical study has shown that the number of first breeders strongly affects population growth in a short live passerine (*Parus major*), by affecting recruitment and survival rates of the other age classes (Gamelon *et al.*, 2016). Fluctuations in population structure can also induce important differences in the dynamics of strata, independently of population size (Coulson *et al.*, 2001).

Despite this apparent complexity, fluctuations in abundance in an open population always result from birth, death and movements, and can thus be accounted for by four processes only : recruitment and survival probability, emigration and immigration rates (Sibly & Hone, 2002; Schaub & Abadi, 2011). Hence, estimating these demographic parameters is the basic step of any empirical study of population dynamics, because these parameters are the expression of individual life history and behavioural strategies (Saether & Bakke, 2000; Saether *et al.*, 2013). There is a growing recognition that separated analyses of demographic parameters do not allow a full understanding of variation and covariation of demographic rates and their contribution to fitness (Cam *et al.*, 2002; Schaub, von Hirschheydt & Gruebler, 2015). Until recently, meaningful demographic analyses of population dynamics have indeed required detailed data from structured populations with a minimum level of uncertainty (*e.g.*, very good detection of individuals, knowledge of breeding status and age, etc.), which can seldom be achieved in empirical study unless artificial conditions are introduced in the environment, such as nest boxes for birds, for example (Grøtan *et al.*, 2009).

In recent years, several modelling techniques have been developed that offer the possibility to use several sources of data simultaneously (*e.g.*, data from capture-recapture, hereafter CR, and counts) and to deal with for all known sources of bias and stochasticity at the same time (Besbeas *et al.*, 2002; Morgan, Brooks & King, 2004; Schaub & Abadi, 2011; Kéry & Schaub, 2012). These methods also enable to investigate potential interactions between demographic parameters, and their influence on the population growth.

Among the innovative features of the recent modelling approaches, the estimation of quantities that are difficult or impossible to directly measure in the field (*e.g.*, immigration, emigration), become easier and their integration ensures more precise estimations. Indeed, immigration is generally not assessed in local scale studies, because immigrant birds generally come from non monitored areas. Emigration, either temporary or permanent, is easier to estimate with CR methods, but this requires monitoring a large proportion of the species range for accurate estimates, especially if survival differs between resident and migrants (Bird *et al.*, 2014). In geographically open populations, movements, *i.e.* emigration and immigration, can have important effects on population dynamics, some populations absorbing individuals, some exporting individuals, and others doing both (at the same time). Immigration can contribute to sustain populations but little is known about the importance and the consequences of immigration on population dynamics (Abadi *et al.*, 2010b; Schaub, Jakober & Stauber, 2013). Importantly, ignoring emigration can bias the estimation of demographic parameters, such as survival rate (Schaub & Royle, 2014). Studies encompassing the analysis of the four key demographic parameters (recruitment, survival, emigration and immigration) in open populations are rare, although the knowledge of all these rates is necessary to device a comprehensive description of the population dynamics (Schaub, Jakober & Stauber, 2013; Weegman *et al.*, 2016).

Open and structured populations, where individuals experience different life-histories, offer opportunities to understand these relationships in relation with growth rate fluctuations and potential regulation mechanisms. In the presence of partial migrant populations, whose persistence mechanisms remain largely unknown (Chapman *et al.*, 2011), the use of open population model is thus particularly appealing. Indeed, while partial migrants expe-

rience a large set of range of environments during their annual cycle, the two phenotypes are maintained in a large number of species (Berthold, 1999), which raises the question of polymorphism maintenance in these populations. Residents and migrants generally coexist during the breeding period, then, the former stay on breeding ground during winter, while the latter migrate. As temporal variations in the growth rate (*i.e.* in fitness, as pointed by Stearns, 1976, 2000) are driven by differences in life history traits (Saether & Bakke, 2000; Saether *et al.*, 2013), we expect different temporal dynamics, resulting from different demographic rates, between the two sub-population. Hence, each sub-populations composed by individuals sharing the same traits, will possess a specific demography that will contribute to the overall population. It is then fundamental to consider the specificity of both sub-populations to disentangle the demographic processes at work in population size variations.

In the present study we propose a mechanistic analysis of the dynamic of the population of a partial migrant shorebird, the Pied Avocet (*Recurvirostra avosetta*). The population of Pied Avocet of Brittany (France) is restricted to a small number of closely related colonies, on the Atlantic coast, in the vicinity of the Morbihan Gulf (South). Previous studies (see chapter II and III) have shown that the two wintering strategies (sedentary and migrant individuals) experience different dynamics, that led to a decrease in the relative frequency of the migrants. No differences in survival rate between the two wintering strategies have been found. In addition, the recruitment of residents took place earlier, which can partly explain the difference in dynamics between the two sub-populations. However, demographic informations obtained so far did not provide a definite conclusion concerning potential fitness differences between the two strategies. Specifically, the previous studies focused on sub-samples of the dataset, restricted to individuals observed during winter. A comprehensive approach for the investigation of the demographic mechanisms responsible for changes in population size over time should include, in addition to the exploration of the major life-history traits, a study of the population flux (emigration and immigration) and of the evolution of the population structure. In the present study we used Bayesian integrated population models (IPMs) to combine several sources of demographic data, in order to (i) assess the entire population trend and the key demographic parameters (*e.g.*, adult and

juvenile survival, productivity, emigration, immigration), (ii) identify the most influential demographic rates on the temporal variations of the population growth rate and the possible regulation mechanisms, (iii) assess the fitness within the two sub-populations (defined by wintering strategies) and their demographic drivers, (iv) investigate the "critical" age classes which contribute most to population growth rate fluctuations.

4.3 Methods

4.3.1 Study area and data source

The population of interest corresponds to a small number of breeding colonies of Pied Avocets in the South of Brittany, on the Atlantic coast of France (47°37'N, 2°42'W; Morbihan Gulf). From summer 1996 to summer 2014, 539 juveniles were captured and individually marked with coloured plastic bands when 3-4 weeks old (close to fledging). The combinations of colour bands were visible from up to 300m using a 20-60× spotting scope. The main colony, in the natural reserve of Séné, was monitored weekly during all the breeding seasons (from April first to August). The other colonies were close to the main one and also monitored. However, most of the colonies were not stable in time and were subject to colonization and extinction. We thus considered them as extensions of the main colony, which was confirmed by the resightings. Collected data consisted not only in presence/absence data but also in the recording of the breeding behaviour of marked individuals. Annual juvenile counts consisted in the sum of observed fledglings and juveniles observed just before fledging (when 3-4 weeks old) but whose fate is not known. The number of pairs was estimated indirectly using laying dynamics. We used laying accumulation curves to determine the first laying peak, which generally occurred around the first week of May. To assess the number of pairs established in the colonies, we summed the number of active nests active at laying peak, the number of nests active in the previous week and that failed, and the new nests where adults laid eggs in the following week. The breeding population was subject to high predation pressure, and Pied Avocets generally make two or even three breeding attempts during the breeding season in Brittany, with an estimated time interval of at least one week between nest failure and the

laying of the first egg of the replacement clutch. Even if females can make several breeding attempts, we considered that they bred a maximum of one fledges, because we have very few examples of multiple broods raised up to fledging by a unique marked female during the same breeding season (2 cases in the database).

Outside Brittany, the main breeding sites were monitored by professionals in nature reserves and by a network of volunteers in the other sites along the French coast, and over most of the breeding range in Europe (see Fig. 3.1.B). Marked individuals were also resighted during the non-breeding season, during the post-breeding gathering and the wintering periods, with particular attention to the most important wintering places in France, Portugal and Spain. Most of the wintering range was also covered by a large number of volunteers across Europe (see Fig. 3.1.A). Data collected during the wintering period (from December 20th to February 25th) allowed us to assign individuals to one of the two wintering strategies, *i.e.* birds wintering in the North (France and marginally England) versus birds wintering in the South (Portugal and Andalusia). In summary, several types of demographic data are available: annual population counts at breeding colonies (number of pairs), productivity (number of fledging juveniles), survival (from capture-recapture data, CR) and movements outside breeding colony (dispersal) as well as during the wintering season (wintering strategy). All of these data are sufficient to estimate population dynamics (variation in time, gain and loss) and the underlying demographic parameters (*e.g.* survival, site or state transition), as well as lifetime, fitness for the different kinds of individuals.

We distinguished several sub-populations, in the following analyses, which all were composed from individuals born in Brittany. First, we distinguished two sub-populations based on wintering strategy, *i.e.* the North wintering individuals we called "residents" and the South wintering individuals we called "migrants". We also referred to "Brittany population" as all the individuals alive and born in Brittany, *i.e.* breeders in Brittany and emigrants from Brittany. We also consider as the breeding population, only the individuals breeding in Brittany, and not those recruited outside.

4.3.2 Demographic parameters estimation and system description

In order to estimate demographic parameters and their changes through time, we used a female-based aged-classified and multi-state integrated population model (Schaub & Abadi, 2011; Kéry & Schaub, 2012). We used pre-breeding census for the estimation of the population size and split breeding range in two different units. The colonies located in Brittany were considered as a unique colony (separated from all others), because monitoring was more intensive: we then expected an higher resighting probability than elsewhere. This distinction allowed us to estimate movement probability from and to birth colony, *i.e.* fidelity, and to estimate immigration and emigration rates. We used a female-based model with 15 adult age-specific population stages. Previous analysis (see chapter II and III) have indeed provided evidence that survival of Pied Avocets from Brittany varies with age and exhibits individual heterogeneity, but the precision of survival estimates decreases with age. Consequently, we decided to limit the number of age classes. To illustrate the approach, the life cycle for the first three cohorts is shown in Fig. 4.1. Pied Avocets can recruit at age of one year, and virtually all the individuals are recruited at age of four years (see chapter III). Here, annual recruitment implicitly included the fecundity of each cohort.

The expected population structure and age transition processes can be mathematically described as follows (Eqn 4.1):

$$\begin{aligned}
 E(N_{1,t+1}|N_{1,t}, \dots, N_{15+,t}) &= (N_{1,t} + N_{2,t} + \dots + N_{15+,t})\phi_{juv,t}b_t \times 0.44, \\
 E(N_{2,t+1}|N_{1,t}) &= N_{1,t}\phi_{1,t}, \\
 &\vdots \\
 E(N_{15+,t+1}|N_{14,t}, N_{15+,t}) &= N_{14,t}\phi_{14,t} + N_{15+,t}\phi_{15+,t},
 \end{aligned}
 \tag{4.1}$$

where $N_{i,t}$ is the number of individuals in age-class $i \in \{1, \dots, 15+\}$ during year tt , $\phi_{juv,t}$ and $\phi_{i,t}$ are the survival of juveniles and adults in age-class $i \in \{1, \dots, 15+\}$, and b_t is the annual fecundity (number of offspring per female). Juvenile survival is the survival probability from nearly fledged (age of 3-4 weeks, *i.e.* time of ringing) to the following breeding season (this estimate was used for the productivity assessment). Sex ratio was estimated from behavioural observations of copulation events and from DNA samples from fledglings during

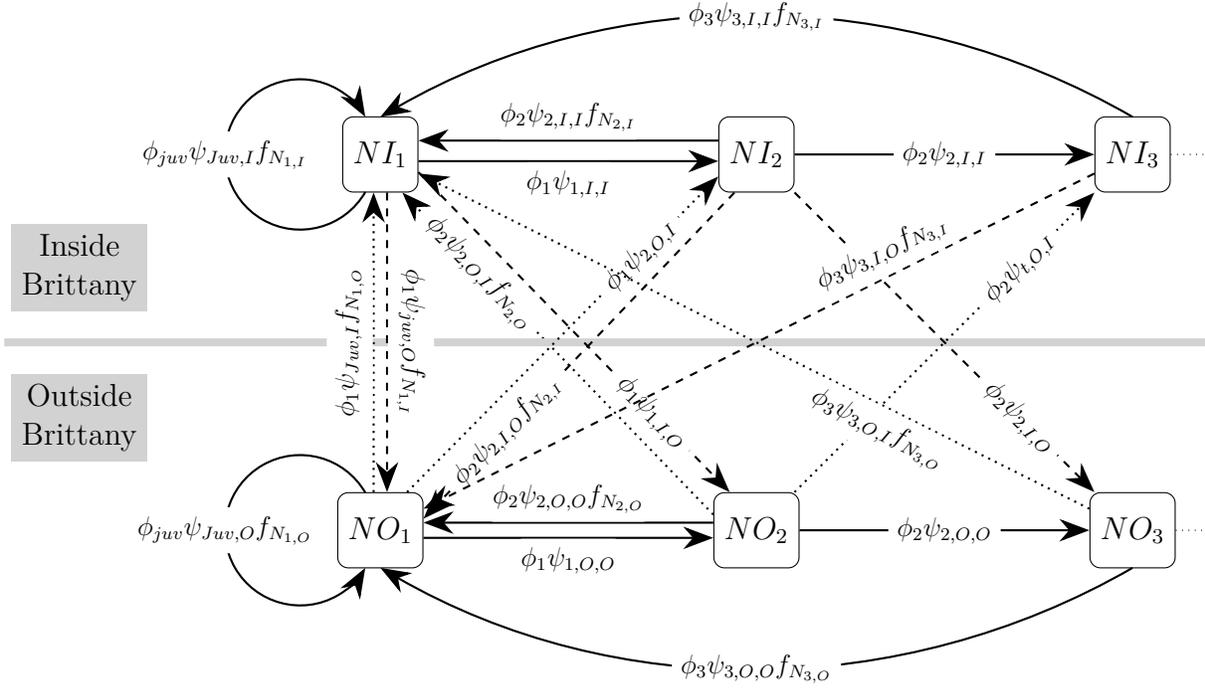


Figure 4.1: **Two-state life cycle graph of the Pied Avocet population from Brittany.** The population is considered geographically closed (all breeding range monitored) with two breeding areas describing birth site, Brittany and elsewhere (outside Brittany). The model is female-based and pre-breeding census. The population stages are defined by age, here only 1-year-old individuals (N_1), 2-year-old individuals (N_2) and 3-year-old individuals (N_3) are represented, for the sake of clarity. Stages also account for location: NI indicates populations breeding inside Brittany and NO populations breeding outside Brittany. The demographic parameters are age-specific, survival ($\phi_i, i \in \{1, \dots, 10\}$), productivity ($f_{N_i}, i \in \{1, \dots, 10\}$), and transition between sites (ψ) depends on time and previous state (I: inside, O: outside) except the first one. Solid lines indicate fidelity, dashed lines indicate emigration from Brittany and dotted lines immigration. Some parameters are not individually identifiable (*e.g.* fecundity of each cohort), but some parameters (*e.g.* annual fecundity) can be estimated thanks to the integration of other data.

capture occasions. As well adults and fledglings shown the same male-biased sex ratio. Thus, we used a sex ratio of 0.44, estimated from 279 individuals (123 females, 156 males; $\chi_1^2 = 3.67, p = 0.06$ suggests a bias sex-ratio) in the whole dataset of marked individuals, including individuals coming from several colonies along the French Atlantic coast.

Annual movement probability of individuals were estimated through CR data outside Brittany. The emigration rate can be estimated from resightings of marked individuals

outside Brittany, while immigration is a hidden component estimated thanks to the IPM. Each adult age-specific population state can result from four possible transitions: $NI_{a,t} = \phi_{a,t} \times (NI_{a,t-1}\psi_{t,I,I} + NO_{a,t-1}\psi_{t,O,I})$ and $NO_{a,t} = \phi_{a,t} \times (NO_{a,t-1}\psi_{t,O,O} + NI_{a,t-1}\psi_{t,I,O})$, where a is the age-class $a \in \{1, \dots, 15+\}$, t the year, ϕ the survival probability, ψ the transition probability between Brittany and the other breeding colonies and the subscripts I and O, which indicate transition directions, referring to inside (I) and outside (O) Brittany, respectively. The number of individuals present in Brittany in year t and belonging to population stage a is then $NI_{a,t}$, *i.e.* philopatric and immigration from locally born individuals, and the number of birds outside Brittany is $NO_{a,t}$, *i.e.* emigrants.

However, immigration (from birds not born in Brittany) potentially concerns birds from all colonies of Pied Avocets in the West Palaearctic breeding range, where there is no ringing programme in the vast majority of cases. Consequently, immigration cannot be entirely assessed with CR data. The estimation of immigration in Brittany was thus made possible by including an extra annual population stage structure ($N_{im,t}$), that accounts for unmarked immigrant birds (Eqn. 4.2):

$$NI_t = \sum_{a=1}^{15+} NI_{a,t} + Nim_t, \text{ and } \omega_t = \frac{Nim_t}{NI_t}, \quad (4.2)$$

where NI_t is the expected number of females in Brittany during year t , NI_t being estimated from the annual counts of breeding pairs, and the sum of the $NI_{a,t}$ terms is the annual population size, estimated from the integrated demographic parameters (counts, survival and fecundity). Finally, the annual immigration rate ω_t was derived from the ratio between the number of immigrants and the population size in Brittany.

We also derived the annual growth rate of the population (λ_t) and the geometric growth rate (λ_G), from population size estimates (Eqn. 4.3):

$$\lambda_t = \frac{N_{t+1}}{N_t} = \frac{NI_{t+1} + NO_{t+1}}{NI_t + NO_t} = \frac{\sum_{a=1}^{15+} NI_{a,t+1} + Nim_{t+1} + \sum_{a=1}^{15+} NO_{a,t+1}}{\sum_{a=1}^{15+} NI_{a,t} + Nim_t + \sum_{a=1}^{15+} NO_{a,t}}, \quad (4.3)$$

$$\lambda_G = \left(\prod_{a=1}^t \lambda_i \right)^{1/t},$$

with $NI_{a,t}$ and $NO_{a,t}$ the numbers of individuals of age-class a in year t inside and outside Brittany, respectively. We used the geometric mean of the population growth rate during the

study as a measure of the individual fitness in this population. The CDL formulation used to analyse the CR data, made it straightforward to derive the annual proportion of North and South wintering birds. We derived the geometric mean growth rate of these sub-populations and used it to assess the fitness measures for both wintering strategies, assuming that the proportion of each strategy in the CR data is the same as in the whole Brittany population.

4.3.3 Integrated population modelling approach

IPMs are defined as "models that jointly analyse data on population size and data on demographic parameters" (Schaub & Abadi, 2011). They are relatively new (Besbeas *et al.*, 2002; Morgan, Brooks & King, 2004). Here, we used a Bayesian approach with a hierarchical formulation, which facilitates the joint analysis of several datasets, including different types of data. The Bayesian approach to IPMs is also a flexible and powerful tool to address demographic and evolutionary questions linked to variation of population size (Schaub, von Hirschheydt & Gruebler, 2015; Bjørkvoll *et al.*, 2016). Implementing these models has become relatively easy thanks to recent developments (Schaub & Abadi, 2011; Kéry & Schaub, 2012). The advantages of this modelling framework are numerous. For example, it allows the analysis of several source of demographic data in one single model. It also accounts for uncertainty in data collection by jointly modelling state and observation processes. The joint likelihood combines three components: a state-space model for population size estimation (count data), a state-space model for survival estimate (CR data) and a model for fecundity estimation (fledglings count data). The population size is linked to underlying demographic rates via an age-structured model with 15 stages (i.e. a Leslie matrix).

The equations 4.1 and equation 4.2 describe the global population structure and a part of the breeding population life cycle graph is provided in Fig. 4.1. In order to include demographic stochasticity, appropriate statistical distributions were set to all annual population stages (for details, see Appendix C.1, p. 199). The likelihood of the state-space model (L_{SS}) for count data is the product of the observation process (error in pairs estimation) and the state process (reproduction): $[C|N][N|\phi_{juv}, \phi_1, \dots, \phi_{15+}, f, \omega]$, where C stands for count data, N is the estimated population size, ϕ the stages-specific survival, f the fecundity and ω the

immigration rate. The likelihood of the state-space model (L_{CR}) for CR data is the likelihood of multistate model, which is also the product of the observation process (error in individual detection) and the state process (survival): $[Y|p, A, z][A|\phi_{juv}, \phi_1, \dots, \phi_{15+}][z|\psi^z]$, with Y the observation matrix, p the detection probability, A the partially latent true alive matrix, z a two states matrix defining reproductive state. Here we used the complete data likelihood approach (Schofield & Barker, 2008; Schofield, Barker & MacKenzie, 2009), for details see Chapter III and Appendix C.1.2 (p. 200). Finally, the likelihood (L_P) of the productivity data is assumed to be unbiased (no measurement error) and dependant on the counts of pairs and fledglings: $[Juv, Fem|f]$, with Juv the annual count of juveniles and Fem the annual count of breeding females (pairs). Assuming independence among the three data sets, we can express the joint likelihood (L_{IPM}) as the product of the component likelihoods:

$$L_{IPM} = L_{SS} \times L_{CR} \times L_P = \\ [C|N][N|\phi_{juv}, \phi_1, \dots, \phi_{15+}, b, \omega] \times [Y|p, A, z][A|\phi_{juv}, \phi_1, \dots, \phi_{15+}][z|\psi^z] \times [Juv, Fem|b]$$

Hence, each likelihood component shares some parameters (see also Fig. C.1, p. 201) with another component. One important assumption for the unbiased estimation of the joint likelihood is the independence of the datasets. However, in this study, the count dataset includes the individuals of the CR dataset. However, Abadi *et al.* (2010a) have shown that the violation of this assumption has limited effects on the estimates of demographics parameters. The use of the same data in more than one dataset mainly affects the accuracy of the estimates and this effect is proportional to the frequency of the redundancy of individuals in the different datasets (Abadi *et al.*, 2010a).

IPMs offer the possibility to estimate quantities that are not measurable or not observable in the field. The immigration rate is a good example of such parameters in wild animal populations, because generally, unmarked immigrants and residents cannot be distinguished (as is the case here). The integration of population size and demographic parameters allows the estimation of this rate. The model also allows the quantification of the population structure (i.e. size of the different age-class segments, never observed).

4.3.4 Model fitting and goodness-of-fit assessment

We used a Bayesian approach (Kéry & Schaub, 2012) for inference on the parameters of the IPM. We performed analyses using Markov Chain Monte Carlo (MCMC) simulations with the software programme JAGS 4.0 (Plummer 2003) called from R 4.4.1 (R Core Team, 2016) through the package jagsUI 1.4.4 (Kellner, 2016). We specified vague prior distributions for the parameters, using reasonable bounds (Appendix C.1.3, p. 203). In particular, we used a uniform distribution for the annual number of immigrants with a left negative bound to account for the possibility that there is no immigration at all (Schaub & Fletcher, 2015). JAGS code is available in Appendix C.3 (p. 206).

For parameters estimation we ran 3 chains for 100000 iterations. We discarded the first 50000 iterations and retained every 2th iteration of the remainder. We used the Brooks-Gelman-Rubin diagnostic to assess convergence (Brooks & Gelman, 1998) and it was satisfactory (all $\hat{R} < 1.07$). To assess model adequacy, as dedicated goodness of fit methods are not yet available (due to the complexity of the IPMs; (Schaub & Abadi, 2011)), we performed separated posterior predictive checks (PPC) for each observation model. We use the χ^2 discrepancy measure (Gelman *et al.*, 2003) and computed Bayesian p-value to test the assumption that the model satisfactorily accounts for the process that gave rise to the data (Hooten & Hobbs, 2015). Details of the methods can be found in Appendix C.5 (p. 220).

We also performed model selection by comparing the deviance information criterion (DIC), to test different biological hypotheses. In particular, we addressed for the hypothesis of a time effect on adult survival, using a random time effect ($\eta_t^\phi \sim Normal(0, \sigma_{\phi t}^2)$). We also studied whether the adult transition probability from Brittany was best accounted for by a year effect treated as factors, or a linear effects. Lastly, we compared models where the first year recruitment probability is constant over time, with a models where recruitment probability varies with time.

4.3.5 Contribution of demographic parameters to population fluctuations

The relationships between demographic parameters and population growth can be assessed by studying correlations between the estimates of annual demographic rates and population growth rates. Demographic rates used in temporal correlations were fecundity, immigration and emigration rate, probability to be resident during the first winter, adult probability to return in Brittany when previously emigrated and juvenile survival. As survival rate was not time dependant, we computed from CR data an annual death rate by dividing the number of dead individuals between year t and $t + 1$ by the number of alive individuals in year t . We computed these correlations using the posterior distribution of each parameter and we estimated the probability that they were positive or negative. Specifically, we estimated the correlations between population growth rate and fecundity, immigration, emigration and transition rates between different wintering and breeding areas.

Moreover, we compared the results of four approaches of population growth rates: (a) taking immigration and emigration into account (Brittany population growth rate); (b) without emigration (overall population growth rate); (c) without immigration (by subtracting number of immigrants); (d) without emigration and immigration (by subtracting number of immigrants from the overall population).

In order to estimate the effects of age-class numbers on population growth, we examined the relationship between annual population growth rate and population structure in a regression framework. We used a linear regression (Schaub, Jakober & Stauber, 2013; Gamelon *et al.*, 2016) between the log population growth rate and the number of individuals in each age class:

$$\log(\lambda_t) = \alpha + \beta_1 N_1 + \beta_2 N_2 + \dots + \beta_{14} N_{14} + \beta_{15} N_{15} + \epsilon_\lambda, \text{ with } \epsilon_\lambda \sim \text{Normal}(0, \sigma_\lambda^2)$$

where α is the intercept, β_i the regression coefficients for age class i and ϵ_λ a random time effect corresponding to the variance not explained by age-specific numbers. The regression was fitted with a simple Bayesian regression model with vague Normal priors on regression coefficients (Appendix C.4, p. 218). This regression was fitted using 15000 random draws

among the 75000 posterior samples of the parameters used.

4.4 Results

The model with the best fit was model 1, see Appendix C.2 (p. 206), where survival is modelled with a linear time trend and an individual random effect, the recruitment probability in first year is constant and subsequent transitions between breeding sites have a linear time trend and a year random effect. Posterior summaries of the complete set of parameters from the IPM is given in Appendix C.6 (p. 225). We found substantial differences in the fitness assessment among the wintering strategies. Hereafter, we report posterior means and 95% Bayesian credible intervals (BCI) of the estimated parameters and derived quantities.

4.4.1 Population dynamics

Estimates of population size closely fit the population counts of pairs in Brittany (Fig. 4.2). The posterior predictive checks provide evidence of a good fit with Bayesian p-values close to 0.5 when all the years were pooled (Appendix C.5, Fig. C.5, p. 224). Annual discrepancy measures also indicate a good fit, except for the first two years (1996, 1997) for count data (Appendix C.5, Fig. C.2, p. 221), and for the first year for fecundity data (Appendix C.5, Fig. C.3, p. 222). There was no lack of fit for the detection probability (corresponding to CR data; detection in 1996 was not estimated). Lack of fit in the first two years of the study for most parameters was due to lack of information in the data. Hence, posterior distributions of parameters mainly reflected prior distributions. Consequently, we discarded samples from the posterior distributions of the parameters concerned by lack of fit, both in the figures and in the pot-hoc analyses.

The detection probability during the breeding season in Brittany was virtually equal to one (Fig. C.6, p. 225), while detection outside Brittany was low, with mean 0.28 (BCI: 0.1, 0.49). Detection probability was very low outside the study area (Fig. 4.2D) but regularly increased, especially after 2005, when similar monitoring programmes were developed all along the French Atlantic coast. During the wintering season, results were similar to those

previously obtained (see chapter II), with mean detection probability equal to 0.4 (BCI: 0.11, 0.59) in the North of Europe and 0.21 (BCI: 0, 0.36) in the Iberian Peninsula.

The population breeding in Brittany experienced important variations with a minimum of 154 pairs (BCI: 133-176; in 2000) and a maximum of 241 pairs (BCI: 213-270; in 1998). For the 1998-2014 period, the geometric mean growth rate of the Brittany population, was 0.97 (BCI: 0.96, 0.98) indicating a 3% decline per year (the BCI interval did not contain the value of 1). Conversely, the breeding colonies in Brittany (population without emigrants) experienced fluctuations around a geometric mean growth rates equal to 1 (BCI: 0.99, 1), indicating that the population is stable or only slightly declining (the BCI included value of 1). From Fig. 4.3, it appeared that the population of Pied Avocet breeding in Brittany will decrease unless there is immigration. The immigration rate compensates emigration and fluctuations in fecundity rate. If we consider emigrants, the population is no more stable but declines even if there are immigrant (Fig. 4.3). The difference between mean growth rates with and without immigration for the overall population was smaller because of the dilution effect of emigrants.

Apparent juvenile survival varied with time (Fig. 4.2B) but was high with a mean value of 0.86 (BCI: 0.57, 1). Adult survival did not vary with time, but showed a linear trend effect with age. The trend of adult survival with age was negative $\alpha_2 = -1.97$ (the BCI: -2.99, -1.05 did not include zero). As previously shown (chapter II and III) Pied Avocet experience senescence in survival (Fig. 4.2C).

Juveniles recruitment, (here geographic recruitment, *i.e.* the place where a one year old individual is observed during the breeding period regardless of its reproductive state), is higher outside Brittany, with a probability of 0.60 (BCI: 0.55, 0.65), than inside. However, annual variations were substantial (Fig. C.6D, p. 225). Adult fidelity to the breeding area increases with time inside Brittany with a strong positive linear trend (Fig. C.6F, p. 225). It was also the case outside Brittany, but temporal variability was more pronounced (Fig. C.6E, p. 225).

The fecundity rate estimate was low (Fig. C.6C, p. 225) with mean 0.24 (BCI: 0.11, 0.49) and highly variable in time. The minimum fecundity rate was 0.13 (BCI: 0.09, 0.19) in 2010

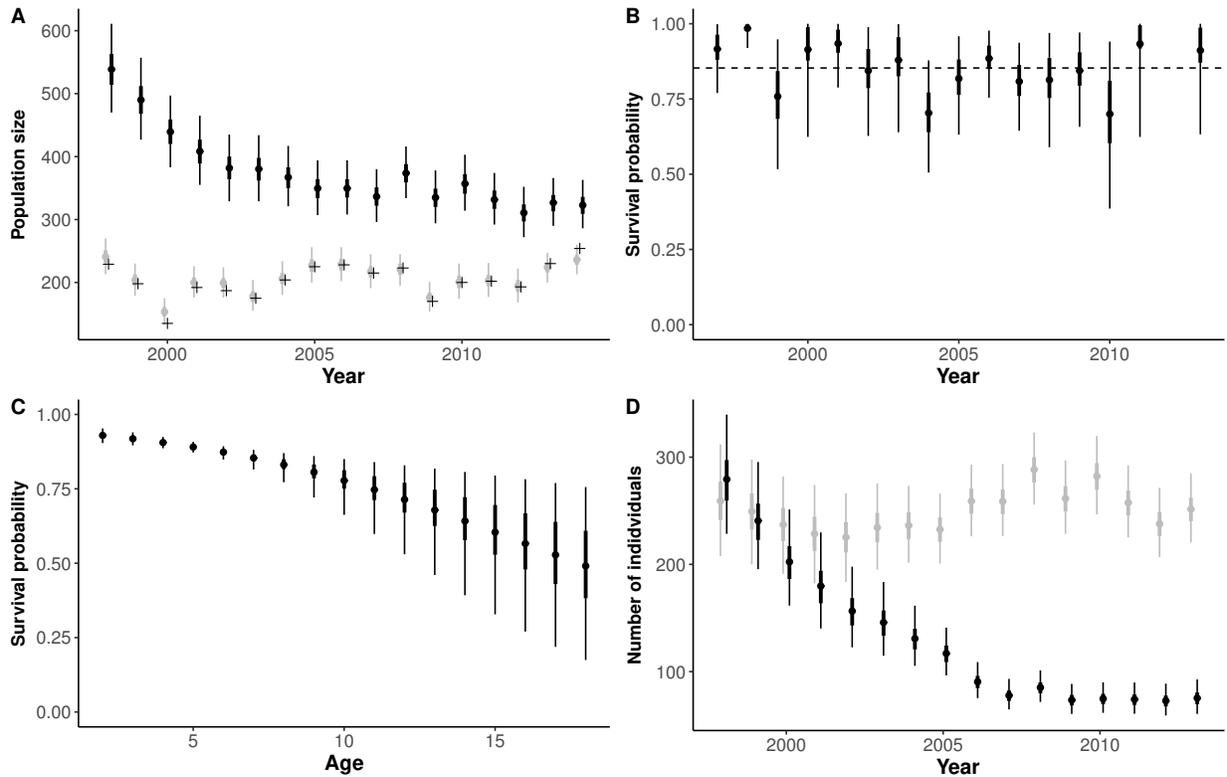


Figure 4.2: **Population size and survival rates variations in the population of Brittany's Pied Avocet.** Panel (A), in black: annual fluctuations of whole population size; grey: annual fluctuations of the breeding population in Brittany (without emigrants); sign plus: observed number of pairs. Panel (B), annual juvenile survival probability, dashed line indicate the mean. Panel (C), adult survival probability according to age class. Panel (D) in black: annual fluctuations of the South wintering sub-population; grey: annual fluctuations of the North wintering sub-population. Fine vertical line: 95% BCI; large vertical line: 50% BCI.

and the maximum was 0.47 (BCI: 0.38, 0.56) in 2008. This rate was in any case not sufficient to maintain population. This was confirmed by the decomposition of the mean population growth rates at different scales (Fig. 4.3), which highlights the major effect of immigration to sustain population growth in Brittany.

4.4.2 Population structure

The immigration rate was not negligible, accounting for a proportion of 0.2 (BCI: -0.02, 0.48) new arrivals in the population during the study period (Fig. C.6B). However, some 95%BCI

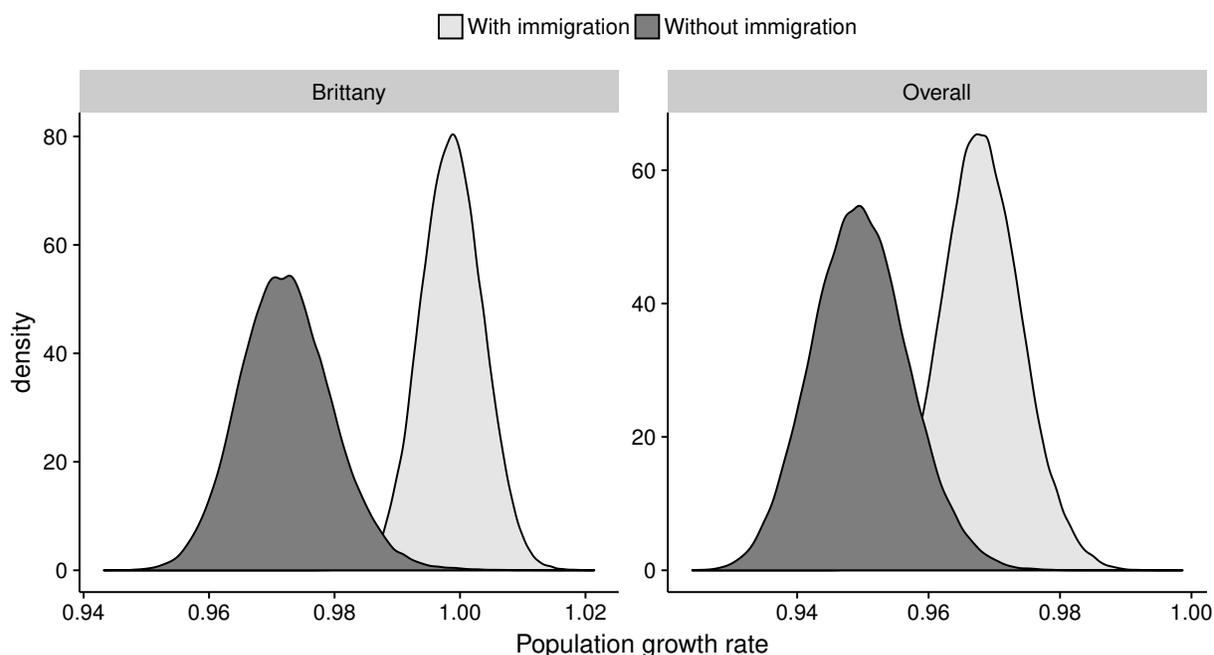


Figure 4.3: **Mean growth rates.** Density plots of the posterior distribution of the geometric mean growth rate with and without immigration pulse in Brittany (left) or for the overall population, *i.e.* population from Brittany and emigrants, (right). Population persistence requires a growth rate equal to one (population in Brittany). It is clear that Brittany’s population was sustained by immigration.

contained negative values or zero, which indicated a very low level of immigration, or none. It was the case from 1996 to 2002, and in 2008. The estimated immigration rate had thus low precision except in the years with the highest immigration rate, *i.e.* 2007, 2013 and 2014. Hence immigration increased during the study period, particularly at the end. The emigration rate of adults, the complement of site fidelity, decreased along the study period in two steps from 0.42 (BCI: 0.25, 0.59) to 0.16 (BCI: 0.09, 0.24) between 1998 to 2007 and from 0.26 (BCI: 0.19, 0.35) to 0.11 (BCI: 0.07, 0.17) between 2008 and 2014 (Fig. C.6A).

The population composition changed over the study. First, the proportion of emigrants was high at the beginning of the study, decreased rapidly until 2002, and then decreased more slowly. The population of emigrants was nearly equal in size to Brittany population and decreased by nearly a factor of 2. Second, immigrants constituted negligible part of the population and were probably absent in the first five years of the study, but then immigration

increased and immigrants represented nearly 40% of the population of Brittany in the last two years of the study. Third, juvenile recruitment remained constant during the study. The transition probability of adults, corresponding to fidelity to the previous breeding site, increased, with a higher fidelity to Brittany's colonies at the end of the study (Fig. C.6F), as this parameter is the complement of emigration rate. This indicates that taking apart immigrant, turn over among breeding birds decreased in Brittany over the study period. A complete graphical representation of the age-class structure of the population between 1996 and 2014 can be found in Appendix C.6.1 (Fig. C.7 to C.9, p. 226 to 228). As expected by the time-dependent structure of age classes (age-dependant survival), variations in the number of individuals in each class is correlated in time and depends on productivity.

The posterior distribution of β_i indicated contrasted effects of age class-specific numbers on population growth rate. The β_i corresponding to ages class 1, 8, 10 and 15 were positive with probability $p(\beta_i > 0) = 1$ and those corresponding to the other age classes were negative with probability $(p(\beta_i < 0) = 1)$, except age class 13 where no effect on population growth rate was detected. A negative sign indicates that an increase in the number of females in age class i is associated with a decrease in the population growth rate. Conversely, a positive sign indicates a similar trend between growth rate and number in age class. The effect of age class number on population growth was progressive from age class 10 ($\beta_{10} \approx 0.002$) to age class 9 ($\beta_9 \approx -0.002$) and there was no clear relationship between ageing and trend effect (Fig. C.10A, p. 229). Correlations between Brittany population size and age classes size were all positives but the first six age classes seemed to have the higher contribution in population changes (Fig. C.20, p. 239). Considering 3 population stages (first 6 ages classes, the following six and the third last age classes), Fig. C.10B (p. 229) showed that the proportion of the three last classes (with the highest reproductive senescence) did not varied during the study. However, the decrease in proportion of the first six ages classes correspond to the period of larger decline of the entire population (1996-2006), while increasing proportion of the first six ages classes correspond to the period of lower decline of the entire population (2007-2014).

4.4.3 Influence of demographic rates on population dynamics

The sign and the strength of correlations between breeding population growth rates in Brittany and demographic parameters strongly depended on the parameter considered. Most of the estimated correlations were negative or close to zero (Fig. C.11, p. 230). The correlation between Brittany's population growth rate and immigration rate was the only positive correlation whose credible interval clearly excluded zero (0.51, BCI: 0.24, 0.76). Surprisingly, this provided evidence of the influence of immigration in population growth. Fecundity was negatively correlated (-0.33, BCI: -0.53, -0.1) with population growth. However, juvenile survival probability was not correlated with population growth (0.04, BCI: -0.44, 0.47). The entire population (Brittany population and emigration) growth rate (Fig. C.12, p. 231) was also positively correlated with immigration rate (0.75, BCI: 0.53, 0.86) and was negatively correlated emigration rate (-0.43, BCI: -0.65, -0.18).

Population size in Brittany (Fig. C.13, p. 232) was positively correlated with the number of immigrants (0.64, BCI: 0.33, 0.82), the number of residents (0.36, BCI: 0, 0.63), the fecundity rate (0.24, BCI: -0.05, 0.53) and the return rate of previously emigrant individuals (0.37, BCI: 0.01, 0.62). It was also logically negatively correlated with the number of emigrants (0.3, BCI: -0.58, -0.04) and the emigration rate (-0.31, BCI: -0.6, 0.02). The entire population size (Fig. C.15, p. 234) was strongly (positively) correlated with the number of emigrant (0.94, BCI: 0.82, 0.96), the number of migrants (0.96, BCI: 0.83, 0.98) the emigration rate (0.87, BCI: 0.57, 0.94) and one year old individuals (0.53, BCI: 0.29, 0.69). Negative correlations existed with immigration rate (-0.7, BCI: -0.83, -0.43), the number of immigrants (-0.45, BCI: -0.69, -0.05).

The size of the Brittany population was positively correlated with input rate (natality + immigration; 0.55, BCI: 0.25, 0.74) but not with demographic output (mortality + emigration; -0.03, BCI: -0.36, 0.3; Fig. C.14, p. 233).

4.4.4 Change in wintering population composition

The geometric mean growth rate of the North wintering sub-population was slightly lower than 1 (BCI: 0.98, 1.01), suggesting a very small decrease ($p(\lambda < 1) = 0.62$). However, the decline in the South wintering sub-population (Fig. 3.5) was strong until 2006. This sub-population was nearly stable afterwards. The geometric mean growth rate indicates a 8% decline per year (0.92 BCI: 0.9, 0.93), with a decline of 13% (0.87 BCI: 0.84, 0.89) between 1998 to 2007 and of *c.a.* 0.5% (0.995 BCI: 0.956, 1.03; with $p(\lambda < 1) = 0.60$) after 2007. These results are consistent with the trend observed in chapter II. The North wintering individuals progressively formed the largest proportion of the population, while the overall population was substantially declining, at least since the late 90s. The North wintering sub-population dynamics is more variable in time than the other, but the two sub-populations approach stability with a proportion of *c.a.* 77% of North wintering birds. The main demographic parameters influencing the two sub-populations growth rates was immigration rate, the correlation being positive with $p(\lambda > 0) = 1$. The South wintering sub-population growth rate was also negatively influenced by emigration rate (-0.43, BCI: -0.65, -0.13).

During the study period, the trajectories of the entire population size and of the South wintering sub-population size were very similar (Fig. 4.2A and 3.5). This was confirmed by correlations with the demographic metrics (Fig. C.17 and C.19, p. 236 and 238). Temporal variations in the migrant sub-population were highly positively correlated with entire population size (0.96, BCI: 0.83, 0.98), the number of emigrants (0.93, BCI: 0.8, 0.96) and the emigration rate (0.9, BCI: 0.63, 0.96). Conversely, but not surprisingly, the correlation with immigration rate was negative (-0.66, BCI: -0.82, -0.36) as with the number of immigrants -0.6 (BCI: -0.78, 0.2). There was also evidence of a negative correlation between fecundity and migrant population size -0.22 (BCI: -0.37, -0.06) and a positive correlation with one year old class 0.43 (BCI: 0.14, 0.43). These relationships suggest that the emigration from Brittany's colonies and the migrant phenotype are closely linked. The migrant sub-population growth rate was negatively correlated with emigration rate -0.41 (BCI: -0.66, -0.12). The

resident sub-population growth rate (Fig. C.18, p. 237) was strongly correlated with the immigration rate (0.65, BCI: 0.27, 0.83). There was also evidences for a positive correlation between the size of the sub-population of residents (Fig. C.16, p. 235) and the number of immigrants (0.6, BCI: -0.06, 0.8) and a negative correlation with return rate in Brittany of previously emigrant individuals (-0.45, BCI: -0.68, -0.04).

4.5 Discussion

Our approach of the dynamics of the Brittany's breeding population of Pied Avocet reveals several unexpected patterns, *i.e.* patterns that had been undetected so far and that were not observable. It also allow to assess the fitness corresponding to each the wintering strategy. At the scale of Brittany, the apparent stability in the total number of pairs, despite fluctuations (Fig. 4.2), hides in fact a decline that was already at work at the beginning of the study.

4.5.1 Population dynamics

The integrated approach of the temporal variations in the population size of Pied Avocet from Brittany allowed us to quantify major demographic metrics either helpful for understanding the dynamics of the population, or for conservation purpose. In particular, we identified a global trend in the entire population that differed from the trends estimated at more local scale. Indeed, the breeding population in Brittany was nearly stable (geometric mean growth rate close to one), while accounting for emigration, the entire population actually experienced an annual decline of *c.a.* 3%. A dramatic decrease occurred between 1996 and 2007, followed by a period of slower decrease, until 2014. These contrasting findings were mainly explained by two demographic processes: emigration and immigration. While immigration significantly increased at the end of the study (*c.a.* 40% of the Brittany population in 2014), emigration decreased linearly and dramatically. We thus demonstrated that the population under study was no more self-sustainable and its stability at the Brittany scale is due to immigration. This study highlighted the major interest of taking movements into account, including both immigration and emigration, when assessing population trend.

Accounting for emigration especially allows, by enlarging the geographic scale of the study, a more accurate estimation of the true population dynamics (and vital rates) that when reasoning only on local dynamics (Schaub & Royle, 2014). Ignoring emigration would, in our case, lead to consider that the population growth was stable, while the population was actually declining.

In terms of conservation, there are several implications: (i) Brittany population is dependant on other populations, which raises the question of the origin of the immigrants and the state of their original populations; (ii) the breeding population exports only few individuals, which raises the question of the absorbing effect of the breeding colonies and of the management policies; (iii) finally the question is raised of both the durability of the population and the possible adaptations of the management policies. Answering these inquiries is beyond the scope of this paper but we can give elements of discussion. Our findings showed that juvenile survival is high, and not correlated with population growth rate, which is not an important issue for conservation policies. However, the results assessed a large variability in fecundity rates. In the context of a declining population, this is a key parameter to take into account for management purpose. Indeed, it would be interesting to understand the reasons for the temporal variability of this demographic rate, in the absence of specific data, we did not investigate it. Different factors could affect fecundity. Observations showed that this colonial species was not exempt of intra-specific competition for nest settlement or breeding territory defence and chicks mortality was sometimes attributed to intra-specific competition. However, the effects of predation on eggs and chicks, which could reach locally *c.a.* a 100% rate certain years (authors pers. obs.), seemed from far the main driver of productivity (authors pers. com.). The predators were numerous and might affect productivity opportunistly but possible density-dependent predation are suspected. Indeed, the settlement of a new colony generally led to higher success during the first years than afterwards. As annual recruitment is dependant on both productivity and immigration, the influence of immigration would decrease if productivity increases. The high juvenile survival implied that the critical period was brooding and breeding of chicks until fledgling and should be take into account in conservation and management policies.

Emigration is the other important parameter of population dynamics. With a higher natal dispersal (0.6, BCI: 0.55, 0.65) than breeding dispersal (0.26, BCI: 0.1, 0.5), Pied Avocet is not an exception in birds (Greenwood & Harvey, 1982). We did not explore here the drivers of dispersion, but previous analyses have shown that recruitment is mainly delayed in migrant birds, but also took place in sedentary birds (see chapter III). Pre-breeding individuals indeed either stayed on wintering grounds during the breeding period (*e.g.*, Iberian Peninsula) or outside Brittany. Some of the first breeders likely bred outside Brittany. Adult dispersal was massive at the beginning of the study, then gradually decreased. The negative correlation between emigration and Brittany population size, as well as the strong positive correlation between emigration and the entire population size can be explained by the conjunction of population decline and the overwhelming effect of immigration. Indeed, individuals could reduce competition for nest sites by emigrating (Matthysen, 2005), which could be the case at the beginning of the study. However, some confounding factors could also contribute to explain adult dispersal. As an example, nest predation could have an important effect on dispersion. Our CR dataset had especially shown that after reproduction failure, individuals could change their breeding site within the reproductive season, for a new breeding attempt. We have no idea of the effects of the accumulation of reproductive failures in time, and of social interactions, on dispersal behaviour. Incidentally, if this IPM allowed to estimate immigration rate, we have no specific information on these individuals and the reasons why they were attracted by Brittany colonies. We only have information on the return rates of adults from Brittany that previously emigrated. This annual return rate was quite large (0.31, BCI: 0.14, 0.5), but neither the life-history nor the composition of this sub-population was addressed here. These individuals probably constitute a mixture of previously pre-breeding and breeding birds with different motivations to return (*e.g.*, experience, reproductive failure).

4.5.2 Population persistence

Our results showed that the Brittany population was connected, through emigration and immigration flows, to many other colonies (CR data on breeding periods are displayed in

Fig. 3.1B, chapter III), with a recruitment rate mainly depending on the dynamics of the other colonies at the end of the study. Indeed, Pied Avocets from Brittany belong to the vast network of colonies of the West European population, which forms a large metapopulation functioning (Hanski, 1991). Hixon, Pacala & Sandin (2002) classified such open populations in the type five, *i.e.* a combination of import (immigration), export (emigration) and self-recruitment (internal recruitment), with the level of each process varying through time. In our case, population decline was associated with a decrease in emigration partially compensated either by immigration, or by an increase in philopatry. This was, however, not accompanied by any temporal change in survival or recruitment rate, as none of these parameters was time dependant. Hixon, Pacala & Sandin (2002) argues that if a population does not grow exponentially to infinity or get extinct, this proves the existence of a regulation process. Our population does not necessary satisfied the basic requirements of regulation. In particular, the persistence of the population is questionable, in the sense that this population is relatively young, less than 40 years old, which one can hardly describe as a long-term succession of generations. However, fluctuations in population size appeared to be bounded (Fig. 4.2A) and the negative or positive correlations between Brittany population size and demographic rates could possibly demonstrate some feedback processes.

Demographic regulation processes, such as density-dependence, are expected to generate negative correlations between variations in population size and demographic rates which measure individual success (*e.g.*, survival, recruitment, fecundity). We only found evidence of a negative correlation between the Brittany population and emigration rate from Brittany. Other demographic rates of importance, such as fecundity, death rate, juvenile survival, immigration rate and adult return rate were poorly or positively correlated. In addition, input rate is positively correlated with growth rate which rather suggests an inverse demographic density-dependence phenomenon (Hixon, Pacala & Sandin, 2002). In summary, we were not able to demonstrate any density-dependent regulation in this open population, except when considering the link between density and emigration. It is always challenging to find such effects and their strength in open populations (Tavecchia *et al.*, 2007). Empirical studies demonstrating density-dependence often fall in the trap of considering only the geographic

scale (Hixon, Pacala & Sandin, 2002) and overlook the importance of emigration and immigration in demographic processes (Cam *et al.*, 2004). In addition, migrant population size was not correlated with Brittany population size, which does not support theoretical findings showing that partial migration persistence is unlikely without density-dependence (Lundberg, 2013).

Surprisingly, fecundity was poorly linked to population dynamics showing the strength of emigration and immigration rates. We found only evidence of a negative correlation of fecundity with Brittany population growth and a positive with Brittany population size. The high variability of the fecundity rate, was essentially the result of stochastic or density-dependant predation events, which generated a poor mean fecundity rate, insufficient to ensure the persistence of the population. Years with high fecundity rates were indeed scarce and seemed insufficient to compensate years with low fecundity. Moreover, the investigation of the effect of an age-dependant life history on population size showed contrasted results. We did not identify any "critical age group" (Charlesworth, 1972) but rather a gradient from positive to negative effects of adult age classes on population growth rate. The temporal variations in the six first age classes sizes showed the strongest positive correlation with population size, supporting the important role of the youngest age classes in the temporal variation of the population. However the six first age classes were the classes with the largest size which explain their effect on the population size variations. If first age classes play an important role in short live species regulation (Gamelon *et al.*, 2016), in long live species with age-dependant survival, we do not expect such direct relationships, especially due to delayed effects of high age-structure. However, we noticed that the decreasing in the proportion of the first six age classes was concomitant to the decline of the entire population until 2007. Afterwards, the former proportion increase which correspond to the period of lowest decline of the entire population. These findings highlighted how variations in population size can results in contrasted variations in population structure, some age-classes increased while others decreased or stayed stable. This is consistent with other empirical studies showing that age-classes are not affected in the same manner by environmental factors responsible for temporal changes in population size (Pardo *et al.*, 2017).

4.5.3 Wintering sub-populations

The two wintering sub-populations of Pied Avocets experienced different dynamics, with migrants clearly having a lower fitness than residents. The resident sub-population size, while fluctuating over time, was close to equilibrium during the period ($p(\lambda_N > 1) = 0.4$). By contrast, the dynamics of the migrant sub-population showed two distinct phases of decline. The emigration rate from Brittany showed the same pattern. It is clear that the decrease in the emigration rate was associated with the decline in the migrant sub-population. This suggests that most of the migrants were actually individuals that bred outside Brittany. Conversely, the positive correlation between resident sub-population size and emigration rate from Brittany, and the positive correlation between the resident sub-population size and the number of immigrants from outside Brittany, suggested that the resident sub-population was composed both by breeders in Brittany and outside, and was sustain by immigration. Indeed, recent increased in immigration toward Brittany coincide with migrant sub-population decrease, suggesting that these immigrants were mainly resident and that the phenomenon of relative decrease in migratory phenotype could apply at larger scale.

The reasons for the decline in the partial migrant population is still unknown, but our results highlight the impact of life history traits on the demographic changes. Despite the decline of the entire population size, residency, or, more precisely, wintering in the North, seems to be the best strategy. Conversely, migrating (*i.e.* wintering in the Iberian Peninsula) and breeding outside Brittany seem to be covarying traits, and both associated with the lower fitness. Life-history traits are well known to covary, forming life-history strategies (Stearns, 1976), and we pointed out the importance to account for them in demographic studies. The persistence of partial migration in Pied Avocet nevertheless raises the question of the evolutionary significance of such covariation. The population structure and size at the beginning of the study provided a possible explanation. In 1998, indeed, migrants and residents were present in equal numbers in the population, indicating that unknown environmental factors used to favours also migrant strategy. Changes in environmental factors appeared favourable

to residents, while migrants were disadvantaged during the study period. Along the slow-fast continuum of life-histories, long-lived species are supposed to favour survival probability rather than reproduction probability (Gaillard & Yoccoz, 2003). Pied Avocet, which is rather a long-lived specie, seems in accordance with this hypothesis as the two migratory strategies have identical survival probability and differences occur in reproductive performances. These findings are consistent with an adaptive process to environmental variability and could either illustrated a case of adaptive demographic lability (Koons *et al.*, 2009) or a bet-hedging strategy (Nevoux *et al.*, 2010).

In this context, we can expect, if influencing factors reappear, that the migrant strategy will be favoured again and, as a demographic consequence, that the sub-population will again increase in size. If these factors no more reappear, we expect, as it is actually the case under the demographic rates estimated in this study, that this latter sub-population will persist at a low level (if actual environmental conditions persist).

4.5.4 Limitations of the modelling framework

Here, as in the recently growing literature using integrated population models, we demonstrated the major benefits and the flexibility of these models in demographic studies, and for investigating numerous ecological and evolutionary questions. Several studies (Schaub, von Hirschheydt & Gruebler, 2015, this study) mention the strong adequacy between the population counts and the estimated population sizes and the low standard deviation associated. In absence of a specific protocol for error process estimations, we used a Poisson distribution to account for observation errors in the count estimation. Due to the joint likelihood formulation of the model, bias in this measure induces bias in the other estimated parameters. Schaub, von Hirschheydt & Gruebler, 2015 wrote:

“The accurate estimation of immigration relies on the assumptions that the other demographic rates are estimated correctly and that the observation process in the state-space model is adequately modeled. The estimated population size is biased if the detection probability of breeding pairs has deterministic trends (Kéry & Schaub, 2012), which in turn would result in a biased estimate of the number of immigrants.”

If bias is systematic, estimated population size should not be taken at face value but should rather be interpreted as an index of the real population size. However, stochastic bias or deterministic bias, without appropriate monitoring methods (*e.g.*, robust design) to estimate detection error, lead to unreliable estimated parameters. Moreover, we tested different distributions (Normal and Log-Normal) instead of Poisson and they lead to different estimations of population size (results not shown). Thus in our case at least, the state-space model seemed sensible to the choice of the distribution used for the observation error in the population count component.

IPMs are a powerful and flexible modelling framework for inference about population ecology. Their ability to accurately estimate demographic parameters depends on the quality of the data and on the design of the population monitoring. In the absence of a dedicated method to account for observation errors in one component of the model, results might be biased, depending on the quality and the accuracy of the data collection. These remarks are obviously general, but, considering IPMs, unreliable data in one data set can lead to important bias in the estimation of the other components of the model, due to its integrating design (the joint likelihood imposes dependency among the components). The above observations suggest that count data strongly influence estimation of the other components of the model. As IPMs are still in development, investigations (*i.e.* simulation studies) on how data bias can be transferred from one component to another, *e.g.* and mainly how bias in counts affects estimation of CR parameters, are still needed.



"A colonial bird"
Picture: G.Gélinaud

Chapter 5

General discussion

The effects of global warming and of increasing anthropic damages to habitats on wildlife are now unambiguous; this is particularly true of damages done to wetlands. There is growing evidence of changes in species distribution and dynamics, particularly in migrant birds (Hickling *et al.*, 2006; La Sorte & Thompson, 2007; Maclean *et al.*, 2008; Chen *et al.*, 2011). Mobile species have been the first species to suffer the consequences of environmental changes, and in a more intensive manner than others. Among them, shorebirds are particularly interesting models; they are already used as indicators of wetland health (Piersma & Lindstrom, 2004, see also <https://www.wetlands.org/>). Indeed, these species provide opportunities to understand ecological, behavioural and evolutionary processes that underlie their ability to adapt (or not) to changes in the most threatened habitats (*e.g.* estuaries, coastal lagoons, inner wetlands). Nowadays this is a major challenge in many areas of research, but also for conservation purpose (Sutherland *et al.*, 2012). The most remarkable features of the recent changes observed in birds are the distribution changes, the shift towards the pole of population ranges, the shift in the timing of migration, the shortening of migration distance and even the switch toward residency (Maclean *et al.*, 2008; Visser *et al.*, 2009; Pulido & Berthold, 2010; Chen *et al.*, 2011; Miles *et al.*, 2017). Redistribution of individuals in the population range, can be attributed to demographic and behavioural responses to environmental changes, which leads to colonization and extinction phenomena. Recent northward shifts in the wintering distribution of many bird species are supposed to result from a combination of newly favourable environmental conditions in the North due to global warming, and to changes in migratory behaviour (Lehikoinen *et al.*, 2016), but others factors (human disturbance) also mediate these shifts (Lehikoinen & Virkkala, 2016). In the North part of the range, breeding individuals decide to become resident, whereas none of them used to remain in the North during winter in the past, *i.e.* either individuals that used to migrate in winter decide to switch wintering strategy and become resident or newly recruited individuals are resident. The extreme South part of the range is abandoned because migrants no longer use this area; either they switch migration strategy toward residency or they migrate less South. Individuals have to choose between different strategies, and we expected to observe differences in vital rates according to their phenotypes. In any case, there are changes in the

frequency distribution of migratory strategies, with local demographic consequences.

Recent changes in the distribution of Pied Avocets in Europe

In this work we first investigated temporal variations in the distribution of Pied Avocets at the European scale. We did not find evidence of a range shift northward, but we found that density has been increasing in the North range in the past two decades, and decreased in the South (Iberian Peninsula), which support others recent empirical studies (Lehikoinen & Virkkala, 2016). This phenomenon is particularly clear in England, where there is a constant increase in the wintering population size, whilst Portugal experienced a pronounced decline. This redistribution is consistent with general patterns described in many other species in the same area and may ultimately lead to the colonisation of new areas Northward (*e.g.*, North East of Netherlands, Germany). The reasons for the decline in the wintering population in the Iberian Peninsula and the substantial temporal variations in local density are unclear; we were unable to address these questions in this study because we lack appropriate data. However, we suspect that stochastic events in winter such as variable rainfall can be responsible for this instability in Spain. Indeed, the wintering habitats of Pied Avocet in Andalusia are mainly man-made wetlands (*e.g.*, saltponds, fishfarms) and food availability depends on water level. Flood events can lead to important distribution change at the Iberian scale, as shown in inland lakes (Goncalves *et al.*, 2016), but we suspect that this also occurs in the North of Africa. It would be interesting to use all the CR data from all the CR programs on Pied Avocets in Europe and assess the effect of climatic variables on winter site fidelity both at the intra- and inter-wintering season scales.

Demographic processes underlying observed changes in the distribution of Pied Avocets

Using data from Pied Avocets marked in Brittany, we estimated the number of individual wintering in the North or the South. We also addressed whether a key demographic

parameter differed according to the strategy: survival probability (as a long-lived species, the Pied Avocet is considered as a “survivor species”, Saether & Bakke, 2000). At the individual scale, the multistate CR modelling framework also allowed us to ask the question of whether individuals change wintering strategy during their life. Indeed, if the proportions of the two segments of the population (migrants and residents) vary over time, this can be because mortality is higher in one of the segments than in the other, because individuals change strategy over life, or because the proportion of individuals adopting a strategy at the beginning of their life increases (under the assumption that they subsequently adopt this strategy). Of course, both mortality and fidelity to the strategy can be involved simultaneously. Our results confirmed the above ones: residents have become more abundant than migrants in Brittany. The number of residents has been increasing rapidly since the early 2000’s, while size of the migrant population remained stable. The initial intuition, which inspired this work was confirmed: not only the frequency of the migrant component of the population was declining but we also observed a reversal in strategy frequencies.

Fidelity to wintering strategy

The change in the proportion of migrants and residents in the individuals marked in Brittany was not due to a switch in wintering strategy from migrant to resident, but to an increase in the number of residents among recruited individuals. Indeed, fidelity to the migration strategy was high. We showed that the majority of the individuals chose their strategy during their first winter and retained this strategy for life. However, it is interesting to note that the probability of switching from migrant to resident is higher than the probability of moving from residency to migration ($< 7\%$ versus $< 1\%$, respectively). This higher probability of switching from migration to residency is consistent with results of experimental the Pied Avocet for life, but the existence of few individuals switching strategy pleads more for a conditional strategy (Lundberg, 1988).

Moreover, we did not find evidence of an effect of climatic variables on the probability that juveniles spend their first winter in the South (NAO, winter harshness index), which is

inconsistent with the hypothesis that the choice of a migration strategy is affected by local climatic variables that are related to global climate warming.

Survival probability

Interestingly, our results did not support the hypothesis of a difference in survival probability between the two strategies. Consequently, the difference between the demographic dynamics of the alternative strategies can't be explained by differences in survival rate. In all our investigations on the drivers of survival probability, at different scales (annual or seasonal, between winters or between breeding seasons), we found the same evidences that survival probability in this population depends mainly on age and individual "frailty".

Nevertheless, it would be unwise to ignore the possibility that winter cold spells affect survival. First, it has been shown that harsh winters (particularly long cold spells) are associated with changes in the abundance and distribution of the species in north-west Europe (Mahéo, Le Dréan Quénéec'hdu, S & Triplet, 2007). We are not aware of particular past cold spells that could have led to high mortality rate in the Pied Avocet (either on the French Atlantic coast or elsewhere in Europe). However, several studies have documented such effects in other shorebirds species in north-west Europe, with high mortality and a dramatic decline in local population, which deeply affected population structure (Johnson, Green & Hirons, 1991; Goss-Custard, 1996). Third, most harsh winters occurred before the beginning of the study period and the frequency of these events has been decreasing during this period (IPCC, 2014). Hötker (1998a) has shown that such events can affect the fidelity of Pied Avocets wintering in north-west Europe. We believe that the hypothesis that fitness depends on winter harshness should be considered seriously, even if no major cold spell occurred during the study period. In addition, the proportion of migrants and residents in the population can also vary over time because of differences in reproductive performance between strategies: we addressed this question in the following step (Chapter III).

Evolutionary demography of migration strategies: a life history perspective

If there are costs associated with migration (either because of the journey or because of the environmental conditions on the wintering ground), migration offers advantages in terms of fitness only if this strategy outweighs residency costs, *e.g.*, lower demographic rates (survival, reproduction) due to harsh winters in the location that residents use for breeding and wintering. Conversely, residency is assumed to be advantageous in terms of reproductive success in years characterized by mild winters, *e.g.* individuals can adapt their breeding phenology to local climate and settle before migrants, they access to high-quality breeding sites thanks to a reduced competition level (Kokko, 1999; Hötker, 2002). In long-lived species, even though migration or residency costs could be expressed every year (at all ages), costs incurred at the beginning of life could also have long-term consequences during life. Such costs could also fade as individuals gain experience. This is why we chose a longitudinal approach and considered the hypothesis that the consequences of strategies could differ according to age, and we put a particular emphasis on age at recruitment and its relationship with subsequent breeding occasions in the life of the individual.

In chapter III, we addressed the question of the relationship between reproductive performances, recruitment age and migration strategy. In “survivor species” variation in survival is assumed to be disadvantageous (Saether & Bakke, 2000; Gaillard & Yoccoz, 2003). In such species, the elasticity of the population growth rate to changes in survival is larger than the elasticity to changes in fecundity (Caswell, 1989). In this framework, natural selection might be able to weed life history features associated with large costs on survival probability (*e.g.*, a migration strategy). In this study, we did not find evidence of a relationship between survival rate and migration strategy (see above). It was reasonable to consider the hypothesis of variation in reproductive performances among migration strategies. Our aims were to test for (i) a cost of migration on recruitment age and on the cumulative reproductive investment (hereafter CRI), (ii) the effect of recruitment age on the CRI and seasonal survival, (iii) the effect of both migration strategies and recruitment age on late life CRI and (iv) the covariation between survival and reproduction. We lacked data to work on the probability of breeding successfully; direct observations of individual reproductive success during sampling

sessions is extremely rare. Even though we used an analytical approach taken uncertainty in breeding state assignment (*i.e.* multi-event models), the data we were able to collect led to a too small number of cases of ascertained successful reproduction. However, available data allowed us to estimate the probability of breeding, using a large number of observed criteria. Sample sizes were sufficient to address the relationship between migration strategy and estimated breeding probability. We estimated the transition probability from a specific winter state to a specific breeding state (breeding, or not), and the cumulative breeding investment: *i.e.* the age-specific cumulative number of breeding attempts.

Migration strategy, age at recruitment and pattern of age-related variation in CRI

We clearly identified a cost of migration, characterised by a delayed age at recruitment in migrants. Migrants mainly recruited after one year ($\approx 90\%$), while residents mainly recruited at the age of one year ($\approx 60\%$). Very few studies have focused on the fitness of the two migration strategies in populations of partial migrants. At least two studies have shown differences in reproductive performances in partial migrants, but they have not investigated age at recruitment (Adriaensen & Dhondt, 1990; Grist *et al.*, 2017).

We detected senescence in both strategies (Fig. 3.5A). Senescence translates into a reduced pace of growth of CRI as individuals get older. Surprisingly, we did not find evidence of a difference in the onset of senescence between the alternative migratory strategies (Fig. 3.5A).

Individual recruiting at the age of one year have the highest CRI regardless of age, and they do not show any senescence in CRI (Fig. 3.5B). These results are not consistent with theories of ageing that predict an early onset of senescence in individuals recruiting earlier. We detected senescence in the two other categories of individuals: those that recruited age two and three years. The onset of senescence occurred at the same age in individuals recruiting at the age of two and three. In addition, there was an unambiguous effect of recruitment age on the pace of growth of CRI. Individuals recruiting at the age of one

year exhibited the largest slope of age-specific CRI curve, with no inflexion point (i.e., no senescent decline in CRI). The CRI curve was similar to a straight line slowly diverging from the bisecting line (Fig. 3.5B). For those recruited at age of two or three years, the smaller the age at recruitment, the smaller the pace of increase in CRI with age. These CRI curves intersected around the age of seven years.

Unfortunately our CR data were insufficient to assess the effect of recruitment age and migration strategy on CRI in a simultaneous manner. A larger dataset combining information from different ringing sites could be useful to investigate this issue. However, these programs began in 2005 and it is very likely that longer time series will be necessary to address senescence. Interestingly, when we compared the slopes of the age-specific CRI curves before the onset of senescence (Fig. 3.5A), we found that the slope associated with residents was smaller than the slope associated with migrants, which led to a similar cumulative reproductive performances around the age of six years (*i.e.* the BCIs intersect, see Fig. 3.5A). With the data at hand, it is impossible to determine if recruitment age alone or migration strategy alone affects the slope of CRI, or if both factors affect this slope. However, it is possible that delayed recruitment age leads to a faster increase in CRI because of benefits associated with experience, behavioural or physiological maturity (*e.g.*, better body condition, competitiveness, more efficient somatic repair systems). If we can not exclude the possibility that residency carries costs on CRI, we suspect a positive effect of delayed recruitment on the pace of growth of CRI in migrants. In this study, we did not address intra season reproductive investment, but there might be differences between wintering phenotypes in terms of number of breeding attempts within the same season in relation with arrival date on the breeding ground.

Reproductive senescence

Our results did not provide evidence of a relationship between recruitment age and seasonal survival, neither in spring nor in fall. It is interesting to note that spring seasonal survival declines with age. There is also some indication of a decline in fall survival, but this

is more ambiguous because of large credible intervals. At the annual scale (Chapter II), we had also found evidence of senescence in survival probability.

Detection of senescence in observational studies can be hampered by differences in mortality risk among individuals in populations (Zens & Peart, 2003). Here we found evidence of positive correlations between the individual seasonal survival and in breeding probabilities: individuals that outperformed the others in terms of survival rate also outperform them in terms of reproductive investment. Observational studies commonly provide evidence of such positive correlations (Cam *et al.*, 2002; Beauplet *et al.*, 2006; Weladji *et al.*, 2008; Hamel *et al.*, 2009; Cam *et al.*, 2013), which is usually interpreted as a consequence of heterogeneity in mortality risk or fecundity in populations and the failure to control for environmental confounding factors in non-experimental studies (Stearns, 1992). Our results support the heterogeneity hypothesis (van Noordwijk & de Jong, 1986), but we were able to detect senescence in survival thanks to models incorporating individual random effects on both survival and breeding probabilities.

Our results did not allow us to understand mechanisms relevant to natural selection that could be responsible for differences in CRI according to recruitment age and migratory strategies. However, the results provided evidence that migration strategies and recruitment age have long-term consequences on reproduction. This could explain the divergent dynamics of the residents and migrants described in chapter II.

To summarize, residents recruit earlier than migrants but the pace of growth of CRI is larger than that of residents. In this framework it is difficult to know if the two strategies actually differ in terms of fitness. In the following step we estimated overall fitness.

The big picture: dynamics and overall fitness of migration strategies

In chapter IV we addressed the question of strategy-dependent fitness directly, (in chapter II and III, we investigated only some fitness components: survival and reproduction). We considered the overall population of birds born in Brittany in an integrated modelling framework (IPM) that also included another breeding site located outside Brittany (any breeding

colony outside Brittany). Birds marked in Brittany when young could be philopatric and return to breed there, or not. Thanks to this approach, movement of breeders among sites is possible (this corresponds to breeding dispersal), and birds born in one site can also disperse to breed in the other one (natal dispersal). The migratory strategy of individuals in winter was also taken into account. We estimated the mean geometric growth rate of the Brittany population and of sub-populations defined on the basis of migratory strategy. We used data from population monitoring at the scale of Brittany (annual number of pairs and annual fecundity), and at the species range (CR data), to estimate this quantity.

The geometric growth rate estimate of breeding pairs in Brittany was very close to one, indicating that the population size was stable. However, when we included the estimated number of emigrants from Brittany, *i.e.* breeders dispersing outside Brittany, the estimated growth rate is clearly lower than one, which indicates a decline in the Brittany population. This decline was strong between 1996 and 2006, followed by a slower phase of decline until 2014 (Fig. 4.2A). This decline was mainly due to the decrease in the number of individuals in the migratory sub-population (Fig. 4.2D). Indeed, the pattern of decline in this sub-population over time was similar to that of the Brittany population, whilst the growth rate of the resident sub-population remained close to one (*i.e.*, this sub-population remained stable). The number of emigrants from Brittany exhibited a similar pattern than the Brittany population: they experienced the same decline. However, this decrease in emigration rate from Brittany was not sufficient to stop the decline of the Brittany population. Immigration from outside Brittany (breeding dispersal of individuals born outside Brittany) was the main factor explaining the apparent stability of the number of breeding pairs in Brittany, while increasing philopatry in Brittany contributed to a lesser extent to this stability. In this metapopulation system (Hanski, 1991), the dynamics of Brittany population is characterised by an unbalanced ratio between “importation” (recruitment of individuals born outside Brittany), “exportation” (dispersal of individuals born in Brittany) and “self-recruitment” (philopatric individuals born in Brittany), where exportations exceeded the sum of importation and self-recruitment.

The demographic mechanisms that could explain temporal variation in population size

are fourfold: emigration and immigration, birth and death. Despite the temporal fluctuations of the number of deaths, all our analyses provided consistent evidence that survival is time-independent. The birth rate was highly variable over time; we suspect that predation is the main factor affecting this vital rate. In this context, emigration and immigration are the key demographic parameters whose variations are responsible for the temporal fluctuations of the population size. This highlights the necessity to include emigration when assessing population growth rates and temporal variations in size; local studies can lead to biased estimates of both of them (Schaub, von Hirschheydt & Gruebler, 2015). The difference between local and “true” demographic rates lays in the geographical scale of the study. Here, CR data have been collected in the whole range of the species, scale for which we considered the Palaearctic West population as closed. We are confident that our estimates are close to “true” rates. Nevertheless, we must acknowledge that the estimate of the number of pairs was sensitive to the choice of the prior distribution for the detection process. We must take these estimates with caution: they should rather be considered as indices than real population size estimates. We are not aware of an approach that would allow us to quantify the bias in the estimated detection probability, in the context of this study. Indeed Kéry & Schaub (2012) showed that in case of systematic bias (false-positive or negative), the modelling approach we used for count data is no longer suitable.

We also investigated the relationships between the size or growth rate of different sub-populations and demographic rates. Namely, (i) the entire population of Brittany (regardless of breeding site and migratory strategy), (ii) the breeding pairs in Brittany, (iii) the segment of the population wintering South (the migrants), (iv) and the segment of the population wintering North (the residents). We used correlations to assess these relationships; the sign and estimated value of the correlation indicate the direction and the strength of the relationships. Terminology was kept from the modelling framework. Hereafter, we call “emigration” (*i.e.*, “emigration rate”, “emigrants”) as the movement of individuals ringed in Brittany and that left this area to breed outside. The term “immigration” (“immigration rate”, “immigrant”) will be restricted to movement of unmarked individuals, born outside Brittany that joined the breeding population in Brittany.

Our results confirmed the contribution of emigration and immigration to the dynamics of this Pied Avocet population. Immigration toward the breeding population in Brittany varied over time in the same way as the growth rate of all sub-population, while emigration from Brittany varied in an opposite way. The “input rate” (rate of natality + rate of immigration from outside Brittany) was positively correlated with the breeding population in Brittany, which indicated an inverse density-dependence type of regulation at the scale of Brittany. This suggests that the population decline is not linked to an issue of carrying capacity in Brittany. Interestingly, emigration, *i.e.* breeding dispersal from Brittany, varied over time in the same way as the number of migrants. This suggests a “strong” relationships between two life-history traits in the Pied Avocet of Brittany: dispersal from Brittany and migration phenotype. In addition, the resident sub-population was positively correlated with the immigration rate from outside Brittany, which suggested that these immigrants (birds that were born outside Brittany) are mainly a residents in winter. These findings suggests that the increase of the resident segment of the population is a phenomenon involve phenomena taking place at a larger scale (as highlighted in chapter II), shared with colonies outside Brittany. At such a large spatial scale, environmental effects affecting the North of Europe), such as cold spells, could drive the frequency distribution of wintering phenotypes (see chapter II).

The fitness of the migrant sub-population was clearly lower (0.92) than that of residents (≈ 1). This is consistent with the lower reproductive performance of the latter (see chapter III) and the strong decline in the migrant phenotype among recruited individuals. Table 5.1 synthesizes the possible effects of winter severity on the wintering sub-populations and how such extreme climatic events could explain variations in phenotypes frequency as in the Brittany population size. We hypothesize that extreme weather conditions in winter do not affect survival, recruitment age, CRI or fitness of migrants, only migratory behaviour and the frequency of the migrant phenotype are affected. Residents suffer from lower survival, lower CRI, delayed recruitment and lower fitness during harsh winter, but also higher switch to migration phenotype (Hötker, 1998a), which lead to a decrease in frequency of this phenotype in the population.

Phenotype	Mild winter	Harsh winter
Resident	survival ↗	survival ↘
	recruitment age ↘	recruitment age ↗
	CRI ↗	CRI ↘
	fitness ↗	fitness ↘
	switch to migration ↘	switch to migration ↗
	phenotype frequency ↗	phenotype frequency ↘
Migrant	survival =	survival =
	recruitment age =	recruitment age =
	CRI =	CRI =
	fitness =	fitness =
	switch to residency ↗	switch to residency ↘
	phenotype frequency ↘	phenotype frequency ↗

Table 5.1: **Effect of winter severity on demographic parameters.** In this scenario only residents are affected by winter conditions but frequency of migrant is indirectly subject to variations.

Conservation implications

Another key result of this paper was the variability of fecundity and its low value, which was not sufficient to sustain population. Our fieldwork experience clearly suggests the massive effect of predation on breeding success. Predation varied over time but was generally high (> 60% of the active nests failed at an early states, eggs to young chicks, authors pers. obs.). Complete breeding failure occurred in some years in some colonies. There was evidence of a negative correlation between the Brittany breeding population growth rate and fecundity but no clear correlation with the entire population growth rate or size. This suggests a small contribution of fecundity in the temporal variations of the population size. This situation calls conservation policies into question at local scale if the objective is to maintain this population. Indeed, self-recruitment was not able to sustain the population, stability was mostly attributable to immigration. Immigration does not depend exclusively on local management policies: the dynamics of others colonies outside Brittany is also involved. Most breeding colonies in Brittany are settled in protected areas. Predation is likely

to be the main cause of reproductive failure in these areas. The question of anti-predatory policies must be tackled in the context of the population trend at larger scale. If the Brittany population is the only one to decline on the Atlantic coast there is no special need to control predation, but if all other colonies are also declining specific measures should be envisaged. This implies the estimation of breeding population trend at least at the scale of the French Atlantic coast. Predation seems to be a general issue in the breeding colonies of the French Atlantic coast (authors pers. com.) and also in Europe (Thorup & Bregnballe, 2015) and probably an important driver of the metapopulation dynamics. Another issue is immigration and the factors affecting movement probability among declining populations. While we don't know the factors driving immigration, we suspect that the rare years with high productivity are attracting immigrants in the following year (Danchin, Boulinier & Massot, 1998). Minor changes in the IPM code we used would allow us to test the relationships between immigration rate and productivity in the previous year. Of course, adding complexity would probably lead to a loss in accuracy in the parameter estimates (Schaub & Fletcher, 2015). IPMs can nevertheless be used for estimating future population trend or as a conservation tool by simulation; this could be used to estimate the minimum fecundity rate that would allow this population to be stable without immigration.

Importantly, this study highlights the necessity of demographic approaches to understand the complexity of the mechanisms underlying the changes in population size and the evolution of life-history traits. We also plead for long-term monitoring programs. Fundamental mechanisms in population dynamics such as senescence in vital rate can not be assessed accurately with short studies; which can lead to improper projections of population changes and can lead to inappropriate conservation policies (Robert *et al.*, 2015).

Future works

This dissertation describes the demographic dynamics of the Pied Avocets population in Brittany with the objective to better understand its temporal variations in relation to migration strategies. It is a pioneer study in France, and this species is little studied in

Europe, except previous work from H. Hötker. This dissertation lays the foundations for a deeper development in the knowledge of this specie. Among the different topics studied here, we highlighted several questions which could not be answered. For example, the factors that determine juvenile dispersal in winter remained unknown. This question has been recently addressed in of another paper (Chambon *et al.*, 2017), that focussed on first winter dispersal in colour-marked Pied Avocets in several colonies along the French Atlantic coast. This work did not make use of individual CR data collected between fledging and arrival at wintering sites. In particular, social interactions still have to be studied. Future analyses should take post-breeding gatherings into account, when individuals from many colonies gather in a few estuaries late in summer and in fall. Social interactions could influence individual behaviour, and group of individuals could migrate in the same direction. Moreover previous investigations of the migration have shown that individual of a same brood tend to have the same wintering phenotype (unpublished results). This will require additional work to test hypothesis about the genetic or environmental determinants of migratory behaviour. Moreover, one of our main hypotheses about factors affecting juvenile dispersal, the effect of harsh winters, can-not be tested unless new extreme climatic events occur. Individual data from a German monitoring program that started in the early 90s exists and could help to better understand factor affecting migration patterns, there is a strong limitation: all these bird were migrants (they did not winter in Germany).

Another important project would be to extend analyses to other colonies on the French Atlantic coast. At least four Southern colonies have been monitored since 2005, in the same way as the Brittany colonies. It would be possible to address whether the size of all these colonies varies in a synchronised manner, whether some demographic rates (*e.g.*, population growth, fecundity, emigration) vary synchronously. Synchrony is common in many taxa (reviewed in Liebhold, Koenig & Bjornstad, 2004). Three main mechanisms lead to “population synchrony”. (i) Spatial autocorrelation of environmental covariates, the so-called the Moran effect. In this case, similar environmental conditions lead to synchronous population size variations (Saether *et al.*, 2007). (ii) Asymmetrical dispersal of individuals among populations generate homogenisation in population density, which can lead to synchronisation (Paradis

et al., 1999). (iii) Populations variations in size can be synchronised with the variations of the trophic resources (Jones, Doran & Holmes, 2003). IPMs such the one described in chapter IV, are particularly well suited tools to assess synchrony in populations (Schaub, von Hirschheydt & Gruebler, 2015). We could estimate the intra-class correlation (Grosbois *et al.*, 2009), which allows decomposing temporal variations of demographic rates into local and global variation. Last, to disentangle the factors affecting movement (emigration and immigration), it is necessary to estimate transition rates between several colonies. This could be achieved using multi-event models for open population (see chapter III) in a multi-site context. Tacking breeding state onto account and age would allow the estimation of intra- and inter-season transition probabilities between breeding sites.



”Avocets of Europe”

Appendix A

Supporting information to chapter II

A.1 Wintering population trend estimates of the Pied Avocet of the East Atlantic flyway for European countries.

A.1.1 European count modelling framework

In time series of counts, temporal autocorrelations, when present, must be taken into account in the modelling framework. Fig. A.1 shows clear autocorrelation for Belgium, Great Britain and Netherlands at least at lag one. In case of spatio-temporal replicates, a second source of autocorrelation should be considered: spatial autocorrelation. Indeed, in the context of bird census at wintering sites, factors such as particular weather conditions can generate important population shifts leading to decreasing numbers in some sites or regions and increasing numbers in other, more favourable, sites or regions. Likewise, effects at longer time scale can result in positive or negative correlations in numbers between sites. The cross-correlation function (CCF) Fig. A.2 indeed shows such significant correlations between sites.

Moreover, observation errors associated with large scale monitoring must be also accounted for. In the present study, we have few details on the error process (over or underestimation during counts, missing counts) for each country and each year.

In order to account for all these aspects in one modelling framework we adopted a Bayesian approach using a state-space model for population counts inspired by Kéry &

Schaub (2012). To model population size, we used a simple population model, with an exponential growth and a random year \times site effect:

$$N_{i,t+1} = N_{i,t}\lambda_{i,t} + \varepsilon_{i,t}, \quad (\text{A.1})$$

$$\lambda_{i,t+1} \sim \text{Normal}(\bar{\lambda}_i, \sigma_{\lambda_i}^2), \quad (\text{A.2})$$

where the growth rates λ of population i are normally distributed with a mean $\bar{\lambda}$ and a variance σ_{λ}^2 . This autoregressive formulation accounts for temporal autocorrelation.

Because of the possible errors in counts, we modelled observation as a normal process:

$$y_{i,t} \sim \text{Normal}(N_{i,t}, \sigma_{y_i}^2), \quad (\text{A.3})$$

where the observed count y in site i and in year t is a realization of the true, but unknown, population size N in the same site and year, and the difference due to uncertainty varies annually around population size. The magnitude of annual observation error in site i of the reported count is then normally distributed with mean zero and variance $\sigma_{y_i}^2$.

Spatial autocorrelation, correlation between the 6 countries, is accounted through the parameter $\varepsilon_{i,t}$, a random site i and year t effect with a multivariate normal distribution: $\varepsilon_{i,t} \sim \text{Normal}(0_i, \Omega)$. The variance-covariance matrix Ω takes the following form:

$$\Omega = \begin{bmatrix} \sigma_{1,1}^2 & \text{cov}_{1,2} & \cdots & \text{cov}_{1,6} \\ \text{cov}_{2,1} & \sigma_{2,2}^2 & \cdots & \text{cov}_{2,6} \\ \vdots & \vdots & \ddots & \vdots \\ \text{cov}_{6,1} & \text{cov}_{6,2} & \cdots & \sigma_{6,6}^2 \end{bmatrix}$$

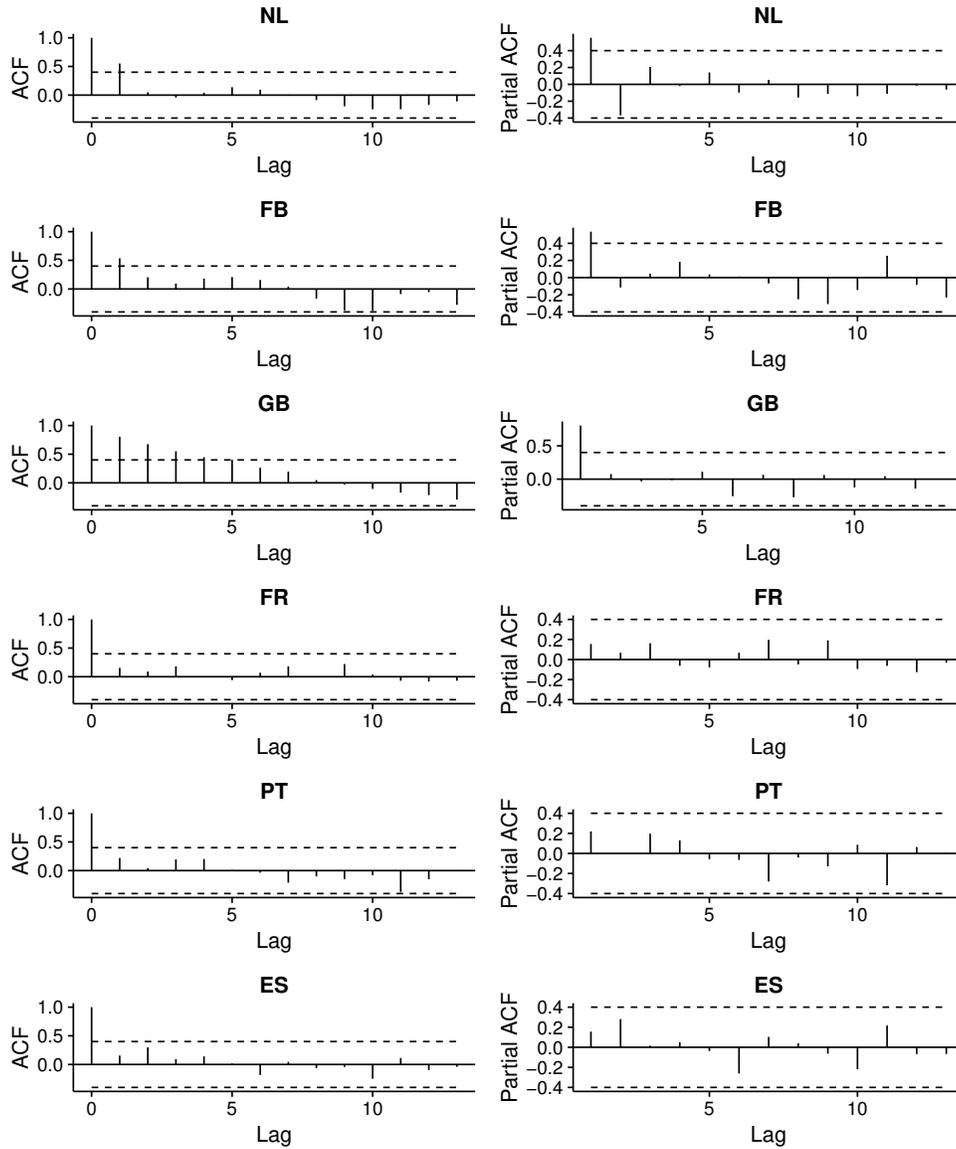


Figure A.1: **Autocorrelation function (ACF) in winter counts of Pied Avocets for the West European countries between 1990 and 2015.** The left column shows the ACF for the each contry count and the right one the partial ACF for the same counts. Vertical lines indicate correlation value at each time lag and horizontal dashed lines, the 95% credible interval. Values out of the 95% credible interval indicate significant autocorrelation. ES = Spain; FB = Belgium; FR = France; GB = England; NL = Netherlands; PT = Portugal.

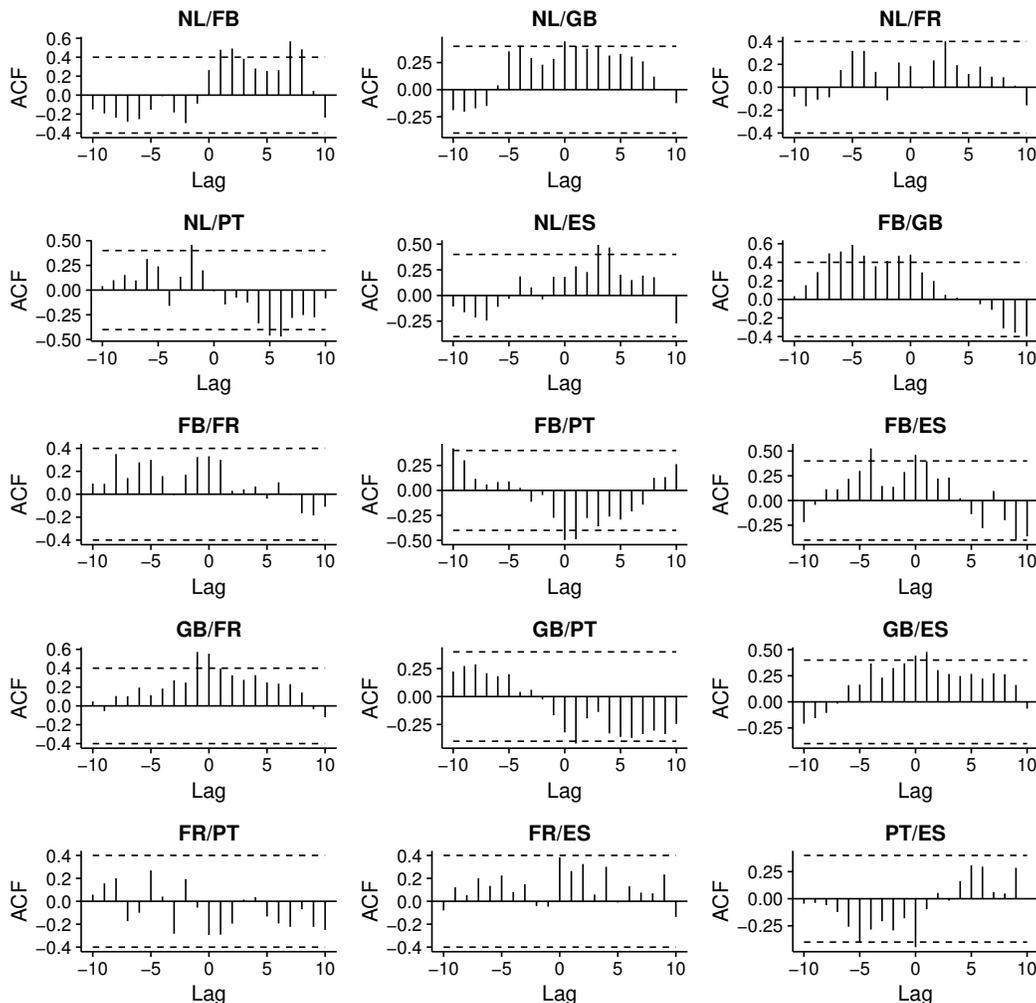


Figure A.2: **Cross-correlation function (CCF) between winter counts of Pied Avocets for the West European countries between 1990 and 2015.** Vertical lines indicate correlation value at each time lag and horizontal dashed lines, the 95% credible interval. Values out of the 95% credible interval indicate significant autocorrelation. ES = Spain; FB = Belgium; FR = France; GB = England; NL = Netherlands; PT = Portugal.

In order to increase computer efficiency we used the Cholesky decomposition proposed by Chen & Dunson (2003). They suggested using a factorization of the variance-covariance matrix Ω into a diagonal matrix D and lower triangular matrix L with a diagonal of 1: $\Omega = DL(LD)' = DLL'D$. Here we used a parameter expanded formulation proposed by Authier (2016, unpublished): $\Omega = AL\Delta L'A$, where $A = \text{diag}(\alpha_1, \dots, \alpha_i)$ and $\Delta = \text{diag}(\delta_1, \dots, \delta_i)$ are two diagonal matrices. To induce marginal half-t priors $T^+(0, \alpha^2, \nu)$ on the standard

deviations of the random effects (σ_i^2) we used the following priors: $\alpha \sim N^+(0, 1.5)$, $\delta \sim \Gamma^{-1}(1.5, 1.5)$ and $l \sim N(0, 4)$ the lower diagonal element of L . Correlations between sites were computed from the elements of Ω :

$$\rho_{i,j} = \frac{cov_{i,j}}{\sqrt{\sigma_i^2 \sigma_j^2}} \quad (\text{A.4})$$

where $i \in \{2, \dots, 6\}$, $j \in \{1, \dots, 5\}$ and $i > j$.

We estimated the parameters with a Bayesian approach using Gibbs sampling, *i.e.* a Markov Chain Monte Carlo (MCMC) algorithm. The observed counts were log transformed before performing the model fitting, in order to reduce the important scale difference between country counts.

A.1.2 JAGS code

```

model {
# Priors and constraints
for (i in 1:ns){
  # Initial population size
  N.est[i,1] ~ dunif(0, 20)
  # Mean growth rate
  mean.lambda[i] ~ dunif(0, 10)
  # sd of state process
  sigma.proc[i] ~ dunif(0, 10)
  sigma2.proc[i] <- pow(sigma.proc[i], 2)
  tau.proc[i] <- pow(sigma.proc[i], -2)
  # sd of observation process
  sigma.obs[i] ~ dunif(0, 100)
  sigma2.obs[i] <- pow(sigma.obs[i], 2)
  tau.obs[i] <- pow(sigma.obs[i], -2)
}

```

```
# Likelihood
# State process (population variations)
for (i in 1:ns){
  for (t in 1:(ny-1)){
    lambda[i,t] ~ dnorm(mean.lambda[i], tau.proc[i]) # eq.3
    N.est[i,t+1] <- N.est[i,t] * lambda[i,t] + eps[i,t] # eq.2
  }
}
# Observation process
for (i in 1:ns){
  for (t in 1:ny) {
    y[i,t] ~ dnorm(N.est[i,t], tau.obs[i]) # eq.1
  }
}

for (t in 1:ny) {
  N.estn[t] <- sum(ExpN.est[1:4,t]) # sum of count in the North
  N.ests[t] <- sum(ExpN.est[5:6,t]) # sum of count in the South
}

for (i in 1:ns){
  for (t in 1:ny) {
    ExpN.est[i,t] <- exp(N.est[i,t])
  }
}

for (i in 1:ns){
  for (t in 1:ny) {
    # European country proportion
```

```
    prop[i,t] <- ExpN.est[i,t]/sum(ExpN.est[,t])
  }
}

# Choleski decomposition (with priors) for the year random effects
for (i in 1:ns) {
  A[i, i] ~ dnorm(0.0, 1.5)T(0.0,)
  Delta[i, i] <- 1/tau[i]
  tau[i] ~ dgamma(1.5, 1.5)
  L[i, i] <- 1.0
}

for (i in 1:(ns-1)) {
  for (k in (i+1):ns) {
    L[i, k] <- 0.0
    A[i, k] <- 0.0
    Delta[i, k] <- 0.0
    L[k, i] ~ dnorm(0.0, 4.0)
    A[k, i] <- 0.0
    Delta[k, i] <- 0.0
  }
}

# covariance matrix
Omega <- A%%L%%Delta%%t(L)%%A

# random effects: multivariate normal
for(t in 1:(ny-1)){
  eps[1,t] <- A[1, 1]*(L[1, 1]*xi[t, 1])
}
```

```

eps[2,t] <- A[2, 2]*(L[2, 1]*xi[t, 1] + L[2, 2]*xi[t, 2])
eps[3,t] <- A[3, 3]*(L[3, 1]*xi[t, 1] + L[3, 2]*xi[t, 2] +
L[3, 3]*xi[t, 3])
eps[4,t] <- A[4, 4]*(L[4, 1]*xi[t, 1] + L[4, 2]*xi[t, 2] +
L[4, 3]*xi[t, 3] + L[4, 4]*xi[t, 4])
eps[5,t] <- A[5, 5]*(L[5, 1]*xi[t, 1] + L[5, 2]*xi[t, 2] +
L[5, 3]*xi[t, 3] + L[5, 4]*xi[t, 4] + L[5, 5]*xi[t, 5])
eps[6,t] <- A[6, 6]*(L[6, 1]*xi[t, 1] + L[6, 2]*xi[t, 2] +
L[6, 3]*xi[t, 3] + L[6, 4]*xi[t, 4] + L[6, 5]*xi[t, 5] + L[6, 6]*xi[t, 6])
for(i in 1:6){
  xi[t, i] ~ dnorm(0.0, tau[i]);
}
}

```

Covariances

```

covar[1] <- Omega[2,1]
covar[2] <- Omega[3,1]
covar[3] <- Omega[4,1]
covar[4] <- Omega[5,1]
covar[5] <- Omega[6,1]
covar[6] <- Omega[3,2]
covar[7] <- Omega[4,2]
covar[8] <- Omega[4,3]
covar[9] <- Omega[5,2]
covar[10] <- Omega[5,3]
covar[11] <- Omega[5,4]
covar[12] <- Omega[6,2]
covar[13] <- Omega[6,3]
covar[14] <- Omega[6,4]

```

```
covar[15] <- Omega[6,5]

# Correlations (eq.4)
rho[1] <- Omega[2,1]/pow(Omega[1,1]*Omega[2,2],0.5)
rho[2] <- Omega[3,1]/pow(Omega[1,1]*Omega[3,3],0.5)
rho[3] <- Omega[3,2]/pow(Omega[2,2]*Omega[3,3],0.5)
rho[4] <- Omega[4,1]/pow(Omega[1,1]*Omega[4,4],0.5)
rho[5] <- Omega[4,2]/pow(Omega[2,2]*Omega[4,4],0.5)
rho[6] <- Omega[4,3]/pow(Omega[3,3]*Omega[4,4],0.5)
rho[7] <- Omega[5,1]/pow(Omega[1,1]*Omega[5,5],0.5)
rho[8] <- Omega[5,2]/pow(Omega[2,2]*Omega[5,5],0.5)
rho[9] <- Omega[5,3]/pow(Omega[3,3]*Omega[5,5],0.5)
rho[10] <- Omega[5,4]/pow(Omega[4,4]*Omega[5,5],0.5)
rho[11] <- Omega[6,1]/pow(Omega[1,1]*Omega[6,6],0.5)
rho[12] <- Omega[6,2]/pow(Omega[2,2]*Omega[6,6],0.5)
rho[13] <- Omega[6,3]/pow(Omega[3,3]*Omega[6,6],0.5)
rho[14] <- Omega[6,4]/pow(Omega[4,4]*Omega[6,6],0.5)
rho[15] <- Omega[6,5]/pow(Omega[5,5]*Omega[6,6],0.5)

# Assess model fit: compute Bayesian p-value for SSQ-type discrepancy
for (i in 1:ns) {
  for (t in 1:ny) {
    resid[i,t] <- y[i,t] - N.est[i,t]
    sq[i,t] <- resid[i,t]^2
    y.new[i,t] ~ dnorm(N.est[i,t], tau.obs[i])
    sq.new[i,t] <- (y.new[i,t]-N.est[i,t])^2
  }
  fit[i] <- sum(sq[i,])
  fit.new[i] <- sum(sq.new[i,])
}
```

```

test[i] <- step(fit.new[i] - fit[i])
bpvalue[i] <- mean(test[i])
}

}

```

A.1.3 Posterior predictive checks

Model adequacy was assessed using a graphical posterior predictive check for the estimation of each country count. As a measure of discrepancy we chose the sum of squares of the residuals. Graphical check consists in plotting lack of fit of the data set against the lack of fit of replicated data using the parameters estimated by the model. A good fit is achieved if half the points are below the 1:1 line and the second half above. Fig. A.3 indicates good fit even if the data are not strictly symmetric. This is confirmed by the calculation of the Bayesian p-value. A lack of fit correspond to a Bayesian p-value closed to zero or one. Here Bayesian p-values are all around 0.54, indicating a good fit.

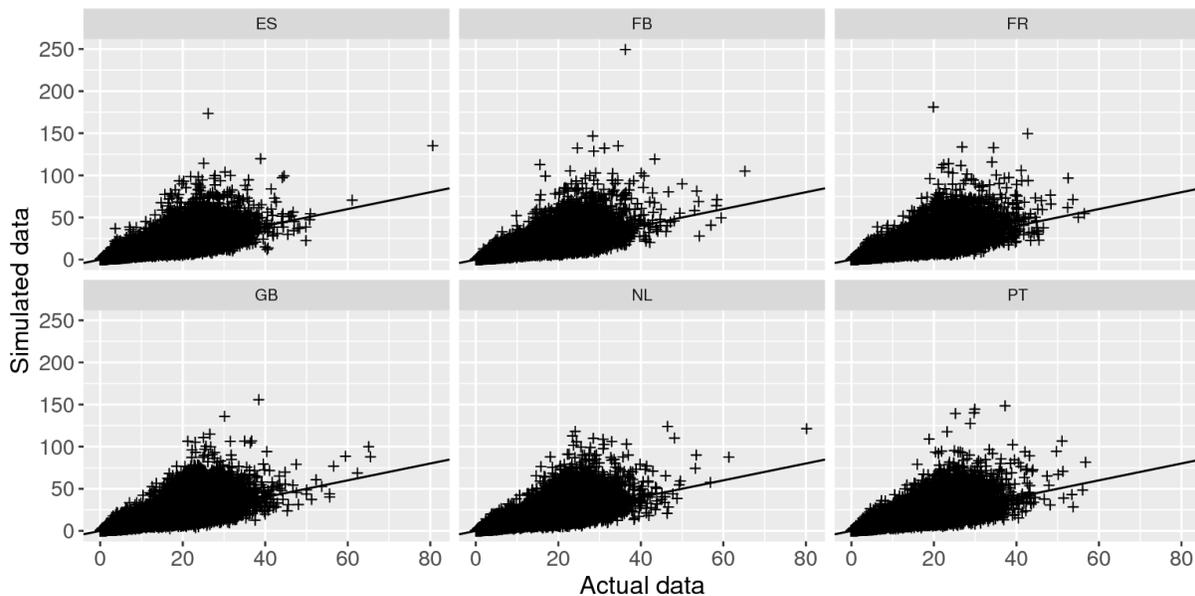


Figure A.3: Plot of discrepancy measures (sum of squares of residuals) for the estimated counts of each European country. Diagonal is the 1:1 line. ES = Spain; FB = Belgium; FR = France; GB = England; NL = Netherlands; PT = Portugal.

A.1.4 Posterior distributions

The 95% Bayesian confidence intervals of the 15 correlations estimated between-country all include zero. Nevertheless the probability of a positive correlation between Netherlands and the three closest countries Belgium, England and France is 95.4%, 93.5% and 97.1%, respectively (Fig. A.4).

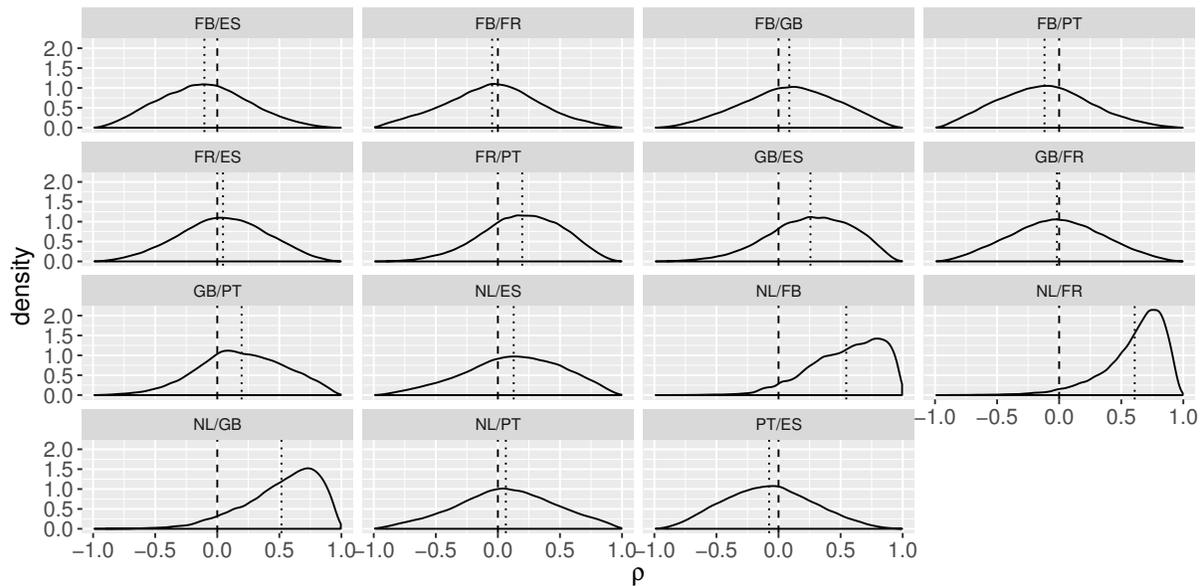


Figure A.4: **Posterior distribution of the correlation between the six West European country counts.** Vertical dotted lines indicate posterior mean and dashed line the zero line. ES = Spain; FB = Belgium; FR = France; GB = England; NL = Netherlands; PT = Portugal

Sum of counts for the North of Europe (Belgium, England, France and Netherlands) and the South of Europe (Portugal and Andalusia) are reported in Fig. A.5. The mean growth rate from 1990 to 2013 for each country is reported in Fig. A.6.

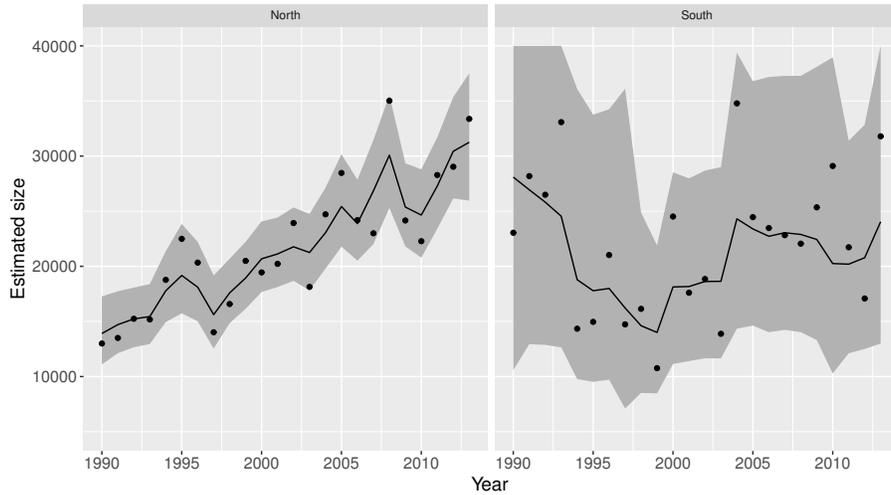


Figure A.5: **Estimated wintering population size of Pied Avocets in the North and the South of Europe between 1990 and 2013.** North European countries gather Belgium, England, France and Netherlands and South of Europe Portugal and Andalusia. Dots indicate observed counts, the line indicates estimated counts and the light grey area the 95% credible interval.

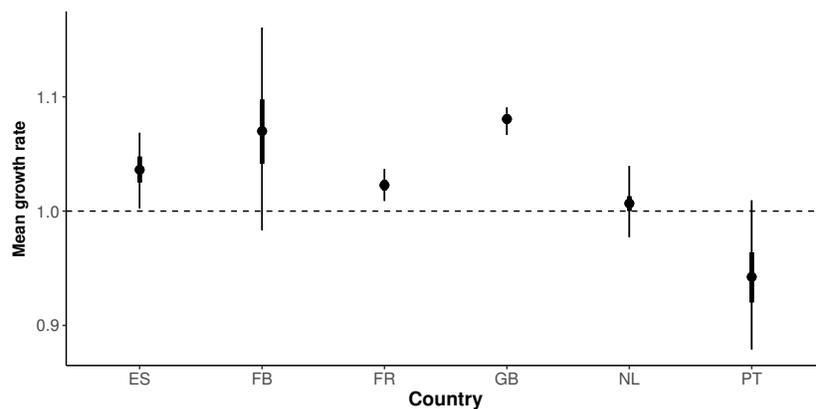


Figure A.6: **Estimated geometric mean growth rates of Pied Avocet wintering population in European country between 1990 and 2013.** Horizontal dashed line indicates population growth at equilibrium. The thin vertical line indicates the 95% credible interval, the thick vertical line the 50% interval and the point the mean estimate for each parameter. ES = Spain; FB = Belgium; FR = France; GB = England; NL = Netherlands; PT = Portugal.

A.2 Technical details on individual data modelling approach, code and models description.

A.2.1 Modelling framework

Hierarchical formulation

The complete data likelihood (CDL) approach facilitates the multistate modelling of demographic processes for open populations by implicitly integrating missing data in the likelihood estimation and by using data augmentation (Schofield & Barker, 2008; Schofield, Barker & MacKenzie, 2009). The modelling framework can be described preliminary through likelihood decomposition, which includes for this study three components, the detection process, the mortality process and the state process, *i.e.* individual time-varying covariates (Schofield & Barker, 2011):

$$\underbrace{[Y|a^b, a^d, \theta^Y, N]}_{\text{Detection}} \underbrace{[a^d|a^b, \theta^d, N]}_{\text{Mortality}} \underbrace{[z|\theta^z, N]}_{\text{Covariate}} \quad (\text{A.5})$$

The detection (encounter) process defines how individuals appeared over the sampling occasions (winter re-sightings) and enables to estimate capture probability. Y is a matrix of random variables (containing the resightings of birds) given a^b (the matrix defining birth dates) and a^d (the matrix defining death dates). θ^Y is the set of parameters describing the observation process and N the total number of individuals entering in the population during the study period. The population dynamics is also described by the death process. As all individuals were marked as chicks, birth date is known. The matrix a^b is then given as data. However, we had no recovery of Pied Avocets, then a^d is a full latent matrix of death histories whose process is described by parameters θ^d . Finally, the state process is defined by the random variable z given parameters θ^z describing the choice of the first winter area and the subsequent transitions between wintering areas.

Detection process.

The data structure is a matrix Y of $n=221$ encounter histories with elements $y_{i,t}$, taking the values 1 or 0, to indicate whether or not individual i was detected during survey t , with

$t \in \{1, \dots, 19\}$. The binary observations $y_{i,t}$ are modelled as independent Bernoulli random variables conditional to the availability of individual i in the population at t ,

$$y_{i,t}|a_{i,t} \sim \text{Bern}(p_{s,t}a_{i,t}), \quad (\text{A.6})$$

where s indicates the individual state (wintering area). Thus, if $a_{i,t} = a_{i,t}^b a_{i,t}^d = 0$ (individual i is ever died, $a_{i,t}^d = 0$, or not yet born at t , $a_{i,t}^b = 0$) then $y_{i,t} = 0$ with probability 1, otherwise $y_{i,t}$ is a Bernoulli trial with probability $p_{s,t}$.

As mentioned in the main text we explicitly account for imperfect detection by modelling encounter process as:

$$\text{logit}(p_{s,t}) = \gamma_s + \eta_{s,t}^p, \quad \eta_{s,t}^p \sim N(0, \sigma_p^2), \quad (\text{A.7})$$

with a Student-t prior $T_3(0, 0.16)$ for γ_s , the state dependant intercept and a $T_3^+(0, 0.04)$ for the state \times time random effect. As an alternative to classical vague Normal prior we chose Student-t distributions with small degree of freedom (df=3) for computational reasons. Indeed, they are flat-tail distributions allowing more robust inference in logistic regression (Gelman *et al.*, 2008) and they place iterative weighted on $[-5, 5]$, a reasonable logistic range that stabilizes coefficient estimates, especially with sparse response data.

Ecological process.

A key feature of the CDL is the estimation of the matrix A estimating latent life history of all individuals entering the population during the study, as well as the observed ones as the unknown individuals included via data augmentation (see below Data augmentation and derived quantities). This matrix is implemented with element $a_{i,t} = a_{i,t}^b a_{i,t}^d$. The latent element $a_{i,t}^d$ which defined the mortality process is estimated as

$$a_{i,t}^d \sim \text{Bern}(a_{i,t-1}^d (a_{i,t-1}^b S_{i,t-1} + 1 - a_{i,t-1}^b)), \quad (\text{A.8})$$

where the parameter $S_{i,t}$ is the probability of individual i surviving between sampling occasions t and $t + 1$. The formulation ensures that an individual can only die after being born, and lives only once. Dead recoveries could be included in this analysis, as date of death can be implemented if known, but non dead recoveries appeared during our study.

The survival probability between occasions t and $t + 1$, as mentioned above, is integrated in the mortality process component of the model. We defined survival probability as a robit regression, which is the inverse function of the cumulative distribution function of the standard Student-t distribution.

$$S_{s,t} = cdfT_7(robit(S_{s,t}), 1/\sigma_r^2), \quad \sigma_r = 1.5485, \quad (\text{A.9})$$

$$robit(S_{s,t}) = f_S(\theta_S) + \eta_{s,i}^S, \quad \eta_{s,i}^S \sim N(0, \sigma_S^2), \quad (\text{A.10})$$

with survival, time and wintering area dependant, a function of parameters θ_S describing survival process (see above section Covariates for the details on covariates tested on survival). We included individual random effect accounting for individual heterogeneity (Cam *et al.*, 2002; Cam, Aubry & Authier, 2016) in survival estimates because we expected differences between wintering strategies especially for residents facing less predictable wintering weather conditions.

Multi-states modelling.

The CDL framework allows to treat categorical states (North or South wintering area) as a covariate that is individual-specific and that can vary through time (Schofield & Barker, 2011). Thus we define a matrix Z (same dimension as A) with element $z_{i,t}$ that takes two values, 1 if individual i is in the north of Europe at occasion t or 2 if it is in the south during winter. Unobserved states take the value NA. The latent states $z_{i,t}$ are defined

$$\begin{cases} z_{i,t} \sim \text{Cat}(p_{t,s}^z), & \text{if } t = \text{first winter, } \text{logit}(p_{t,s}^z) = f_{p^z}(\theta_z), \\ z_{i,t} \sim \text{Cat}(\psi_{t,s}^z), & \text{if } t > \text{first winter, } \text{logit}(\psi_{t,s}^z) = g_{p^z}(\alpha_z). \end{cases} \quad (\text{A.11})$$

where $\text{Cat}(\phi)$ is a categorical distribution with probability vector ϕ , ψ^z is the transition probability between state $z_{i,t-1}$ and state $z_{i,t}$ and $p_{t,s}^z$ is the probability of being in state s at occasion t given the individual was not born at $t - 1$ *i.e.*, the first transition state from breeding ground. $f_{p^z}(\theta)$ and $g_{p^z}(\alpha)$ are specific functions of parameter θ_z and α_z we tested on p^z and ψ^z respectively.

Data augmentation and derived quantities.

The CDL uses data augmentation (Schofield & Barker, 2011; Tanner & Wong, 1987) for including missing or unobserved data, which allows to estimate population dynamics parameters (size, growth,...) during the study. The data augmentation is a flexible tool for estimating the number of unmarked or unobserved items belonging to (recruiting in) the population. This method consists in adding to the known- N number of individuals (221 here) a new dataset of a large number of unobserved individuals. The new (augmented) dataset obtained constitutes the "super-population" of size M from which we can estimate the true number of individuals recruited during the study period. The chosen number of pseudo-individuals $n_0 = M - N$ must be sufficiently large to ensure the inclusion of all the potential individuals to the population. Following Royle & Dorazio (2008, 2012), we augmented the observation matrix Y with a matrix of 570 pseudo-individuals (30×19 sampling occasions) of all zero encounter histories. This enables the potential recruitment of 30 unmarked individuals at each sampling occasion. The latent state matrices Z and A^d were also augmented by the same number of pseudo-individuals x sampling occasions, as well as matrix A^b for which 30 pseudo-individuals with element $a_{i,t}^b$ was set to 1 for each sampling occasion t and the subsequent occasions. This parametrisation implies that, considering this zero-inflated version of the model described above, we used an inclusion parameter w_i ,

$$\begin{cases} w_i = 1 & \text{if individual } i \in \text{known-}N \text{ individuals,} \\ w_i \sim \text{Bern}(\psi_i) & \text{if individual } i \in \text{zero-inflated individuals.} \end{cases} \quad (\text{A.12})$$

that determines if pseudo-individual i belongs to the population, with $\psi_i \sim \text{Beta}(1, 1)$, a flat prior on $[0,1]$. Considering this parametrization, we now define $a_{i,t} = a_{i,t}^b a_{i,t}^d w_i$.

This new parameter enables easy calculation of numerous derived parameters, such as the total population size (N_{tot}), the number of individuals alive at occasion t (N_t) or the number of birth (B_t) and death (D_t),

$$N_{tot} = \sum_{i=1}^M w_i, \quad N_t = \sum_{i=1}^M a_{i,t}, \quad B_t = \sum_{i=1}^M (1 - a_{i,t}) a_{i,t+1}, \quad D_t = \sum_{i=1}^M (1 - a_{i,t-1}^d) a_{i,t}^d$$

the population growth rate (λ) and the per-capita entry probability f (Pradel, 1996),

$$\lambda_t = \frac{N_{t+1}}{N_t} \quad \text{and} \quad f_t = \frac{B_t}{N_t}.$$

As covariates have two states we can easily compute quantities of interest according to each state. From the partially latent life history matrix A we can derived individual lifespan as row sum of A equal lifetime history of each individual:

$$lifespan_i = \sum_{t=1}^T a_{i,t} \quad i = 1, \dots, M$$

Covariates

In order to test biological hypotheses on the processes modelled in this analysis we used environmental covariates: North Atlantic Oscillation (NAO) index and a custom winter severity indices. NAO is used as a proxy for global climate. When positive, it indicates that the climate is warmer and wetter in northern Europe, whereas conditions are colder and dryer than average in the southern Europe and Mediterranean region and vice-versa (Visbeck *et al.*, 2001). We particularly used indices for the winter period (December to February), taken from <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>. The winter severity indices were based on the number of successive days with mean daily temperatures $\leq 0^\circ\text{C}$, using freely available climatic data (<http://www.infoclimat.fr/climatologie>) from Nantes airport (47°09'N, 1°36'W) and Bordeaux airport (44°50'N, 0°42'W), situated at the extremity of French Pied Avocet winter Range. We considered these two places as representative of the climate range and then calculated the mean values. We sorted these data in discrete indices between 1 to 4 if consecutive days are in class 0 to 4 days, 5 to 9 days, 10 to 14 days and ≥ 15 days, respectively (see Table A.1).

Winter (years)	Severity indices	NAO
1995-1996	1	-0.62
1996-1997	4	-0.07
1997-1998	1	-0.23
1998-1999	1	0.64
1999-2000	1	1.3
2000-2001	1	0.04
2001-2002	1	0.24
2002-2003	2	-0.05
2003-2004	1	0.07
2004-2005	1	0.89
2005-2006	1	0.11
2006-2007	1	0.36
2007-2008	1	0.65
2008-2009	1	-0.08
2009-2010	2	-1.67
2010-2011	1	-0.68
2011-2012	3	1.37
2012-2013	1	0.02
2013-2014	1	0.86
2014-2015	1	1.66

Table A.1: **Environmental covariates.** These covariates were incorporated in the model at the first stage of selection as explanatory variable for the estimation of survival probability, first wintering area selection and transition between following winters.

It is difficult to obtain a precise hatching date in Pied Avocets because it is a precocial species and our monitoring schema is not daily. Then, hatch dates were estimated from biometrics taken during ringing sessions. Chambon *et al.* (2017) showed that bill length is the best predictor of hatch date with a precision ± 2.2 days (SE=0.24). Estimated hatch date was calculated from the following equation:

$$hd = rd - \frac{1.36 - \log\left(\frac{82.23}{bl} - 1\right)}{0.08} \quad (\text{A.13})$$

where hd is estimated hatch date, rd is ringing date and bl is bill length.

The distribution of the hatching date concerning the whole data set is clearly bivariate (see Fig. A.7.A) and the same pattern exists among the individuals never seen in the Iberian

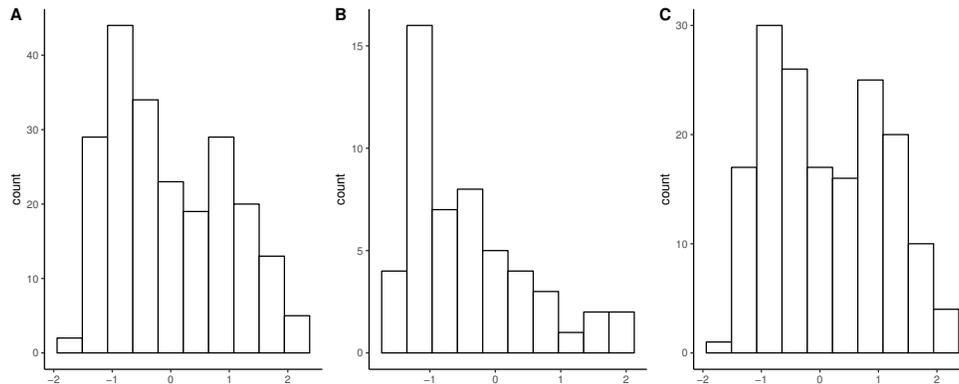


Figure A.7: **Hatch date distributions.** Values were standardized with a mean of 0 and a standard deviation of 1. Graphic A shows the distribution of estimated hatching date for all individuals, graphic B shows the distribution of estimated hatching date for the individuals seen at least once in the Iberian Peninsula and graphic C shows the distribution of estimated hatching dates for the individuals never seen in the Iberian Peninsula.

Peninsula (see Fig. A.7.B). However, the distribution of the hatch date concerning the individuals seen in the Iberian Peninsula has a higher density in negative values (see Fig. A.7.C) indicating a globally earlier hatching date than in other individuals, despite a skew tail toward positive values. As three bill length are missing among the selected individuals and because first winter state was not known for every bird, we consider hatching date as being normally distributed, *i.e.*:

$$Birth_i \sim N(\mu_{S,j}, \tau_S) \tag{A.14}$$

$$\mu_{North,j} \sim N(1, 0.5) \quad \& \quad \mu_{South,j} \sim N(-1, 0.5), \tag{A.15}$$

where $Birth_i$ is the estimated birth date of individual i using equation 9 and $\mu_{S,j}$ is its mean estimated birth date conditionally of his state S (North or South) during the first winter in year j . Informative prior distributions (Eq.A.15) were used for the mean birth dates considering knowledge of birth date due to equation 9 after scaling the date with mean zero and standard deviation equal to one.

Horseshoe prior

In order to select the covariates that affect the main parameters of the model (survival, the choice of wintering site and transition between sites), we made use of the horseshoe prior that

is related to the shrinkage methods, e.g. the Laplacian priors (LASSO) or Student-t priors. The horseshoe prior is a robust estimator at handling sparse data and outlying signals as well as disentangling noise from real signal from data. It assumes that in a regression the coefficients, say β_i , are conditionally independent and their density can be represented as scale-mixture of normal distributions:

$$(\beta_i | \lambda_i, \tau) \sim N(0, \lambda_i^2 \tau^2) \tag{A.16}$$

$$\lambda_i \sim C^+(0, 1), \tag{A.17}$$

with $C^+(0, 1)$ is the half-Cauchy distribution for the standard deviation λ_i . In this context λ_i 's are considered as the local shrinkage parameters (defined for each coefficient β_i) and τ is a global shrinkage parameter. We also defined a half-Cauchy distribution for τ . Following Carvalho, Polson & Scott (2010) we formulated the Cauchy distributions as scale mixture with inverse-Gamma distribution, $IG(1/2, 1/2)$. The interest of the horseshoe prior is to put the posterior probability mass around zero ($\beta_i = 0$), see Fig. A.8, unless signal from a covariate shift posterior probability mass of β_i away from zero.

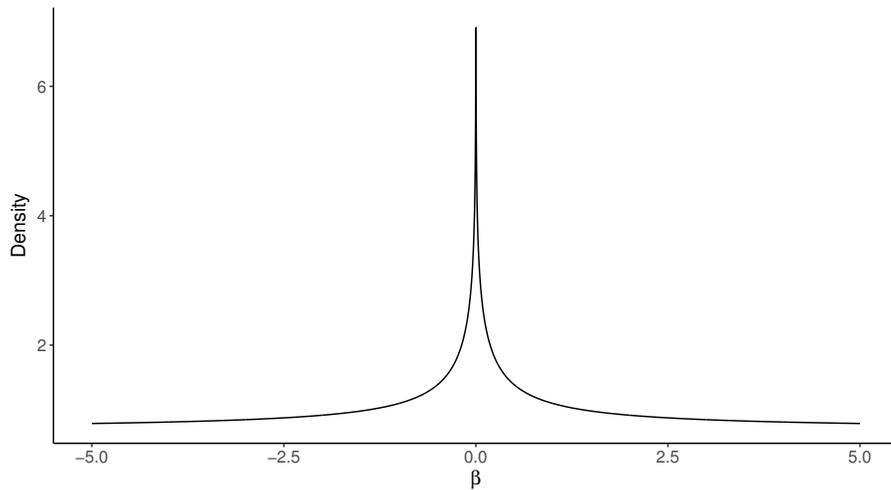


Figure A.8: **The horseshoe prior.** Approximate density function of the horseshoe prior, $\log(1 + 2/\beta^2)$, according to Carvalho, Polson & Scott (2010) on the range $[-5,5]$.

A.2.2 DIC Model selection

Name	DIC	pD	Deviance	ΔDIC	w_i
mod0	3648.5	884.3	2764.2	25.1	0.00
mod1	3663.0	902.8	2760.2	39.6	0.00
mod2	3623.4	865.4	2758.0	0	0.84
mod3	3641.8	876.6	2765.3	18.4	0.02
mod4	3642.3	874.6	2767.7	18.9	0.00
mod5	3646.8	880.4	2766.5	23.4	0.00
mod6	3657.2	896.6	2760.6	33.8	0.00
mod7	3650.0	886.7	2763.2	26.6	0.00
mod8	3637.6	866.3	2771.3	14.2	0.13
mod9	3642.7	882.9	2759.9	19.3	0.00
mod10	3642.2	875.1	2767.0	18.8	0.00
mod11	3649.1	886.2	2762.9	25.7	0.00
mod12	3635.3	872.6	2762.6	11.9	0.00

Table A.2: **Model selection.** The different models were selected using the deviance information criterion (DIC). Best fitted model has the lowest DIC, w_i is the weight of the model ($w_i = \exp(-0.5\Delta DIC_i) / \sum \exp(-0.5\Delta DIC_i)$, with ΔDIC_i the difference between model i and the model with the lowest DIC).

A.2.3 Model code

Jags code for the best fitted model (mod2).

```

model{
  for(i in 1:m){
    w[i] ~ dbern(pw) # inclusion parameter (eq.8)
  }

  pw ~ dbeta(1,1)
  lambda <- sum(w[1:m]) # estimated total individuals recruited

  for(i in 1:m) {
    for(j in 1:(since[i]-1)){

```

```

a[i,j] <- 0
a1[i,j] <- 0
a2[i,j] <- 0
ad[i,j] <- 1
}

for(j in since[i]:until[i]){
  # DEATH
  ad[i,j] ~ dbern(piad[i,j]) # latente death matrix
  # ALIVE
  a[i,j] <- ab[i,j]*ad[i,j]*w[i] # alive matrix for all individuals
  # alive matrix in for individuals in state 1 (North)
  a1[i,j] <- a[i,j]*(2-z[i,j])
  # alive matrix in state for individuals in state 2 (South)
  a2[i,j] <- a[i,j]*(z[i,j]-1)
}

for(j in since[i]:until[i]){
  # Observation process
  x[i,j] ~ dbern(pdets[i,j])
  pdets[i,j] <- a[i,j]*p[i,j] # eq.2
}

for(j in 1:(until[i]-1)){
  # Birth
  b[i,j] <- equals(a[i,j],0)*equals(a[i,j+1],1)
  # Death
  d[i,j] <- equals(a[i,j],1)*equals(a[i,j+1],0)
}

```

```
z[i,since[i]] ~ dcat(zp[since[i],1:ns]) # first state

for(j in (since[i]+1):until[i]){
  # State estimation = Covariate model
  z[i,j] ~ dcat(psi[z[i,j-1],1:ns]) # states transitions (eq.7)
}

# Prob for death
piad[i,since[i]] <- 1
for(j in (since[i]+1):until[i]){
  piad[i,j] <- ad[i,j-1]*(ab[i,j-1]*sv[i,j-1] + (1-ab[i,j-1])) # eq.4
}

# Survival prob (robit link function)
for(j in since[i):(until[i]-1)){
  sv[i,j] <- pt(sv.rob[i,j],0,tau.robit,7) # eq.5
  sv.rob[i,j] <- beta1 + beta2*age[i,j] + etas[z[i,j],i] # eq.6
}

for(j in since[i]:until[i]){
  p[i,j] <- pdt[z[i,j],j]
}
}

# Scale parameter for the robit link
tau.robit <- pow(sigma.res,-2)
sigma.res <- 1.5485
```

```
for(j in 1:n_occ){
  logit(pdt[1,j]) <- gamma[1] + etap[1,j] # North detetection (eq.3)
}

for(j in 1:3){
  logit(pdt[2,j]) <- gamma[2] + etap[2,j] # South detetection (eq.3)
}

for(j in 4:9){
  pdt[2,j] <- 0 # South detetection (eq.3)
}

for(j in 10:n_occ){
  logit(pdt[2,j]) <- gamma[2] + etap[2,j] # South detetection (eq.3)
}

for(h in 1:2){
  # Variance priors
  gamma[h] ~ dt(0,0.16,3)
  taup[h] <- 1/sdp[h]/sdp[h]
  sdp[h] ~ dt(0,0.04,3)T(0,)
  taus[h] <- 1/sds[h]/sds[h]
  sds[h] ~ runif(0,10)
}

for(i in 1:m){
  for(h in 1:2){
    # Survival individual state-dependant random effect
    etas[h,i] ~ dnorm(0,taus[h])
  }
}
```

```
    }
  }

for(j in 1:n_occ){
  for(h in 1:2){
    # detection random year effect
    etap[h,j] ~ dnorm(0,taup[h])
  }
}

for(h in 1:ns){
  psi[h,1:ns] ~ ddirch(alpha[]) # yearly transition probability
}

# Others priors
for(h in 1:ns){
  alpha[h] <- 1
}

beta1 ~ dnorm(0,0.001)T(-10,10)
beta2 ~ dt(0,0.16,3)

for(j in 1:n_occ){
  # yearly selection rate of first wintering area
  zp[j,1:ns] ~ ddirch(alpha[])
}

### Computation of lifespan
for (i in 1:(m-nz)){
```

```
lspan[i] <- sum(a[i,since[i]:until[i]])
}

### Computation of abundance population parameters
for(j in 1:n_occ){
  N[j] <- sum(a[1:m,j])
  N1[j] <- sum(a1[1:m,j])
  N2[j] <- sum(a2[1:m,j])
}

for(j in 1:(n_occ-1)){
  B[j] <- sum(b[1:m,j])
  D[j] <- sum(d[1:m,j])
}
}
```

A.2.4 Model description

Name	Par.	State	Age	Year (fact.)	Time	Wint. Sev.	Time* Wint. Sev.	State*time (r. eff.)	Indiv. (r. eff.)	State*Indiv. (r. eff.)
mod0	p	yes	no	no	no	no	no	yes	no	no
	S	no	yes	no	no	no	no	no	no	no
	p^z	no	no	yes	no	no	no	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no
mod1	p	yes	no	no	no	no	no	yes	no	no
	S	no	yes	no	no	no	no	no	no	yes
	p^z	no	no	no	yes	no	no	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no
mod2	p	yes	no	no	no	no	no	yes	no	no
	S	no	yes	no	no	no	no	no	no	yes
	p^z	no	no	yes	no	no	no	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no
mod3	p	yes	no	no	no	no	no	yes	no	no
	S	no	no	no	no	no	no	no	no	yes
	p^z	no	no	yes	no	no	no	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no
mod4	p	yes	no	no	no	no	no	yes	no	no
	S	no	no	no	no	no	no	no	no	yes
	p^z	no	no	no	yes	no	no	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no
mod5	p	yes	no	no	no	no	no	yes	no	no
	S	no	no	no	no	no	no	no	no	yes
	p^z	no	no	no	yes	yes	no	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no
mod6	p	yes	no	no	no	no	no	yes	no	no
	S	no	yes	no	no	no	no	no	no	yes
	p^z	no	no	no	yes	yes	no	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no
mod7	p	yes	no	no	no	no	no	yes	no	no
	S	no	yes	no	no	no	no	no	no	yes
	p^z	no	no	no	no	yes	no	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no
mod8	p	yes	no	no	no	no	no	yes	no	no
	S	no	no	no	no	no	no	no	no	yes
	p^z	no	no	no	no	yes	no	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no
mod9	p	yes	no	no	no	no	no	yes	no	no
	S	no	yes	no	no	no	no	no	no	yes
	p^z	no	no	yes	no	yes	no	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no

Name	Par.	State	Age	Year (fact.)	Time	Wint. Sev.	Time* Wint. Sev.	State*time (r. eff.)	Indiv. (r. eff.)	State*Indiv. (r. eff.)
mod10	p	yes	no	no	no	no	no	yes	no	no
	S	no	no	no	no	no	no	no	no	yes
	p^z	no	no	yes	no	yes	no	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no
mod11	p	yes	no	no	no	no	no	yes	no	no
	S	no	yes	no	no	no	no	no	yes	no
	p^z	no	no	yes	no	no	no	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no
mod12	p	yes	no	no	no	no	no	yes	no	no
	S	no	yes	no	no	no	no	no	no	yes
	p^z	no	no	yes	no	yes	yes	no	no	no
	ψ^z	no	no	yes	no	no	no	no	no	no

Table A.3: **Parameters of the final models compared.** p = detection probability, S = survival probability, p^z = first transition probability, ψ^z = site fidelity. Par.= parameters, Wint. sev. = winter severity, fact. = variable treated as factor, r. eff. = random effect, Indiv. = Individual effect (treated as random) and * indicates interaction between covariables.

A.3 Additional data and results from CMR modelling.

A.3.1 Cohort data

Cohort	Total ringed	Ringed individuals kept for analysis	Number of Resighting occasions	
			North	South
1996	26	13	10	22
1997	53	24	67	16
1998	26	4	6	9
1999	29	3	4	0
2000	8	4	19	0
2001	38	12	57	10
2002	26	8	41	5
2003	18	12	28	10
2004	43	9	43	3
2005	39	33	29	12
2006	54	22	103	5
2007	46	16	68	6
2008	24	14	37	8
2009	31	9	21	6
2010	16	3	20	1
2011	4	6	2	2
2012	0	0	0	0
2013	16	6	7	3
2014	43	14	12	2
Total	552	221	574	120

Table A.4: **Ringed and resighted Pied Avocets.** Number of Pied Avocets ringed as chicks per cohort, number of individuals resighted at least once during winter and number of resighting occasions (occasion correspond to individual resightings of the considered cohort and per winter) according to wintering area and for each cohort.

Pied Avocets were all ringed as chicks from 3 weeks old to 1 month old, just before fledging. The colour-ring combinations consist of multiple plastic colour-rings or a mix of colour-rings including a flag or engraving rings. The colour-ring combinations can be read through a telescope (zoom 20x60) up to a distance of 300m in good weather conditions. The maximum number of chicks is ringed, each of them with a unique combination, in the

limits of feasibility and volunteers availability. We thank the Museum National d'Histoire Naturelle of Paris for the authorisation to ring Pied Avocets.

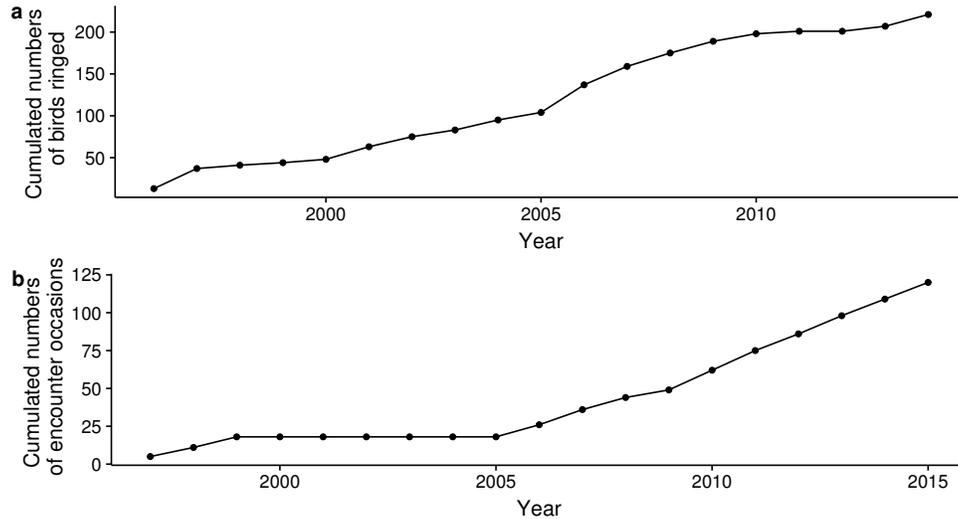


Figure A.9: **Accumulation curve of ringed birds entering the study.** A: accumulation of the number of birds ringed during the study period; B: Accumulation curve of the number of encounter occasions per winter.

Winter 2006 is the cut point date between low rate of ringing and low number of encounter occasions with higher rates of both ringing and observation as showed by the slope of the two curves. These two variables are obviously correlated.

A.3.2 Model adequacy with data

The observed yearly survival was calculated as the number of Pied Avocets borne in year t or before and still alive during year $t + 1$, *i.e.* observed in year $t + 1$ or after.

Apparent detection is the proportion of observed individuals among individuals know to be alive.

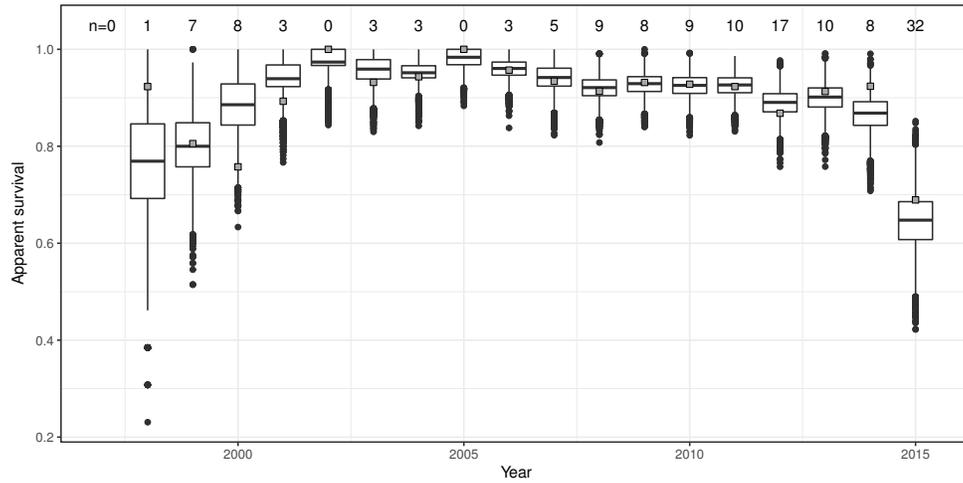


Figure A.10: **Posterior predictive distribution for survival.** The observed yearly survival is shown by grey squares. Boxplots show posterior distribution simulated from 10000 random draws of joint posterior distributions parameters of the best model. The numbers in the upper part of the figure indicate numbers of individuals of the corresponding cohort never observed subsequently during the study period.

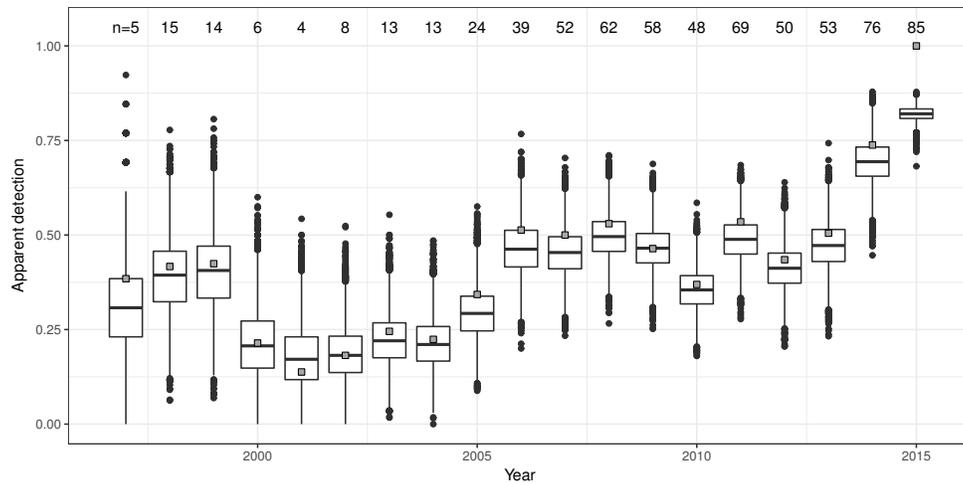


Figure A.11: **Posterior predictive distribution for detection.** Detection probability as calculated from data set is shown by grey squares. Boxplots show posterior distribution simulated from 10000 random draws of joint posterior distributions parameters of the best model. The numbers in the upper part of the figure indicate numbers of detected individuals.

A.3.3 Summary of population dynamics parameters

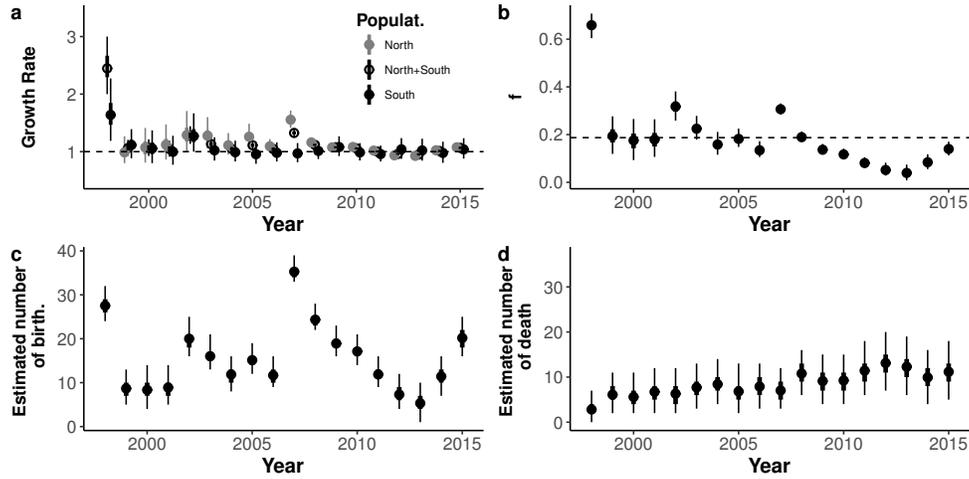


Figure A.12: **Population dynamics.** (a) Estimated annual growth rate (λ_t), horizontal dashed line indicates stability ($\lambda = 1$). For graphical clarity the North population growth rate in 1998 (7.49) was note shown on the graphic. (b) per-capita entry probability (recruitment), horizontal dashed line indicate mean value on the period. (c) Estimated annual number of births. (d) Estimated annual number of dead individuals. For all graphics fine vertical lines correspond to 95% Bayesian confidence interval and large vertical lines correspond to 50% Bayesian confidence interval.

A.3.4 Survival heterogeneity

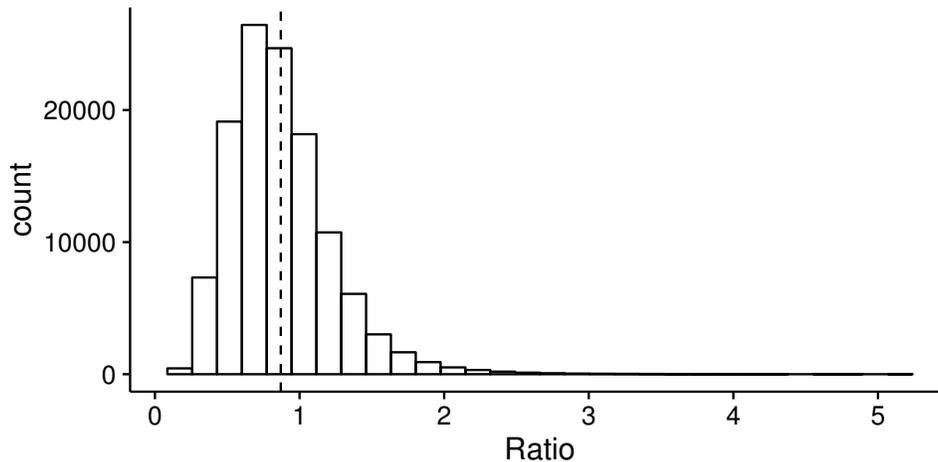


Figure A.13: **Variance ratio.** Distribution of the ratio between the state-specific survival variance of North wintering Avocets, against the South wintering ones. The vertical dotted line shows the mean (0.87).

Survival heterogeneity was estimated as individual and state dependant (Eq. A.9). Dif-

ferences between states (North and South wintering area) was explored via variance ratio (Fig. A.13).

In order to explore individual heterogeneity in survival we tested, using the posterior mean estimates of each individual heterogeneity parameter, potential local wintering area effects by splitting wintering quarters at different scales. To each bird we attributed one winter site, according to its life history. To birds observed in different sites during their life, we attributed as site the one where they were resighted the higher number of winters. We also treated birds moving between different sites as a special category, depending on the scale considered.

Considering the Iberian Peninsula, we compared survival heterogeneity between Spain and Portugal using Wilcoxon rank sum test, but found no significant difference ($W=289$, $p=0.26$). At lower scale, we only compared heterogeneity between the Tagus and the Sado estuary, due to the very small sample size in the other sites. The difference was not significant ($W=108$, $p=0.48$). We excluded from the analyses the 5 birds observed in the two states.

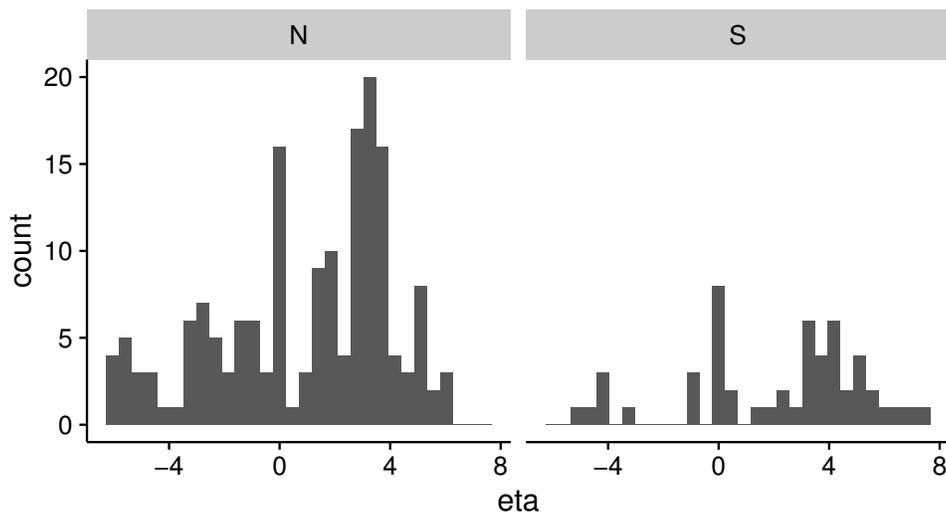


Figure A.14: **Individual heterogeneity.** Distribution of the survival heterogeneity according to bird wintering area. N: North, S: South.

Concerning birds wintering in the North of Europe, we first compared 4 main wintering areas along the French Atlantic coast, using Mood’s median test ($p=0.05$). However, pair-

wise comparison using Mood’s median test indicated no significant p-value, we thus did not concluded to any significant difference between sites. At a lower scale we distinguished birds seen in only one site during their life, consisting in 5 sites along the French Atlantic coast, and a supplementary category for birds seen in different sites (with no more distinction). Mood’s median test ($p < 0.001$) was significant, but a pairwise analysis revealed no significant p-value. We thus did not concluded to any significant difference. However, p-values corresponding to comparisons between birds faithful to 3 sites in winter and birds moving between different sites are all in the interval $[0.05, 0.1]$. These 3 sites correspond to the breeding colony and the two Southern sites of the Atlantic coast, *i.e.* the Northern main wintering sites of this coast.

We excluded from these analyses the 5 birds observed in the two states.

A.3.5 Posterior distributions

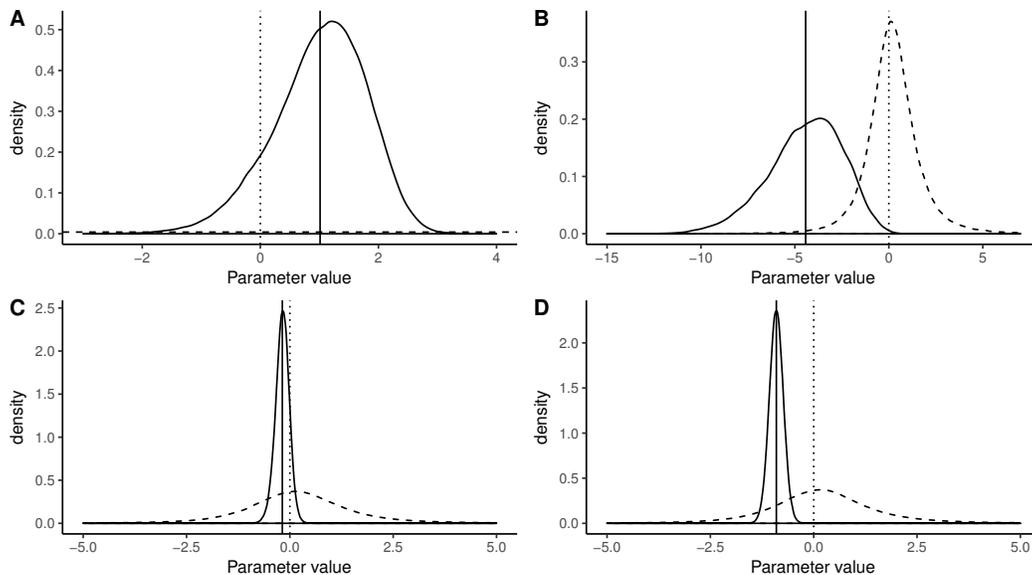


Figure A.15: **Posterior distribution of survival and detection parameters.** A. β_1 : intercept in the survival probability regression. B. β_2 : Age effect in the survival probability regression. C. γ_1 : intercept in the detection probability regression for North wintering birds. D. γ_2 : intercept in the detection probability regression for South wintering birds. Vertical line indicates posterior mean and dotted line zero. Dashed curve indicates prior distribution.

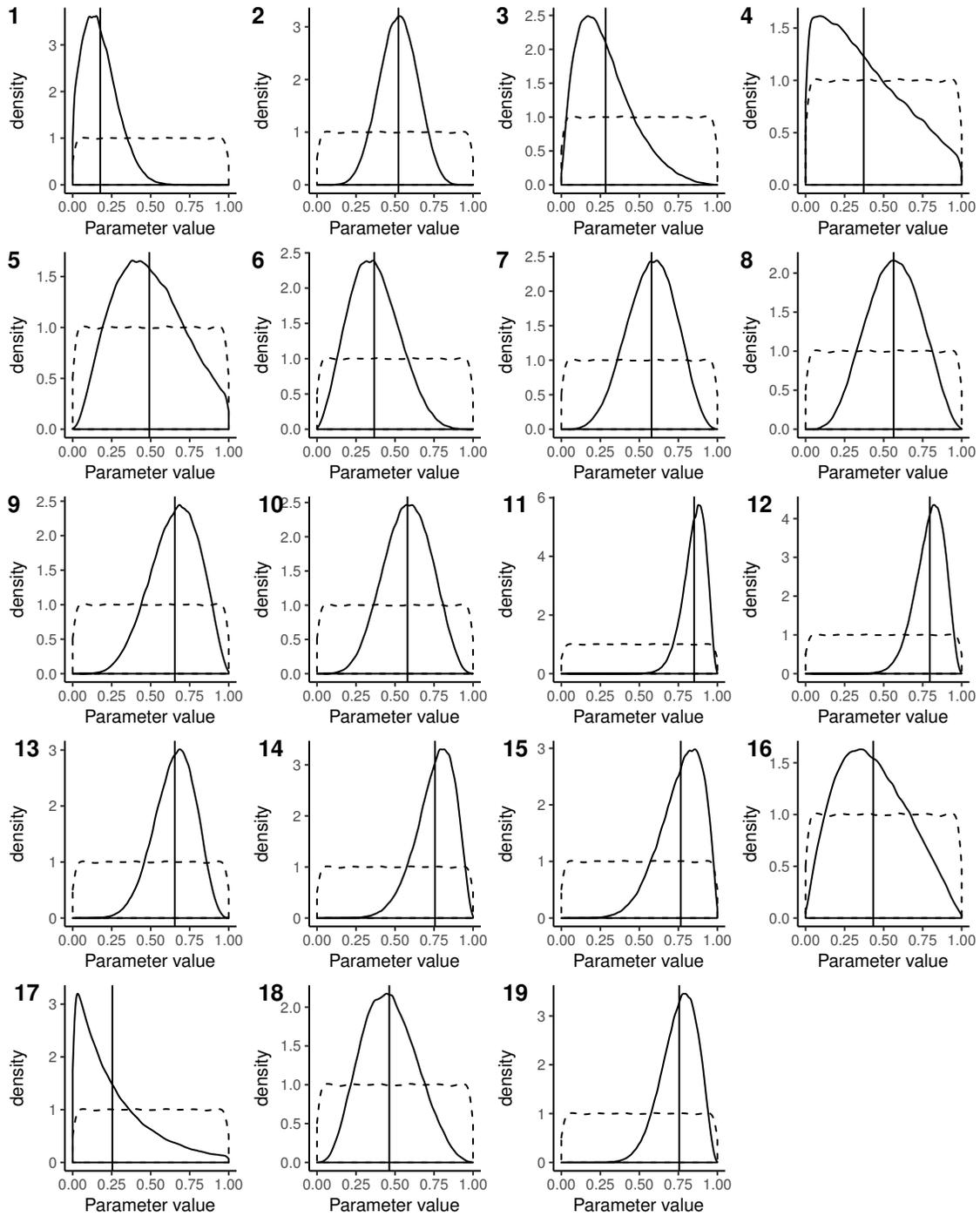


Figure A.16: **Posterior distribution of annual first winter transition to North.** From 1 to 19 respectively $p_{t,1}^z$ for $t = \{1, \dots, 19\}$. Vertical line indicates posterior mean and dashed curves indicate prior distribution (Dirichlet). First winter transition to South ($p_{t,2}^z$) is the complement of $p_{t,1}^z$, *i.e.* $p_{t,2}^z = 1 - p_{t,1}^z$.

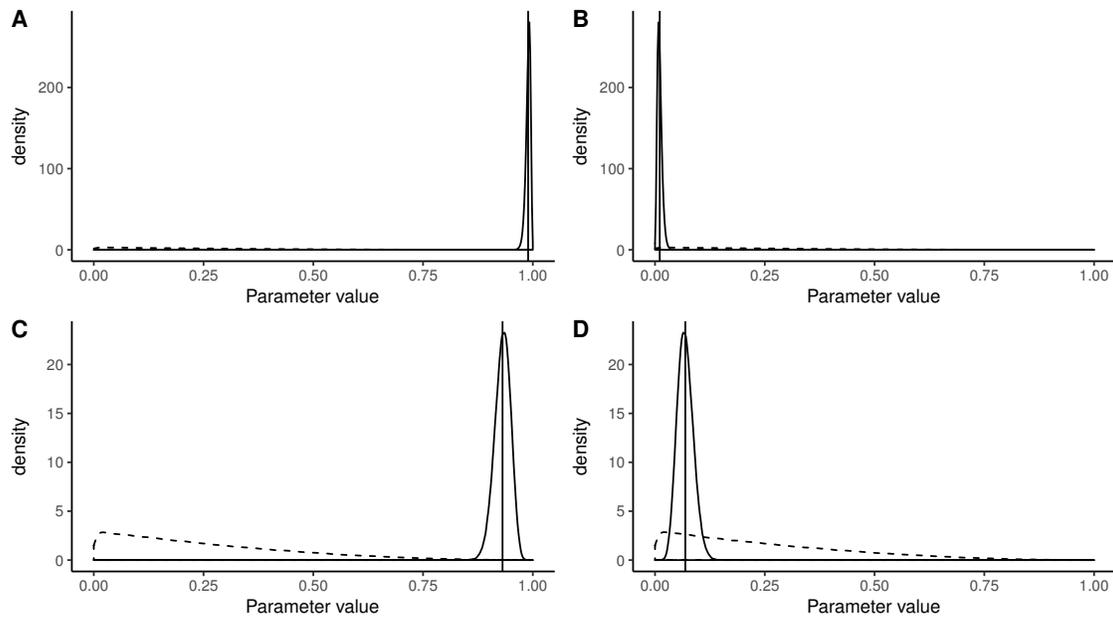


Figure A.17: **Posterior distribution of state transitions after first winter.** A: probability to winter in the North if first wintering in the North ($\psi_{N,N}$), fidelity to the North area. B: transition probability to the South if first wintering in the North ($\psi_{N,S}$). C: probability to winter in the South if first wintering in the South ($\psi_{S,S}$), fidelity to the South area. D: transition probability to the North if first wintering in the South ($\psi_{S,N}$). Vertical line indicates posterior mean and dashed curves indicate prior distribution (Dirichlet).

Appendix B

Supporting information to chapter III

B.1 Breeding Events

We distinguished firstly birds observed at their breeding site from those observed outside. Monitoring of breeding period was more intensive at ringing colony than elsewhere, we then suspected a higher detection rate, as well as a better classification rate of breeding state than outside this colony.

During each breeding season, an individual can only have one of the three possible states: non-breeder, unsuccessful breeder or successful breeder (inside or outside the ringing colony). However, it was not possible to ascertain non breeding state (there is no objective criteria for that), apart from juveniles, as breeding can occur from the breeding season following birth. We then attributed certain non-breeding state mainly to juveniles (at ringing occasion), and also to a few occasions for adults from which a high number of observations during the breeding season indicated no breeding behaviour (34 occasions). Moreover, it was not possible to classify all breeding individuals as certain breeders, because observations were sparse and we can miss the breeding behaviours needed to classify the individual as certain breeder. Some individuals may as well have skipped reproduction (state: non-breeder) and we expected them to exhibit no specific breeding behaviour. Moreover, conspecific nest parasitism is not rare in Pied Avocet (Hötker, 2000) and can hardly never be confirmed in the field. Indeed, those individuals show no brooding behaviour. In this context, we defined five graded observation events (see Table B.1) that reflect our knowledge about the

Event	Behaviour
Certain non-breeder (1)	Juvenile (at ringing)
Possible breeder (2)	No specific behaviour Present at breeding site
Suspected breeder (3)	Nest prospection
	Mate
	Alarming
	Territoriality
	Copulating
Certain breeder (4)	Manipulating nest material
	Digging nest
	Diversion moves
	Incubating Chicks care
Successful breeder (5)	Juveniles care

Table B.1: **Event determination.** List of behaviours observed during fieldwork and their corresponding events.

real breeding state of individual: (1) certain non-breeder, (2) possible breeder, (3) suspected breeder, (4) unsuccessful breeder and (5) successful breeder. These five events were recorded both inside and outside the ringing colony, leading to a total of 10 possible events. For events 2 and 3, no state was attributed, we used the maximum level of information from behavioural observations to set these event grade, reflecting our best knowledge of unknown breeding state. Event 5 is a special case of event 4, indeed it correspond to breeders that were successful in their breeding attempt (observed whit sub-fledgling juveniles). As there was possibly uncertainty in the success of breeding attempts, families escaping the monitoring, we also considered event 4 as uncertain in term of success (see Fig. B.1).

Annual breeding occasions consisted in one unique value in our modelling framework. However, as predation is very high on most of the breeding range (Touzalin pers. com.), multiple breeding attempts are common in Pied Avocets. In order to overcome this problem assigning a single trait to each individuals during each breeding season, we used the higher

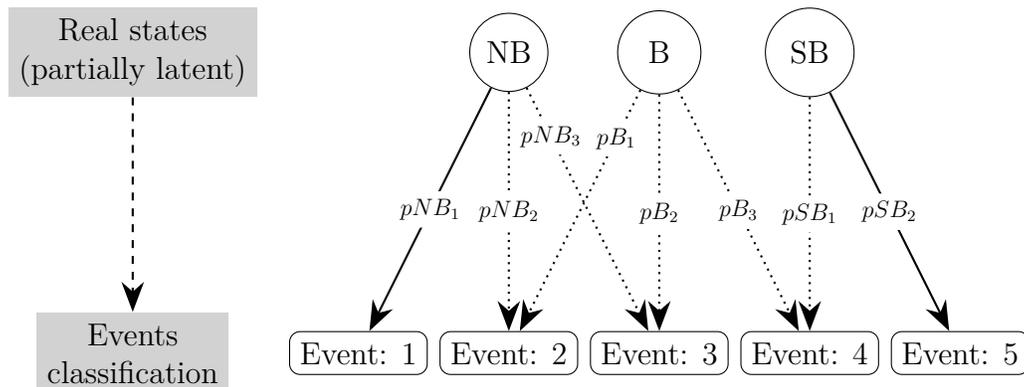


Figure B.1: **States and events relationships.** Diagram describing the hidden Markov process with probability structure for state assignment. Circles indicate real states (NB: non-breeder; B: unsuccessful Breeder; SB: Successful Breeder) and rectangular the event grades established from fieldwork observations (see Tab. B.1). Plain arrows indicate unambiguous links (event 1 and 5 correspond, respectively and exclusively to the state NB and SB) and dotted arrows the latent links. Event 2 and 3 correspond as well as state NB as B. Event 4 correspond as well as state B as SB. The assignment probability are indicated on the arrows with probability rule: $\sum_{n=1}^3 p_{NB} = \sum_{n=1}^3 p_B = \sum_{n=1}^2 p_{SB} = 1$.

event grade observed as a reference. As breeding site was of interest in this study, for individuals observed at several breeding sites during the same breeding occasion, we used as reference the site of the first breeding attempt if breeding events grades were equivalent. In other cases, we used the site with the maximum grade of breeding event. In eighteen occasions, concerning sixteen birds, no data were collected during the breeding season but only on post-breeding gathering sites. We then set these occasions to the event potential breeder outside the birth colony, because the absence of detection on the breeding site was very unlikely with a detection probability nearly equal to one (see results).

B.2 Detail on the multievent modelling

B.2.1 Hierarchical formulation

The complete data likelihood (CDL) approach allows an easy estimation of vital rates by implicitly integrating missing data in the likelihood estimation (Schofield & Barker, 2008; Schofield, Barker & MacKenzie, 2009), by modelling multi-states or multi-events as individual time-varying covariates (Schofield & Barker, 2011). The likelihood of the model can be

decomposed in five components, the detection process, the mortality process and three elements concerning state and event process, *i.e.* individual time-varying covariates (Schofield & Barker, 2011):

$$\underbrace{[Y|p, a, z^r, z_h, t1]}_{\text{Detection}} \underbrace{[a|S, t1]}_{\text{Mortality}} \underbrace{[z^r|\psi_r, t1]}_1 \underbrace{[\omega|\psi_r, \theta_r, t1]}_2 \underbrace{[z^w|\psi_w, t1]}_3 \quad (\text{B.1})$$

In this hierarchical formulation, detection process allows the estimation of the recapture probability p by defining entrance of individuals throughout the sampling process. Y is a matrix of random variables (containing the resightings of birds) given a (the matrix defining alive status) which depends of winter state z_w and reproductive state z_r . Time of entry in the study is indicated by $t1$, *i.e.* the breeding season corresponding to ringing and release. Mortality process defines when individual died (if death occurred before the end of the study). Here we used a Cormack-Jolly-Seber (CJS) formulation of the CDL for survival estimations (Cormack, 1964; Jolly, 1965; Seber, 1965), which is the product of the conditional likelihood component for survival and for capture given the time of death ($\text{Detection} \times \text{Mortality}$ in eq. B.1). The covariates z_r , corresponding to the reproductive events (component 1 in eq. B.1) were modelled as conditional on transition probability ψ_r , using an extra component noted ω (component 2 in eq. B.1) that modelled the uncertainty with parameter θ_r . Finally, covariate z_w corresponding to wintering states (component 3 in eq. B.1) was modelled conditionally to the transition probability ψ_w .

Detection process.

The data structure is a matrix Y of $n=221$ encounter histories with elements $y_{i,t}$ taking the values 1 or 0 to indicate whether or not individual i was detected during survey t , with $t \in \{1, \dots, 19\}$. The binary observations $y_{i,t}$ are modelled as independent Bernoulli random variables conditional to the availability of individual i in the population at t ,

$$y_{i,t}|a_{i,t} \sim \text{Bern}(p_{s,z,t}a_{i,t}), \quad (\text{B.2})$$

where s indicates the season (breeding or wintering) and z the individual state during this season. Detection is conditional on survival with $a_{i,t} = 0$ (individual i is ever dead or not yet

born at t) then $y_{i,t} = 0$ with probability 1, otherwise $y_{i,t}$ is a Bernoulli trial with probability $p_{s,z,t}$.

As mentioned in the main text, we explicitly account for imperfect detection by modelling encounter process as:

$$\begin{cases} \text{logit}(p_{z^r,t}) = \beta_s^p + \gamma_{z^r} + \eta_{g,t}^p, & \eta_{g,t}^p \sim N(0, \sigma_p^2), \text{ if } s=1 \text{ (breeding season),} \\ \text{logit}(p_{z^w,t}) = \beta_s^p + \gamma_{z^w} + \eta_{z^w,t}^p, & \eta_{z^w,t}^p \sim N(0, \sigma_p^2), \text{ if } s=2 \text{ (wintering season),} \end{cases} \quad (\text{B.3})$$

with a vague Normal prior $N(0, 1000)$ truncated on the interval $[-10, 10]$ for β_s , the seasonal intercept. The state dependant intercepts γ_{z^r} and γ_{z^w} were modelled with a Student-t prior $T(0, 0.16, 3)$. However, successful breeder is a particular case among of the breeder states and we modelled $\gamma_{z^r=succ.} = \gamma_{z^r=fail} + \gamma_\epsilon$ to ensure that $\gamma_{z^r=succ.} > \gamma_{z^r=fail}$. Indeed, successful breeders have a higher detection probability because they are successful at all steps of breeding (laying, incubating and chicks care) and as a consequence they spend more time at breeding site than unsuccessful ones. We also added a season-dependent random time effect (η^p) which is state dependant (z^w) during wintering season and site dependent (g) during breeding season (eq. B.3), *i.e.* we distinguish random effects at ringing sites from other sites. We modelled η^p with a half Student-t prior $T^+(0, 0.04, 3)$. As an alternative to classical vague Gamma prior we chose Student-t distributions with small degree of freedom (df=3) for computational reasons. Indeed, they are flat-tail distributions allowing more robust inference in logistic regression (Gelman *et al.*, 2008) and they place iterative weights on a range close to zero that stabilizes coefficient estimates, especially with sparse response data.

Ecological process.

The survival probability between occasion t and t + 1, as mentioned above, is considered as a part of the mortality process component of the model. We defined survival probability as a robit regression, which is the inverse function of the cumulative distribution function of the standard Student-t distribution:

$$S_{i,t} = \text{cdf}T(\text{robit}(S_{i,t}), 1/\sigma_r^2, 7), \quad \sigma_r = 1.5485, \quad (\text{B.4})$$

$$\text{robit}(S_{i,t}) = \beta_1 + \alpha * \text{age}_{i,t} + \eta_{s,i}^S, \quad \eta_{s,i}^S \sim N(0, \sigma_S^2), \quad (\text{B.5})$$

where β_1 is the intercept, α is the linear regression coefficients on age effect. We included an individual random effect $\eta_{s,i}^S$ accounting for individual heterogeneity (Cam *et al.*, 2002; Cam, Aubry & Authier, 2016), which is dependant of individual winter state. The global implementation of survival (age dependence and random individual effects) is inspired by results in chapter II, and show that survival probability in Pied Avocet is mainly driven by a negative linear age effect and by individual heterogeneity.

However, we have no a priori on the possible importance of individual heterogeneity in survival during breeding period. To investigate the relevance of adding an individual random term in the survival regression in breeding season, we used an inclusion variable. Inspired by Royle & Dorazio (2008), we multiplied the individual random term with a binary variable (wp), whose prior distribution is: $wp \sim Bern(0.5)$. If mean posterior distribution of wp is closed to one there is a strong support to keep the random term in the regression. If closed to zero, the term is not informed by the data and should be deleted.

Multi-states modelling in winter.

The CDL framework allows to treat categorical states during winter (North or South wintering area) as a covariate that is individual-specific and that can vary through time (Schofield & Barker, 2011). We used the same implementation as in chapter II for wintering states transition, *i.e.* we defined a matrix Z^w with element $z_{i,t}^w$ that takes two values, 1 if individual i is in the north of Europe at occasion t or 2 if it is in the South. Unobserved states take the value NA. The latent states $z_{i,t}^w$ are defined:

$$\begin{cases} z_{i,t}^w \sim Cat(p_{t,z}^{z^w}), & \text{if } t = \text{first winter,} \\ z_{i,t}^w \sim Cat(\psi_{z_{t-1},z_t}^{z^w}), & \text{if } t > \text{first winter,} \end{cases} \quad (\text{B.6})$$

where $Cat(\phi)$ is a categorical distribution with probability vector ϕ , ψ^{z^w} is the transition probability between the states $z_{i,t-1}^w$ and the state $z_{i,t}^w$ and $p_{t,s}^{z^w}$ is the probability of being in state z at occasion t given not born at $t-1$, *i.e.* the first transition from breeding ground to wintering site. We modelled p^{z^w} as time and state dependant and ψ^{z^w} with a Markovian process (transition between state depends only on previous state), following results in chapter I.

Multi-events modelling in breeding season.

We modelled breeding events as a covariate that is individual-specific and that can vary through time. However we need extra information to model uncertainty on real states. Thus, we defined a matrix Z^r with element $z_{i,t}^r$ that takes 6 values, 1 to 3 if individual i is in the ringing colonies at occasion t or 4 to 6 if it is outside. These three states for each breeding area corresponded to non-breeder, fail breeder and successful breeder, respectively. To cope with uncertainty we considered another matrix W with element $w_{i,t}$ that takes 10 values corresponding to the five events for each breeding area as described in Table B.1 (p. 153). Unobserved or uncertain events take the value NA. The latent events $z_{i,t}^r$ are defined:

$$\begin{cases} z_{i,t}^r \sim \text{Cat}(p_{i,z}^{z^r}), & \text{if } t = \text{first winter}, \\ z_{i,t}^r \sim \text{Cat}(\psi^{z^r}), & \text{if } t > \text{first winter}, \text{ } \text{logit}(\psi^{z^r}) = f_{z^r}(\theta_{z^r}), \\ w_{i,t} \sim \text{Cat}(p^w), \end{cases} \quad (\text{B.7})$$

where $\text{Cat}(\phi)$ is a categorical distribution with probability vector ϕ , ψ^{z^r} is the transition probability between state $z_{i,t-1}^r$ and state $z_{i,t}^r$ and $p_{i,s}^{z^r}$ is the probability of being in state z at occasion t given first wintering state at $t-1$ *i.e.*, the first transition state from wintering area to breeding area. $f_{p^{z^r}}(\theta_{z^r})$ is a specific function of parameter θ_{z^r} we tested on ψ^{z^r} . We particularly tested for age, time and previous reproductive state effects on these transitions. The probability of assignment is p_{z_{t-1},z_t}^w , the probability for an individual i to be observed in the event w at t given that he is in state z .

We included individual heterogeneity in the transition probability between breeding states ($p_{z^r,t}$) which was modelled as an individual random effect (Eq. B.3). As we were interested in the correlation between the different sources of heterogeneity, we assumed these random effects to have a multivariate normal distribution with mean 0 and a variance-covariance matrix Ω . For computational ease we used the Cholesky decomposition proposed by Chen & Dunson (2003). They suggested to factorize the variance-covariance matrix Ω into a diagonal matrix D and a lower triangular matrix L with a diagonal of 1: $\Omega = DL(LD)' = DLL'D$. Here we used a parameter expanded formulation proposed by Authier (2016, unpublished): $\Omega = AL\Delta L'A$, where $A = \text{diag}(\alpha_1, \dots, \alpha_i)$ and $\Delta = \text{diag}(\delta_1, \dots, \delta_i)$ are two diagonal matrices. To induce marginal half-t priors $T^+(0, \alpha^2, \nu)$ on the standard deviations of the random effects

(σ_i^2) we used the following priors: $\alpha \sim N^+(0, 1.5)$, $\delta \sim \Gamma^{-1}(1.5, 1.5)$ and $l \sim N(0, 4)$ the lower diagonal element of L . Correlations between sites were computed from the elements of Ω :

$$\rho_{i,j} = \frac{cov_{i,j}}{\sqrt{\sigma_i^2 \sigma_j^2}} \quad (\text{B.8})$$

where $i > j$.

Derived parameters.

A main advantage of using the CDL is that it allows direct estimation of quantities of interest, allowing in turn the easy calculation of numerous derived parameters of demographic interest. The partially latent life history matrix A can be used to compute individual lifespan as row sum of A equals lifetime history of each individual:

$$lifespan_i = \sum_{t=1}^T a_{i,t} \quad i = 1, \dots, M,$$

where T is the number of occasions and M is the total number of ringed individuals. In a similar way, it is easy to calculate the reproductive lifespan (difference between first and last reproductive attempt) or the number of reproductive attempts ('rltime') in an individual's life:

$$rltime_i = \sum_{t=1}^T a_{i,t} * r_{i,t} \quad i = 1, \dots, M \text{ with } \begin{cases} r_{i,t} = 0 \text{ if } z_{i,t}^r = 1, \\ r_{i,t} = 1 \text{ if } z_{i,t}^r \in \{2, 3\}, \end{cases}$$

where $z_{i,t}^r = 1$ is the state non-breeder for individual i at occasion t and $z_{i,t}^r \in \{2, 3\}$ corresponds to breeding states (respectively unsuccessful and successful). Then, it is possible to calculate the proportion of time devoted to reproduction along life as a ratio between reproductive lifespan and lifespan. Using reproductive and wintering states we can summarize age-related breeding attempts among recruitment stage as well as summarize their survival probabilities.

B.3 CJS code for jags

model{

```
for(i in 1:n) {
  for(j in 1:(since[i]-1)){
    a[i,j] <- 0
    ad[i,j] <- 1
  }

  for(j in since[i]:until[i]){
    # DEATH
    ad[i,j] ~ dbern(pad[i,j]) # latente death matrix
    # ALIVE
    a[i,j] <- ab[i,j]*ad[i,j] # alive matrix
  }

  # Prob for death
  pad[i,since[i]] <- 1
  for(j in (since[i]+1):until[i]){
    pad[i,j] <- ad[i,j-1]*(ab[i,j-1]*sv[i,j-1] + (1-ab[i,j-1]))
  }

  for (j in since[i]:until[i]){
    # This specifies the distribution [Y|a,p]
    Y[i,j] ~ dbern(pdets[i,j])
    pdets[i,j] <- a[i,j]*p[z[i,j],j]
  }

  # model for breeding state asignement
  for(j in f[i]:s_occ){
    obst[i,j] ~ dcat(ps[z[i,idb[j]],1:nso])
  }
}
```

```

}

# model the first transition
z[i,(since[i]+1)] ~ dcat(psi1[((since[i]+1)/2),1:nsw])

# model the breeding state
for(j in (since[i]+2):until[i]){
  z[i,j] ~ dcat(psi2[i,ida[i,j],ids[j],z[i,j-1],1:nsb])
}

sv[i,since[i]] <- 1 # all individuals survive until first winter
for(j in (since[i]+1):(until[i]-1)){
  sv[i,j] <- pt(sv.rob[i,j],0,tau.robit,7)
  sv.rob[i,j] <- beta[1] + alpha*age[i,j] +
equals(ids[j],2)*equals(z[i,j],1)*eta[i,1] +
equals(ids[j],2)*equals(z[i,j],2)*eta[i,2] +
wp*equals(ids[j],1)*eta[i,3]
}
}

# Scale parameter for the robit link
tau.robit <- pow(sigma.res,-2)
sigma.res <- 1.5485

# prior for first event (first winter)
for(j in idw){
  psi1[(j/2),1:nsw] ~ ddirch(alphaw[])
}

```

```

for(h in 1:nsw){
  # prior the values for alphaw
  alphaw[h] <- 1
}

# transition from wintering to breeding
for(i in 1:n) {
  for(j in (f[i]+1):19){
    for(h in 1:nsw){
      qpsi2[i,ida[i,(j*2)],1,h] <- exp(lpsi2[i,ida[i,(j*2)],1,h,1]) +
exp(lpsi2[i,ida[i,(j*2)],1,h,2]) + exp(lpsi2[i,ida[i,(j*2)],1,h,3]) +
exp(lpsi2[i,ida[i,(j*2)],1,h,4]) + exp(lpsi2[i,ida[i,(j*2)],1,h,5]) +
exp(lpsi2[i,ida[i,(j*2)],1,h,6])
      psi2[i,ida[i,(j*2)],1,h,1] <- exp(lpsi2[i,ida[i,(j*2)],1,h,1])/
qpsi2[i,ida[i,(j*2)],1,h]
      psi2[i,ida[i,(j*2)],1,h,2] <- exp(lpsi2[i,ida[i,(j*2)],1,h,2])/
qpsi2[i,ida[i,(j*2)],1,h]
      psi2[i,ida[i,(j*2)],1,h,3] <- exp(lpsi2[i,ida[i,(j*2)],1,h,3])/
qpsi2[i,ida[i,(j*2)],1,h]
      psi2[i,ida[i,(j*2)],1,h,4] <- exp(lpsi2[i,ida[i,(j*2)],1,h,4])/
qpsi2[i,ida[i,(j*2)],1,h]
      psi2[i,ida[i,(j*2)],1,h,5] <- exp(lpsi2[i,ida[i,(j*2)],1,h,5])/
qpsi2[i,ida[i,(j*2)],1,h]
      psi2[i,ida[i,(j*2)],1,h,6] <- exp(lpsi2[i,ida[i,(j*2)],1,h,6])/
qpsi2[i,ida[i,(j*2)],1,h]
      lpsi2[i,ida[i,(j*2)],1,h,1] <- iota[1,h] + delta[1,ida[i,(j*2)],h]
      lpsi2[i,ida[i,(j*2)],1,h,2] <- iota[2,h] + delta[2,ida[i,(j*2)],h] + eta[i,4]
      lpsi2[i,ida[i,(j*2)],1,h,3] <- iota[3,h] + delta[3,ida[i,(j*2)],h] + eta[i,4]
      lpsi2[i,ida[i,(j*2)],1,h,4] <- iota[4,h] + delta[4,ida[i,(j*2)],h]

```

```
lpsi2[i,ida[i,(j*2)],1,h,5] <- iota[5,h] + delta[5,ida[i,(j*2)],h] + eta[i,4]
lpsi2[i,ida[i,(j*2)],1,h,6] <- iota[6,h] + delta[6,ida[i,(j*2)],h] + eta[i,4]
}

# transition from breeding to wintering
for(h in 1:nsb){
  psi2[i,ida[i,(j*2)],2,h,1] <- psi3[h,1]
  psi2[i,ida[i,(j*2)],2,h,2] <- psi3[h,2]
}
}

for(j in 1:ida[i,(f[i]*2)]){
  for(h in 1:nsb){
    for(k in 1:nsb){
      psi2[i,j,1,h,k] <- 0
      psi2[i,j,2,k,h] <- 0
    }
  }
}

for(j in (f[i]+1):19){
  for(h in 3:6){
    for(k in 1:nsb){
      psi2[i,ida[i,(j*2)],1,h,k] <- 0
      psi2[i,ida[i,(j*2)],2,k,h] <- 0
    }
  }
}
}
```

```
for(h in 1:nsb){
  psi3[h,1:nsw] ~ ddirch(alphaw[])
}

# specifies the values for alphab in the prior for psi2
for(h in 1:nsb){
  alphab[h] <- 1
}

# state assignement
ps[1,1:3] ~ ddirch(alphas[])
ps[2,2:4] ~ ddirch(alphas[])
ps[3,4:5] ~ ddirch(alphasb[])
ps[4,6:8] ~ ddirch(alphas[])
ps[5,7:9] ~ ddirch(alphas[])
ps[6,9:10] ~ ddirch(alphasb[])

for(h in 1:5){
  ps[1,(h+5)] <- 0
  ps[2,(h+5)] <- 0
  ps[3,(h+5)] <- 0
  ps[4,h] <- 0
  ps[5,h] <- 0
  ps[6,h] <- 0
}

ps[1,4] <- 0
ps[1,5] <- 0
```

```
ps[2,1] <- 0
ps[2,5] <- 0
ps[3,1] <- 0
ps[3,2] <- 0
ps[3,3] <- 0
ps[4,9] <- 0
ps[4,10] <- 0
ps[5,6] <- 0
ps[5,10] <- 0
ps[6,6] <- 0
ps[6,7] <- 0
ps[6,8] <- 0

# specifies the values for alphas in the prior for ps
for(h in 1:3){
  alphas[h] <- 1
}

for(h in 1:2){
  alphasb[h] <- 1
}

# detection
for(j in idw){
  logit(p[1,j]) <- beta[2] + gamma[1] + etap[1,j]
  p[3,j] <- 0
  p[4,j] <- 0
  p[5,j] <- 0
  p[6,j] <- 0
}
```

```
}

for(j in idw[1:3]){
  logit(p[2,j]) <- beta[2] + gamma[2] + etap[2,j]
}

for(j in idw[4:9]){
  p[2,j] <- 0
}

for(j in idw[10:s_occ]){
  logit(p[2,j]) <- beta[2] + gamma[2] + etap[2,j]
}

for(j in idb){
  logit(p[1,j]) <- beta[3] + gamma[3] + etap[1,j]
  logit(p[2,j]) <- beta[3] + gamma[4] + etap[1,j]
  logit(p[3,j]) <- beta[3] + gamma[4] + gamma[7] + etap[1,j]
  logit(p[4,j]) <- beta[3] + gamma[5] + etap[2,j]
  logit(p[5,j]) <- beta[3] + gamma[6] + etap[2,j]
  logit(p[6,j]) <- beta[3] + gamma[6] + gamma[8] + etap[2,j]
}

# priors
alpha ~ dt(0,0.16,3)

for(i in 1:3){
  beta[i] ~ dnorm(0,0.001)T(-10,10)
}
```

```
for(i in 1:6){
  gamma[i] ~ dt(0,0.16,3)
}

for(i in 7:8){
  gamma[i] ~ dt(0,0.16,3)T(0.0,)
}

for(i in 1:nsb){
  delta[i,1,1] <- 0
  delta[i,1,2] <- 0
  for(j in 2:s_occ){
    for(h in 1:nsw){
      delta[i,j,h] ~ dt(0,0.16,3)
    }
  }
}

iota[1,1] <- 0
iota[1,2] <- 0

for(i in 2:6){
  for(h in 1:2){
    iota[i,h] ~ dnorm(0,0.001)T(-10,10)
  }
}

wp ~ dbern(0.5)
```

```
# Choleski decomposition (with priors) for correlation between survival
#and breeding indivisual heterogeneity
for (i in 1:4) {
  A[i,i] ~ dnorm(0.0, 1.5)T(0.0,)
  Delta[i,i] <- 1/tau[i]
  tau[i] ~ dgamma(1.5, 1.5)
  L[i,i] <- 1.0
}

for (i in 1:3) {
  for (k in (i+1):4) {
    L[i,k] <- 0.0
    A[i,k] <- 0.0
    Delta[i,k] <- 0.0
    L[k,i] ~ dnorm(0.0, 4.0)
    A[k,i] <- 0.0
    Delta[k,i] <- 0.0
  }
}

# covariance matrix
Omega <- A%*%L%*%Delta%*%t(L)%*%A

# random effects: multivariate normal
for(i in 1:n){
  eta[i,1] <- A[1,1]*(L[1,1]*xi[i,1])
  eta[i,2] <- A[2,2]*(L[2,1]*xi[i,1] + L[2,2]*xi[i,2])
  eta[i,3] <- A[3,3]*(L[3,1]*xi[i,1] + L[3,2]*xi[i,2] + L[3,3]*xi[i,3])
}
```

```
    eta[i,4] <- A[4,4]*(L[4,1]*xi[i,1] + L[4,2]*xi[i,2] + L[4,3]*xi[i,3] +  
L[4,4]*xi[i,4])  
  }
```

```
for(i in 1:n){  
  for(j in 1:4){  
    xi[i,j] ~ dnorm(0.0, tau[j])  
  }  
}
```

```
# Covariances
```

```
cov[1] <- Omega[2,1]  
cov[2] <- Omega[3,1]  
cov[3] <- Omega[3,2]  
cov[4] <- Omega[4,1]  
cov[5] <- Omega[4,2]  
cov[6] <- Omega[4,3]
```

```
# Correlations
```

```
rho[1] <- Omega[2,1]/pow(Omega[1,1]*Omega[2,2],0.5)  
rho[2] <- Omega[3,1]/pow(Omega[1,1]*Omega[3,3],0.5)  
rho[3] <- Omega[3,2]/pow(Omega[2,2]*Omega[3,3],0.5)  
rho[4] <- Omega[4,1]/pow(Omega[1,1]*Omega[4,4],0.5)  
rho[5] <- Omega[4,2]/pow(Omega[2,2]*Omega[4,4],0.5)  
rho[6] <- Omega[4,3]/pow(Omega[3,3]*Omega[4,4],0.5)
```

```
for(h in 1:2){  
  taupb[h] <- 1/sdpb[h]/sdpb[h]
```

```
sdpb[h] ~ dt(0,0.04,3)T(0,)
taupw[h] <- 1/sdpw[h]/sdpw[h]
sdpw[h] ~ dt(0,0.04,3)T(0,)
}

for(j in idb){
  for(h in 1:2){
    etap[h,j] ~ dnorm(0,taupb[h])
  }
}

for(j in idw){
  for(h in 1:2){
    etap[h,j] ~ dnorm(0,taupw[h])
  }
}

### Computation of lifespan for all individuals
for (i in 1:n) {
  lspan[i] <- sum(a[i,(since[i]+1):n_occ])/2
}

### Computation of cumulative reproductive attempt by age (derived quantities)
for(i in idn2){
  for (j in 1:s_occ){
    rl[i,j] <- 0
    acrl[i,j] <- 0
    acrln[i,j] <- 0
    acrls[i,j] <- 0
  }
}
```

```
    acrl1[i,j] <- 0
    acrl2[i,j] <- 0
    acrl3[i,j] <- 0
    newa[i,j] <- 0
    newan[i,j] <- 0
    newas[i,j] <- 0
    newa1[i,j] <- 0
    newa2[i,j] <- 0
    newa3[i,j] <- 0
  }

  for(j in 1:(until[i]-1)){
    sv1[i,j] <- 0
    sv2[i,j] <- 0
    sv3[i,j] <- 0
    newas1[i,j] <- 0
    newas2[i,j] <- 0
    newas3[i,j] <- 0
  }
}

for(i in idn){
  fw[i] <- z[i,idw[f[i]]] # individual state at first winter
  for (j in 1:f[i]){
    r1[i,j] <- 0
    r12[i,j] <- 0
    r13[i,j] <- 20
  }
  for(j in (f[i]+1):s_occ){
```

```
    rl[i,j] <- equals(a[i,idb[j]]*z[i,idb[j]],2) +
equals(a[i,idb[j]]*z[i,idb[j]],3) +
equals(a[i,idb[j]]*z[i,idb[j]],5) +
equals(a[i,idb[j]]*z[i,idb[j]],6)
    rl2[i,j] <- rl[i,j]*j
    rl3[i,j] <- ifelse(rl[i,j]==0, 20, rl2[i,j])
    acrl[i,(j-f[i])] <- ifelse(a[i,idb[j]]==1,sum(rl[i,1:j]),0)
    acrln[i,(j-f[i])] <- acrl[i,(j-f[i])]*equals(fw[i],1)
    acrls[i,(j-f[i])] <- acrl[i,(j-f[i])]*equals(fw[i],2)
    newa[i,(j-f[i])] <- a[i,idb[j]]
    newan[i,(j-f[i])] <- newa[i,(j-f[i])]*equals(fw[i],1)
    newas[i,(j-f[i])] <- newa[i,(j-f[i])]*equals(fw[i],2)
}

for(j in since[i):(until[i]-1)){
    sv1[i,(j-since[i]+1)] <- sv[i,j]*a[i,j]*equals(fbreed[i],1)
    sv2[i,(j-since[i]+1)] <- sv[i,j]*a[i,j]*equals(fbreed[i],2)
    sv3[i,(j-since[i]+1)] <- sv[i,j]*a[i,j]*equals(fbreed[i],3)
    newas1[i,(j-since[i]+1)] <- a[i,j]*equals(fbreed[i],1)
    newas2[i,(j-since[i]+1)] <- a[i,j]*equals(fbreed[i],2)
    newas3[i,(j-since[i]+1)] <- a[i,j]*equals(fbreed[i],3)
}

for(j in (until[i]-since[i]+1):(until[i]-1)){
    sv1[i,j] <- 0
    sv2[i,j] <- 0
    sv3[i,j] <- 0
    newas1[i,j] <- 0
    newas2[i,j] <- 0
```

```

    newas3[i,j] <- 0
  }

  for(j in (s_occ+1-f[i]):s_occ){
    acrl[i,j] <- 0
    acrln[i,j] <- 0
    acrls[i,j] <- 0
    acrl1[i,j] <- 0
    acrl2[i,j] <- 0
    acrl3[i,j] <- 0
    newa[i,j] <- 0
    newan[i,j] <- 0
    newas[i,j] <- 0
    newa1[i,j] <- 0
    newa2[i,j] <- 0
    newa3[i,j] <- 0
  }

  # computation of reproductive lifetime, reproductive lifespan, and
  #first breeding attempt indice
  rltime[i] <- sum(rl[i,])
  fbreed[i] <- ifelse(min(rl3[i,])==20,0,min(rl3[i,]))-f[i]
  rlspan[i] <- max(rl2[i,]) - ifelse(min(rl3[i,])==20,
(max(rl2[i,])+1),min(rl3[i,]))) + 1
  qrlspan[i] <- rlspan[i]/lspan[i]
  qrltime[i] <- rltime[i]/ifelse(rlspan[i]<1,1,rlspan[i])

  for(j in (f[i]+1):s_occ){
    acrl1[i,(j-f[i])] <- acrl[i,(j-f[i])]*equals(fbreed[i],1)
    acrl2[i,(j-f[i])] <- acrl[i,(j-f[i])]*equals(fbreed[i],2)

```

```
    acrl3[i,(j-f[i])] <- acrl[i,(j-f[i])]*equals(fbreed[i],3)
    newa1[i,(j-f[i])] <- newa[i,(j-f[i])]*equals(fbreed[i],1)
    newa2[i,(j-f[i])] <- newa[i,(j-f[i])]*equals(fbreed[i],2)
    newa3[i,(j-f[i])] <- newa[i,(j-f[i])]*equals(fbreed[i],3)
  }
}
for(j in 1:(s_occ-1)){
  arlt[j] <- sum(acrl[,j])/sum(newa[,j])
  arltn[j] <- sum(acrln[,j])/ifelse(sum(newan[,j])==0,1,sum(newan[,j]))
  arlts[j] <- sum(acrls[,j])/ifelse(sum(newas[,j])==0,1,sum(newas[,j]))
  arlt1[j] <- sum(acrl1[,j])/ifelse(sum(newa1[,j])==0,1,sum(newa1[,j]))
  arlt2[j] <- sum(acrl2[,j])/ifelse(sum(newa2[,j])==0,1,sum(newa2[,j]))
  arlt3[j] <- sum(acrl3[,j])/ifelse(sum(newa3[,j])==0,1,sum(newa3[,j]))
}

for(j in 1:(n_occ-1)){
  svg1[j] <- sum(sv1[,j])/ifelse(sum(newas1[,j])==0,1,sum(newas1[,j]))
  svg2[j] <- sum(sv2[,j])/ifelse(sum(newas2[,j])==0,1,sum(newas2[,j]))
  svg3[j] <- sum(sv3[,j])/ifelse(sum(newas3[,j])==0,1,sum(newas3[,j]))
}
}
```

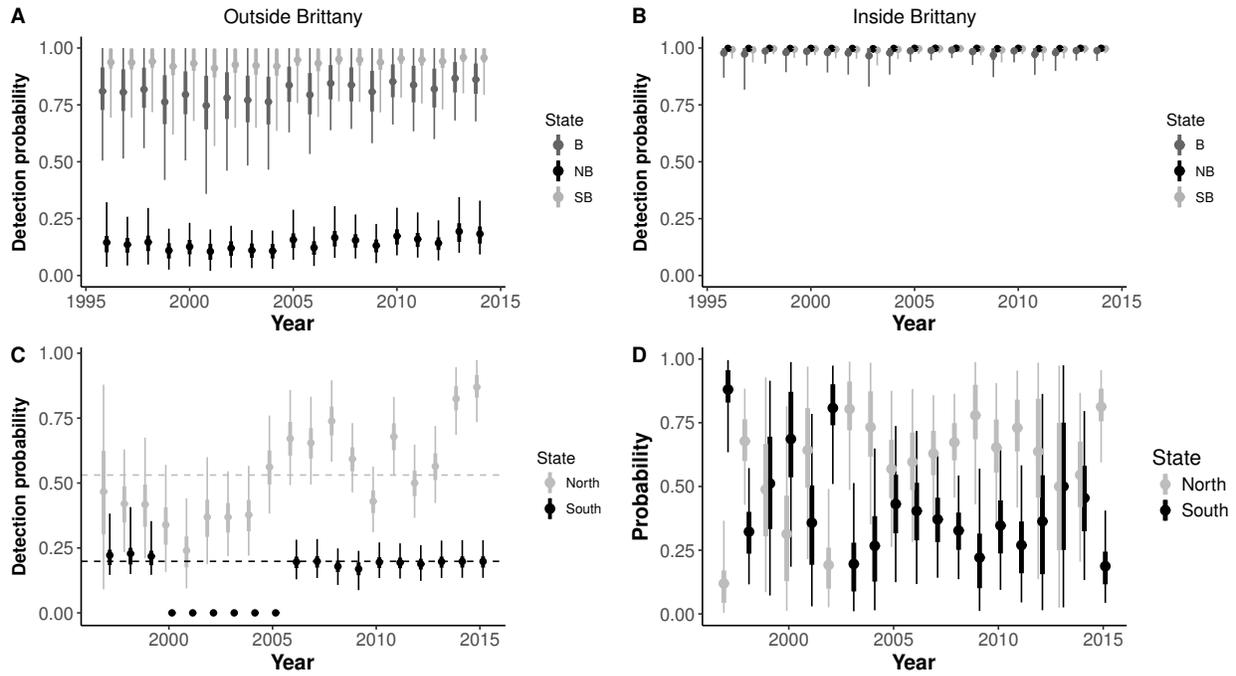


Figure B.2: **Seasonal estimations of detection probability and choice of first winter location.** Annual detection probability of Pied Avocets during breeding season both outside Brittany (panel A) and inside (panel B) according to breeding state (B: unsuccessful breeder; NB: non breeder, SB: successful breeder). Annual detection probability of Pied Avocets during winter according to winter state (North or South wintering, panel C). Annual probability of first winter area choice (North or South, panel D).

B.4 Additional results

B.4.1 Detection Probability

B.4.2 Seasonal transitions

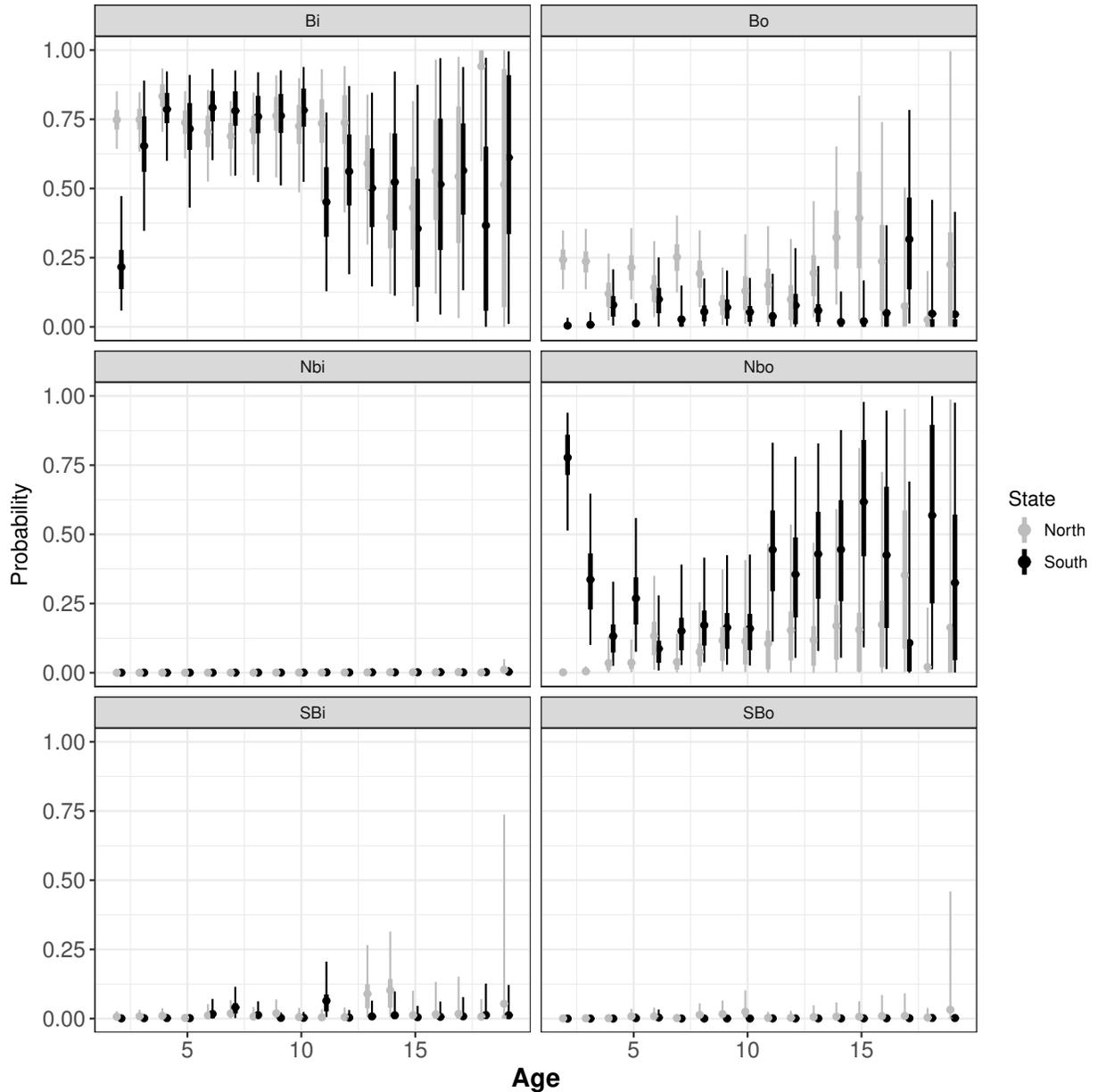


Figure B.3: **Seasonal transition probability from winter state to breeding state.** Age dependant transition probability from winter state to breeding state. Bi: unsuccessful breeder in Brittany; Nbi: non breeder in Brittany, Sbi: successful breeder in Brittany; Bo: unsuccessful breeder outside Brittany; NBo: non breeder outside Brittany, SBo: successful breeder outside Brittany..

B.4.3 Vital rate correlation

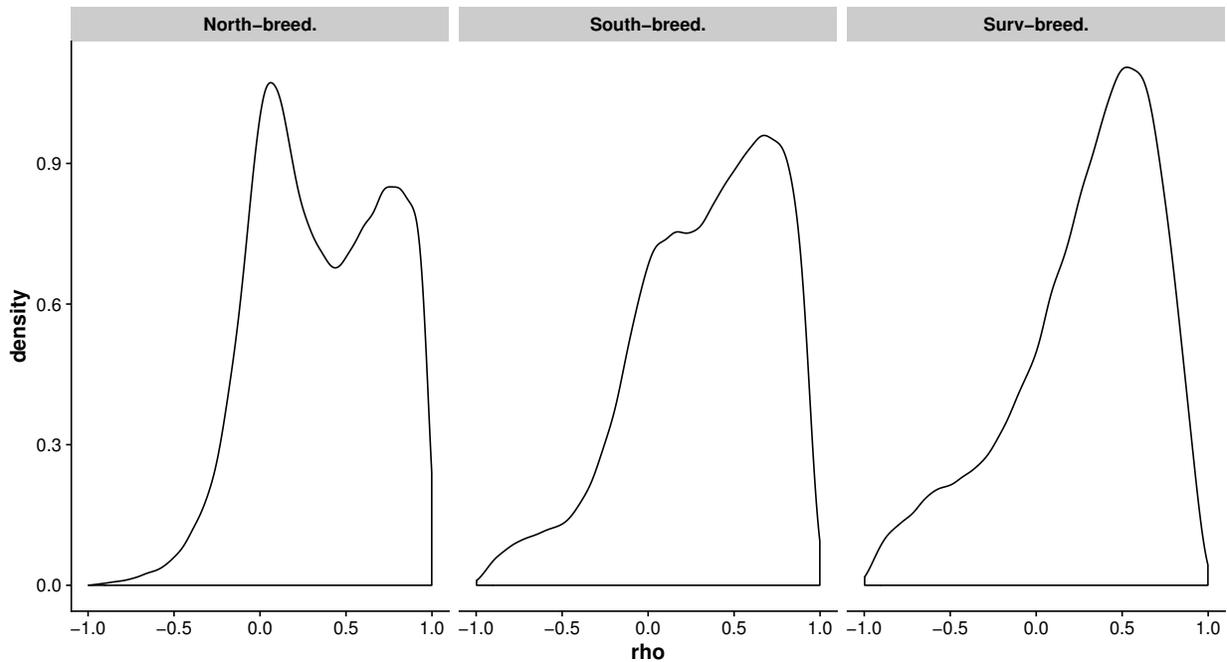


Figure B.4: **Correlation between individual heterogeneity in vital rates.** Correlation between reproductive heterogeneity and survival heterogeneity in winter for North wintering individuals (left panel). Correlation between reproductive heterogeneity and survival heterogeneity in winter for South wintering individuals (middle panel). Correlation between reproductive heterogeneity and survival heterogeneity during breeding season (right panel). See summary statistics in table B.2.

Correlation	Mean	Quantile		$p(r > 0)$
		2.5%	97.5%	
North-Breeding	0.33	-0.65	0.91	0.79
South-Breeding	0.35	-0.34	0.95	0.81
Surv.-Breeding	0.28	-0.74	0.87	0.77

Table B.2: **Summary of posterior distribution of the correlations between heterogeneity in vital rates, see in Fig. B.4.**

B.4.4 Summaries of posterior distribution

Here we display the posterior density of the parameters estimated with the model whose code is give above (p. 159) using Markov chain Monte Carlo simulation.

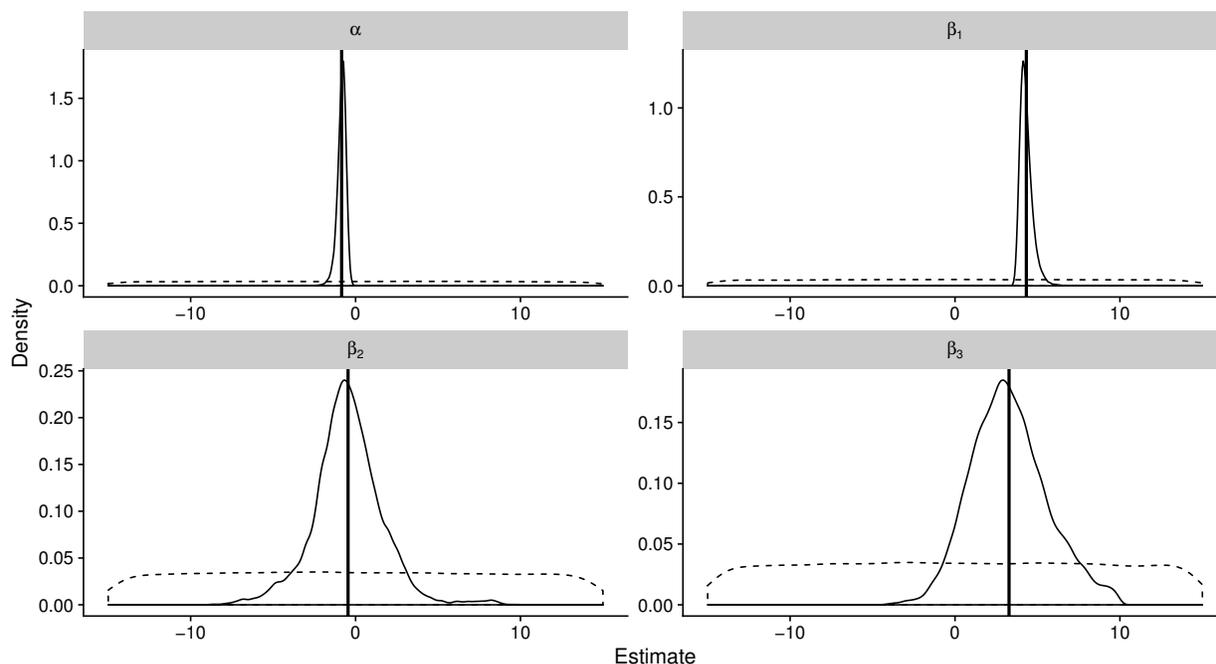


Figure B.5: **Posterior distribution of different parameters.** Density of posterior distributions shown on the robit scale: α is the trend age parameter of adult survival regression with mean -0.85 (BCI: -1.48,-0.40); β_1 is the intercept of the juvenile survival with mean 4.32 (BCI: 3.76, 5.29). Density of posterior distributions shown on the logit scale: β_2 is the intercept of the detection probability during winter with mean -0.46 (BCI: -4.88, 3.8); β_3 is the intercept of the detection probability during breeding period with mean 3.28 (BCI: -0.89, 8.32). Mean value is indicated with a vertical line and prior distribution in dashed line.

Parameter	Effect	Mean	Quantile	
			2.5%	97.5%
γ_1	North	0.62	-3.59	5.08
γ_2	South	-0.96	-5.26	3.44
γ_3	Nbi	5.97	-0.15	18.65
γ_4	Bi	2.69	-2.86	11.9
γ_5	Nbo	-5.16	-10.21	-0.99
γ_6	Bo	-1.19	-7.01	4.26
γ_7	Sbi	2.72	0.08	10.46
γ_8	Sbo	2.58	0.07	10.1

Table B.3: **Parameter estimates.** Mean and BCI are given for each parameter for which the effect is specified. γ_1 and γ_2 are the effect of wintering states on detection probability, *i.e.* wintering in North or South area, respectively. γ_3 to γ_6 are the breeding state effect on detection. γ_7 and γ_8 are positive definite effect corresponding to successful breeding state inside or outside Brittany respectively. For density of posterior distribution see Fig. B.6

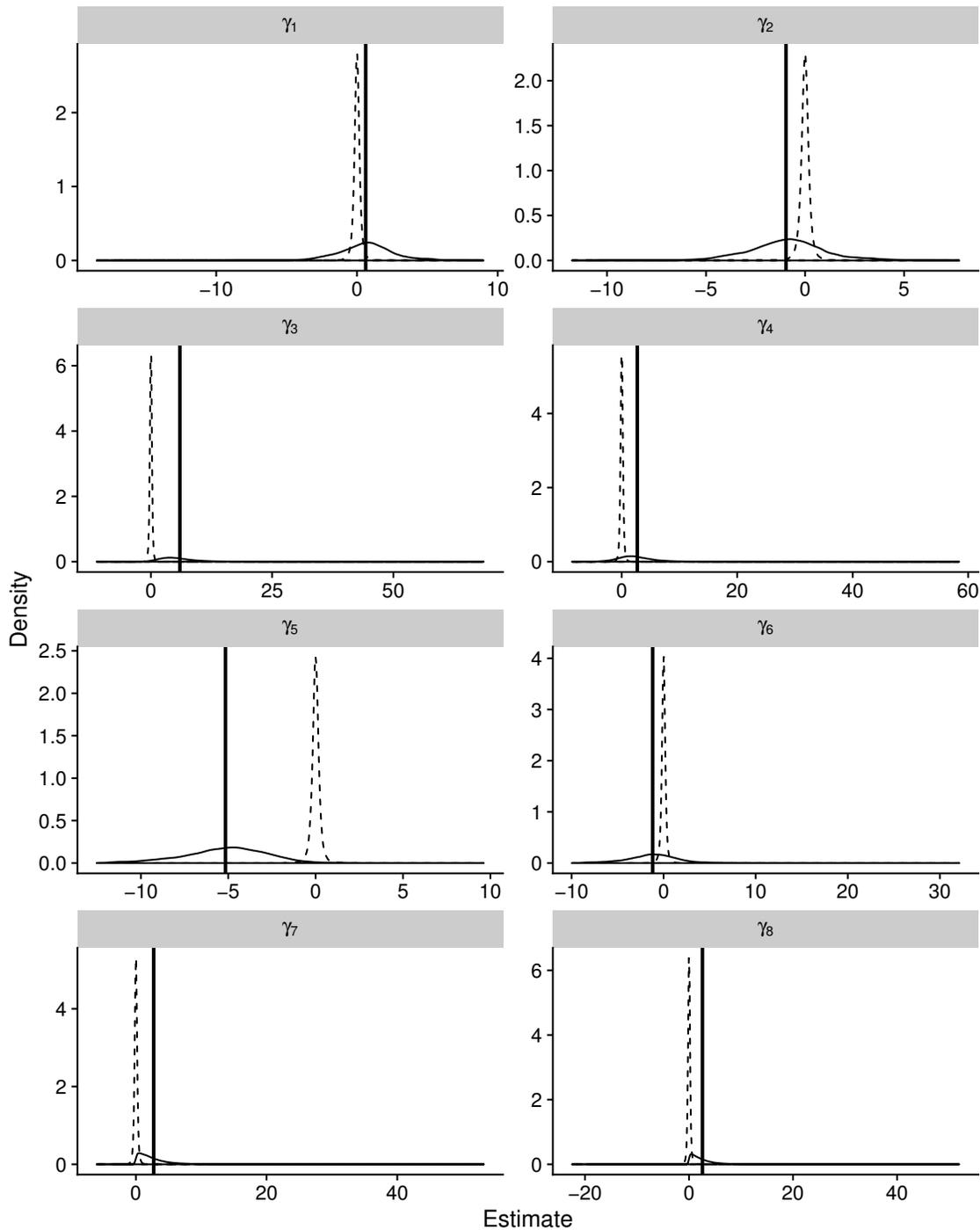


Figure B.6: **Posterior distribution of parameter γ .** γ_1 and γ_2 are the effect of wintering states on detection probability, *i.e.* wintering in North or South area, respectively. γ_3 to γ_6 are the breeding state effect on detection. γ_7 and γ_8 are positive definite effect corresponding to successful breeding state inside or outside Brittany respectively. See mean values and BCI in table B.3. Density of posterior distributions are shown on the logit scale. Mean value is indicated with a vertical line and prior distribution in dashed line.

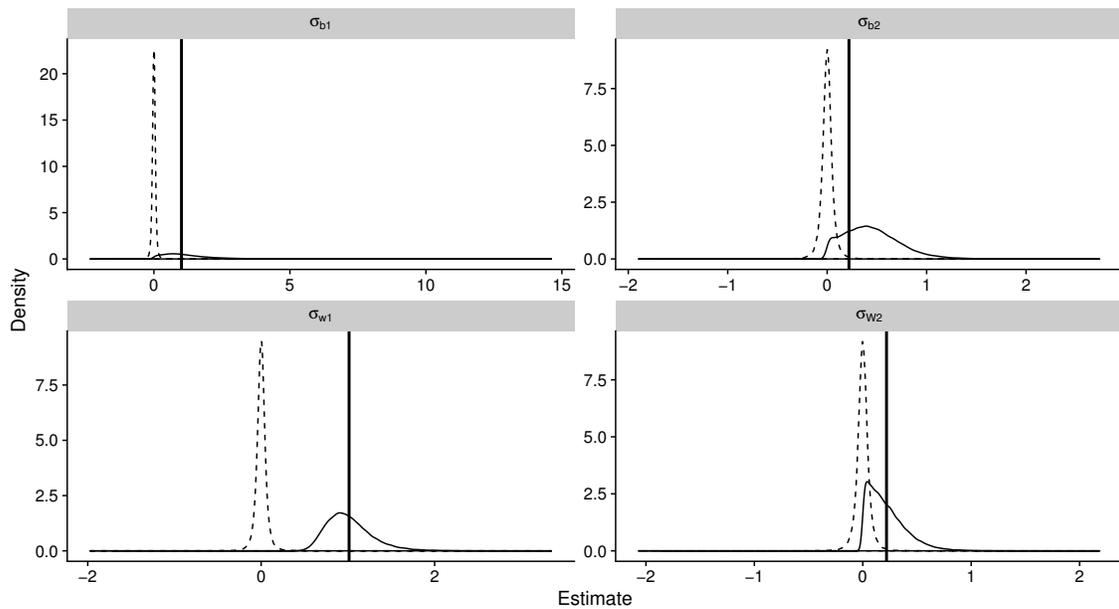


Figure B.7: **Posterior distribution of parameter σ .** σ_{b1} is the standard deviation of the random time effect in detection probability inside Brittany, with mean 1.01 (BCI: 0.61, 1.64). σ_{b2} is the standard deviation of the random time effect in detection probability outside Brittany, with mean 0.22 (BCI: 0.01, 0.65). σ_{w1} is the standard deviation of the random time effect in detection probability in the North during winter, with mean 1.24 (BCI: 0.05, 3.48). σ_{w2} is the standard deviation of the random time effect in detection probability in the South during winter, with mean 0.44 (BCI: 0.02, 1.09). Mean value is indicated with a vertical line and prior distribution in dashed line.

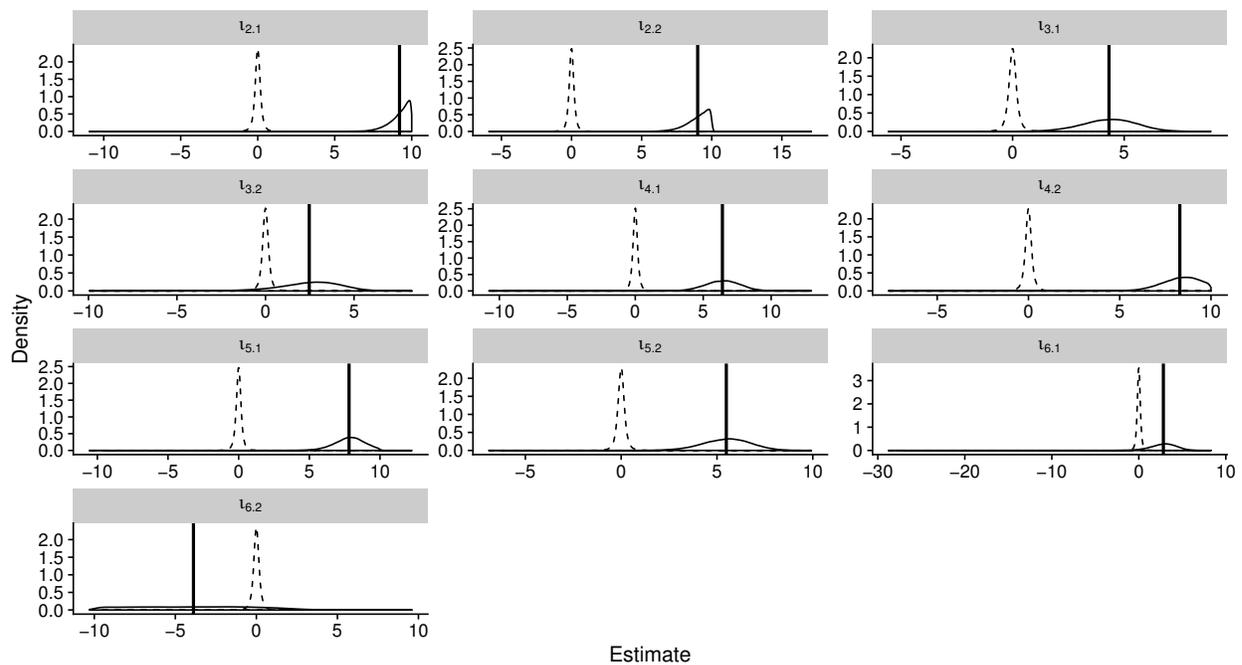


Figure B.8: **Posterior distribution of parameter l .** $l_{g,w}$ correspond to the effect of wintering states w on transition toward breeding state g . $w = 1$ correspond to the North wintering area and $w = 2$ correspond to the South wintering area. $g \in \{2, 3\}$ correspond to state unsuccessful breeder and successful breeder in Brittany, respectively. $g \in \{5, 6\}$ correspond to state unsuccessful breeder and successful breeder outside Brittany, respectively. Mean value is indicated with a vertical line and prior distribution in dashed line.

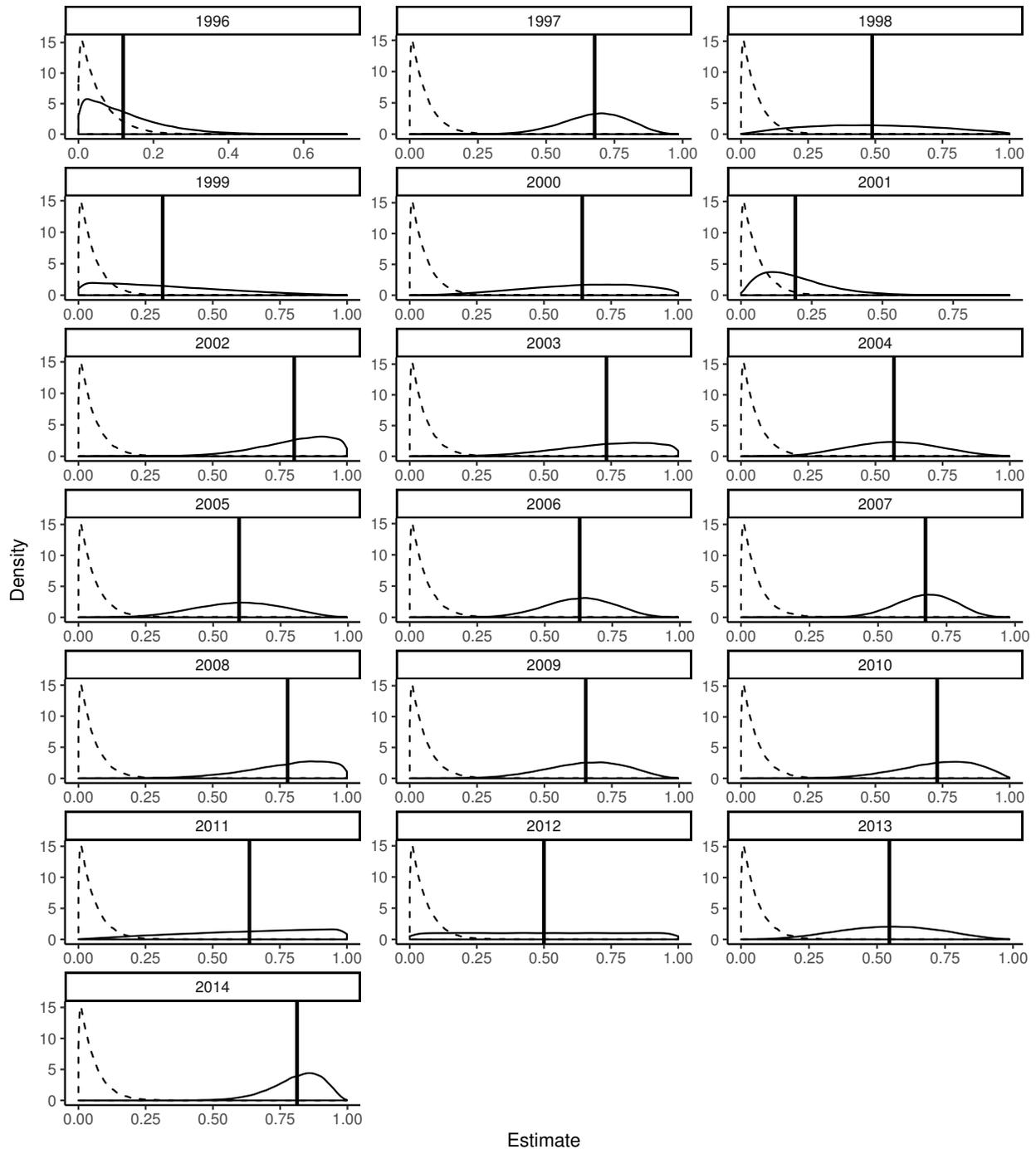


Figure B.9: **Annual posterior distribution of resident frequency during the first winter.** In 2012, there was no bird ringed, parameter is then not identifiable. Mean value is indicated with a vertical line and prior distribution in dashed line.

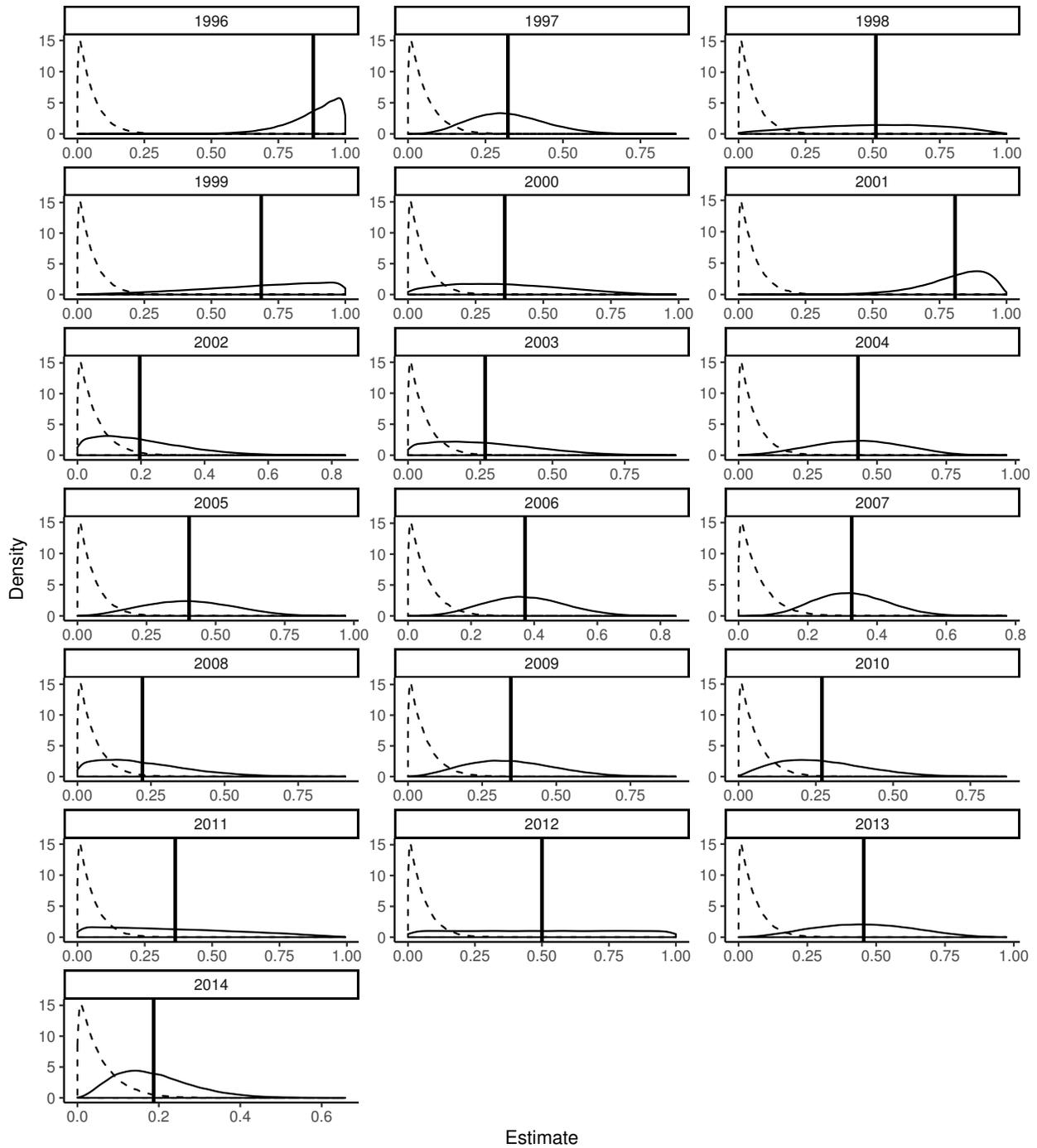


Figure B.10: **Annual posterior distribution of migrant frequency during the first winter.** In 2012, there was no bird ringed, parameter is then not identifiable. Mean value is indicated with a vertical line and prior distribution in dashed line.

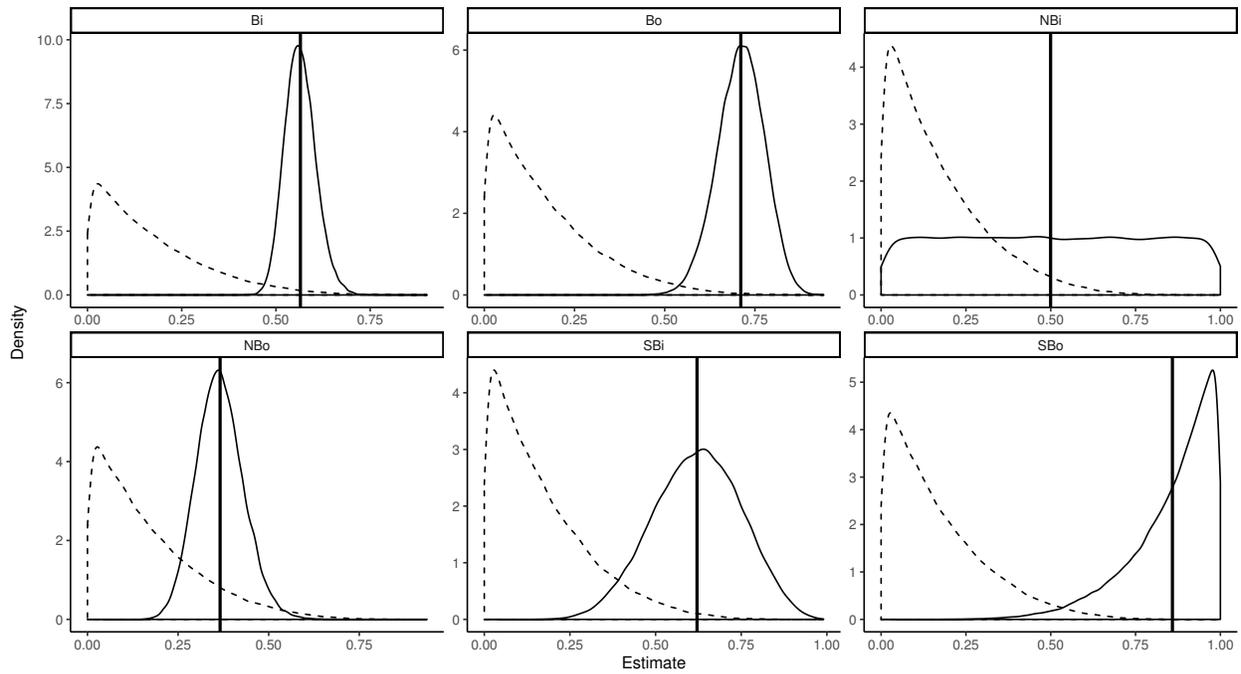


Figure B.11: **Posterior distribution of fall transition probabilities for residents.** Bi: unsuccessful breeder inside Brittany; Bo: unsuccessful breeder outside Brittany; NBi: non-breeder inside Brittany; NBo: non-breeder outside Brittany; SBi: successful breeder inside Brittany; SBo: successful breeder outside Brittany. Mean value is indicated with a vertical line and prior distribution in dashed line.

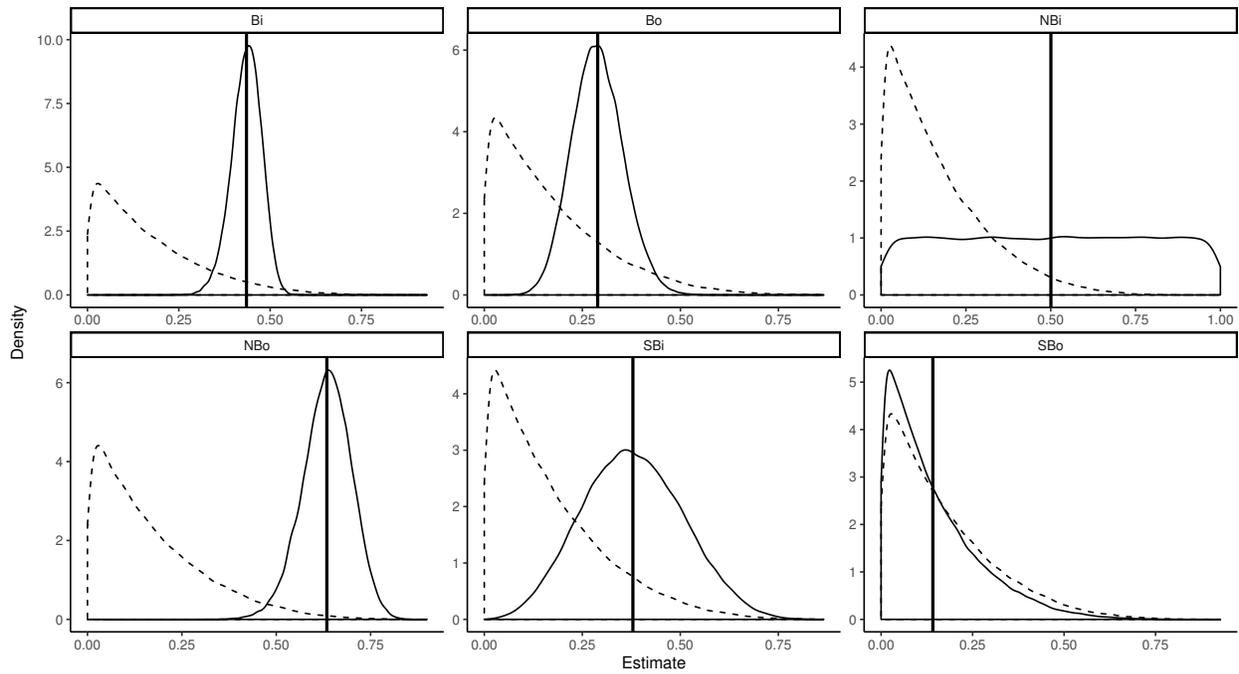


Figure B.12: **Posterior distribution of fall transition probabilities for migrants.** Bi: unsuccessful breeder inside Brittany; Bo: unsuccessful breeder outside Brittany; NBi: non-breeder inside Brittany; NBo: non-breeder outside Brittany; SBi: successful breeder inside Brittany; SBo: successful breeder outside Brittany. Mean value is indicated with a vertical line and prior distribution in dashed line.

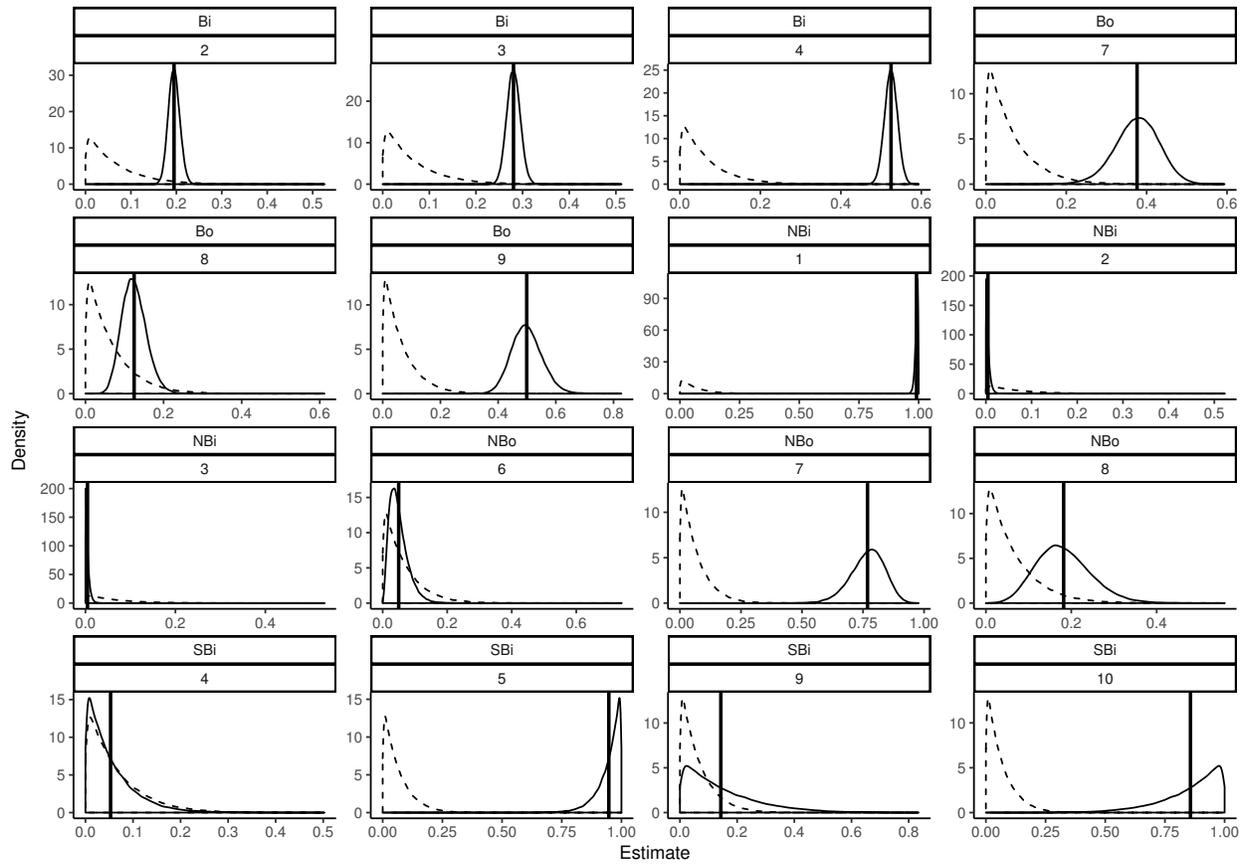


Figure B.13: **Posterior distribution of assignment probabilities.** 1:10: event from observation in the field. Bi: unsuccessful breeder inside Brittany; Bo: unsuccessful breeder outside Brittany; NBo: non-breeder inside Brittany; NBo: non-breeder outside Brittany; SBo: successful breeder inside Brittany; SBo: successful breeder outside Brittany. Mean value is indicated with a vertical line and prior distribution in dashed line.

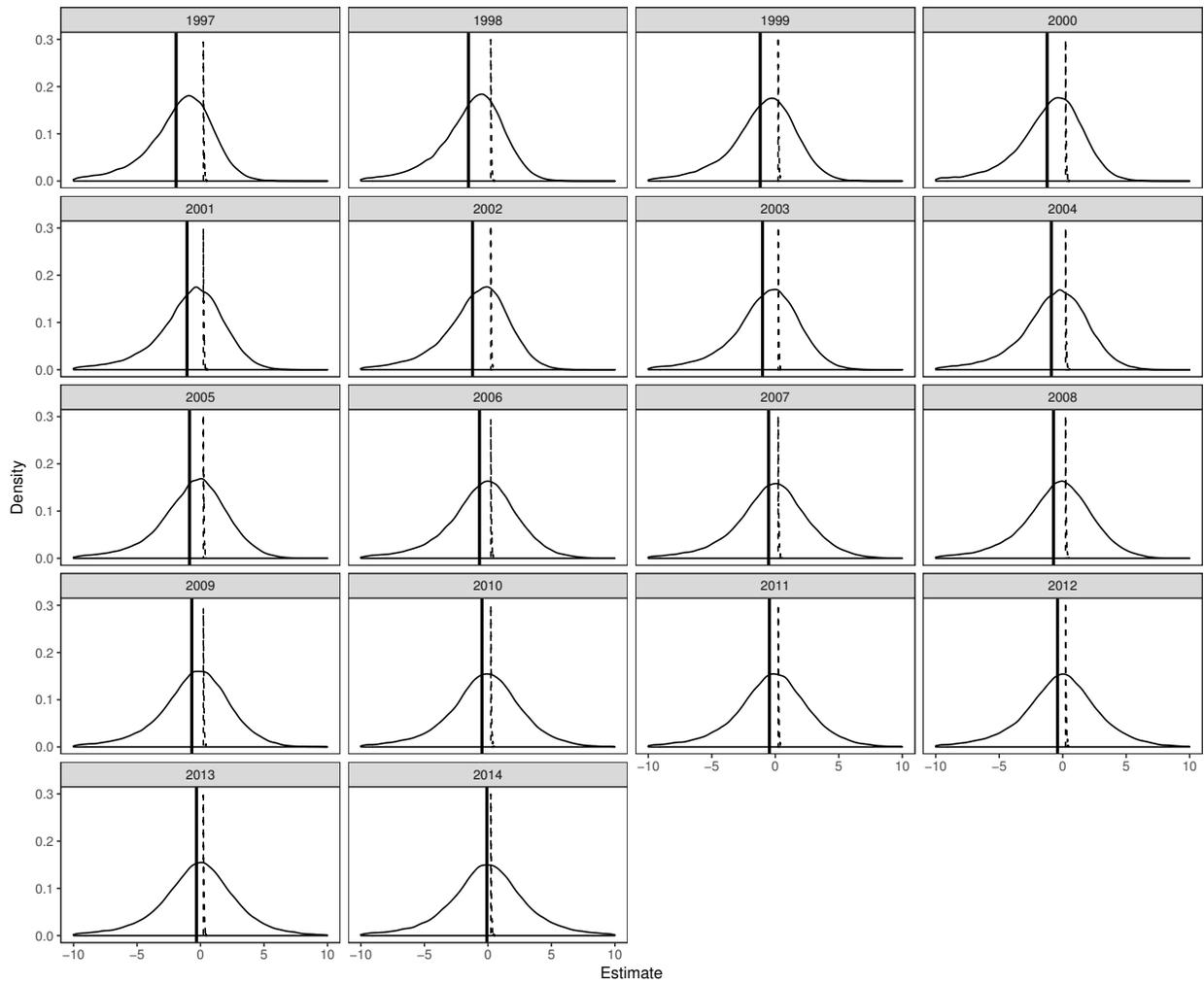


Figure B.14: **Posterior distribution of the age effect on transition probability from non-breeding state inside Brittany for resident.** Mean value is indicated with a vertical line and prior distribution in dashed line.

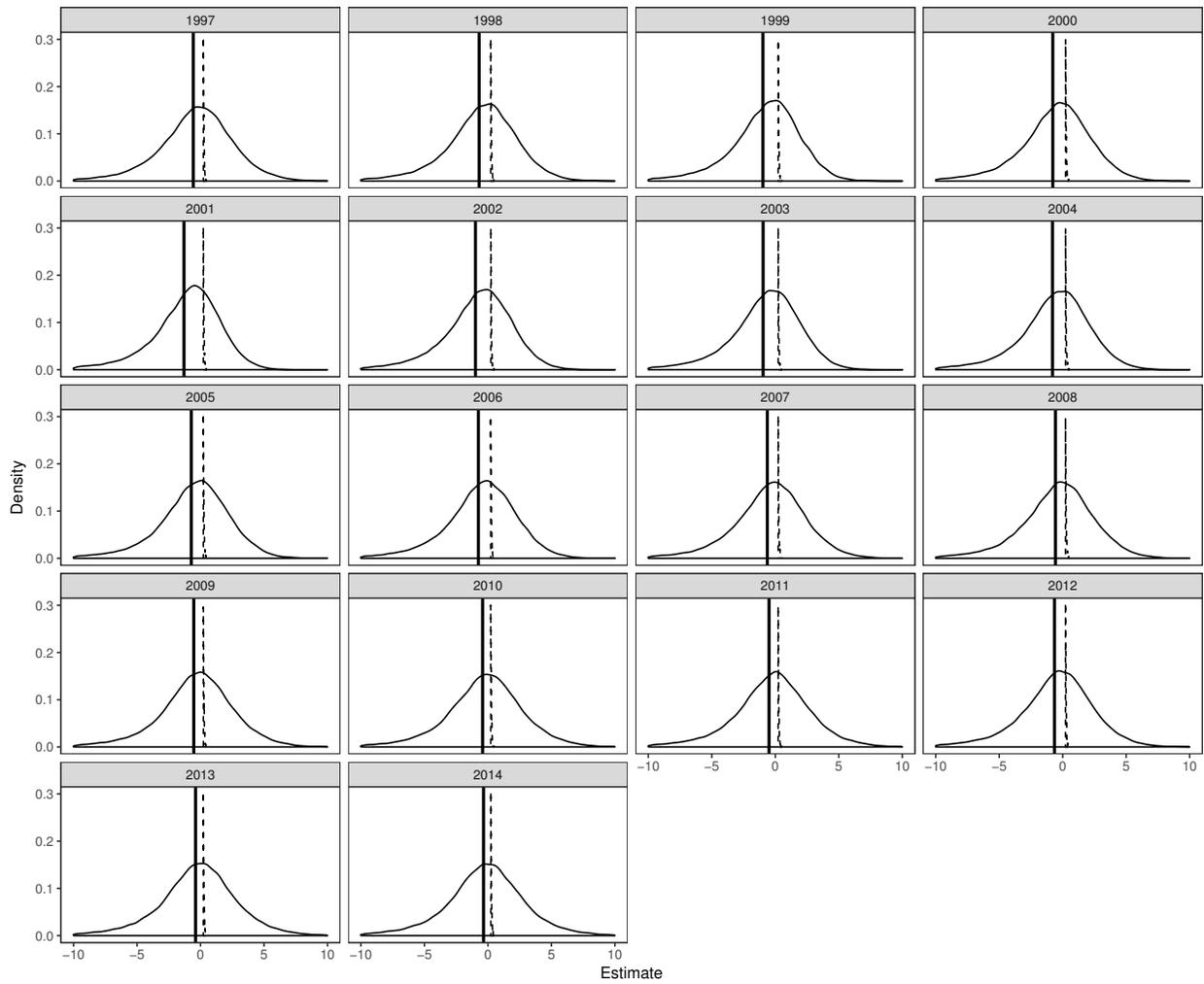


Figure B.15: **Posterior distribution of the age effect on transition probability from non-breeding state inside Brittany for migrant.** Mean value is indicated with a vertical line and prior distribution in dashed line.

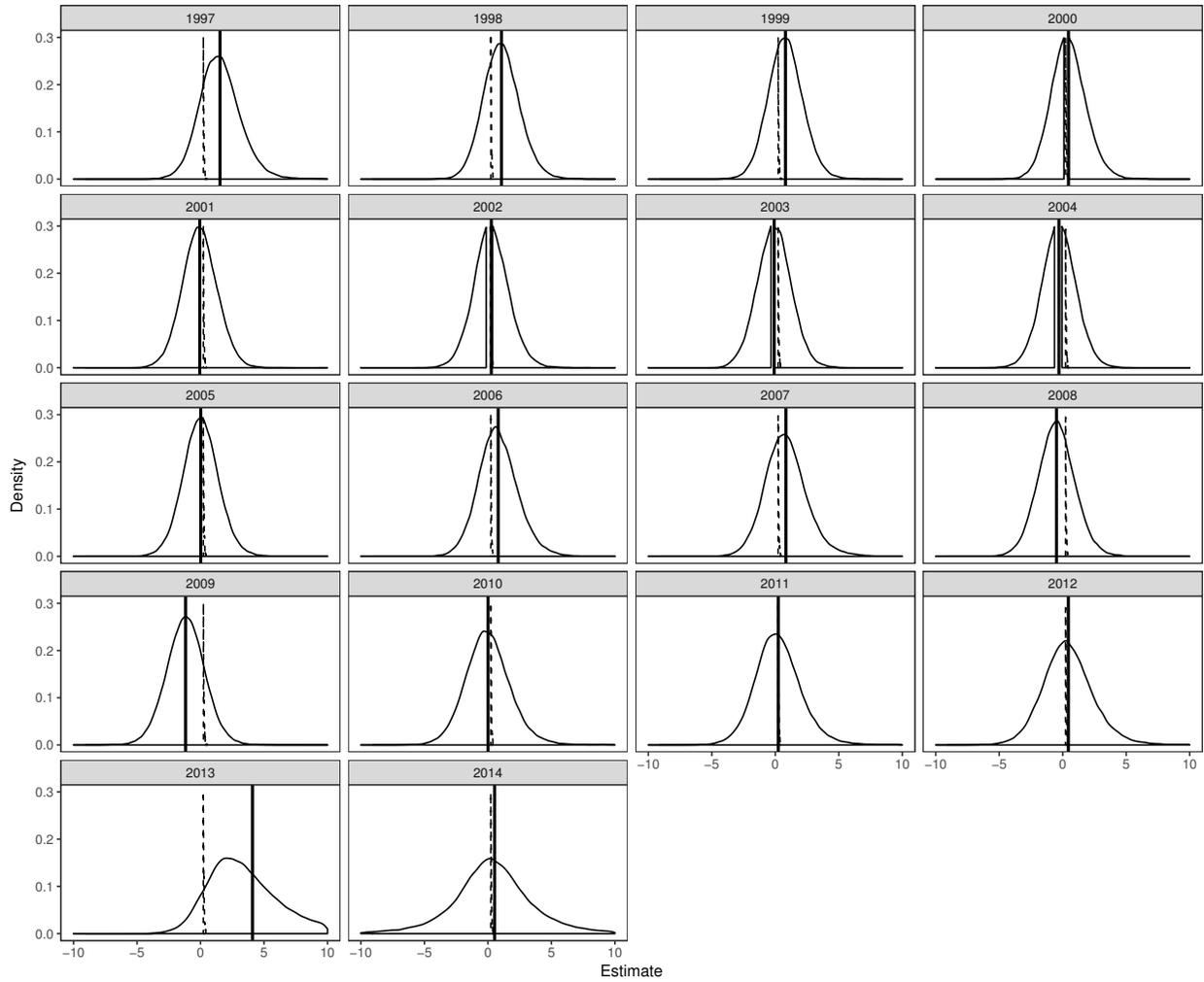


Figure B.16: **Posterior distribution of the age effect on transition probability from unsuccessful breeding state inside Brittany for resident.** Mean value is indicated with a vertical line and prior distribution in dashed line.

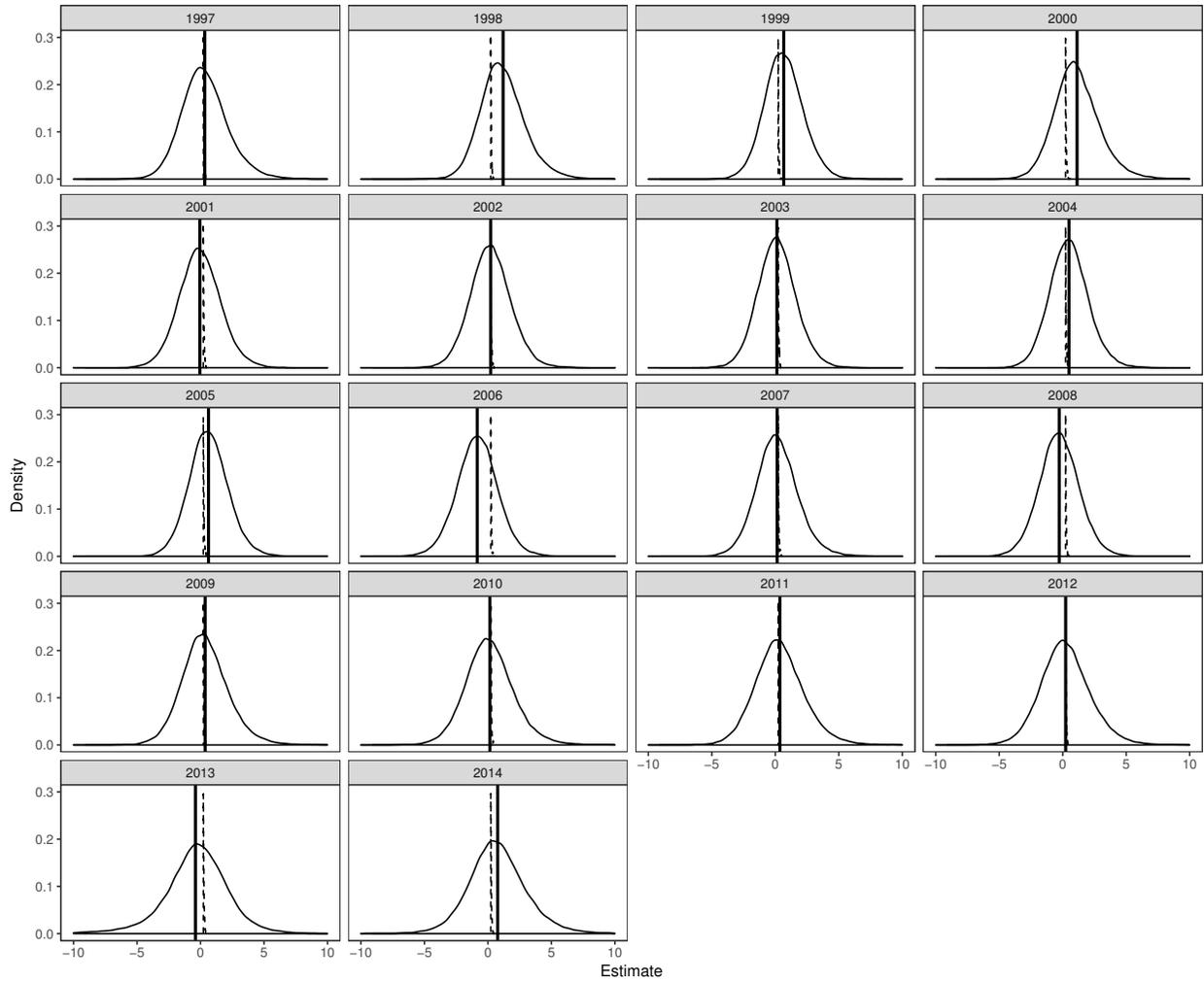


Figure B.17: **Posterior distribution of the age effect on transition probability from unsuccessful breeding state inside Brittany for migrant.** Mean value is indicated with a vertical line and prior distribution in dashed line.

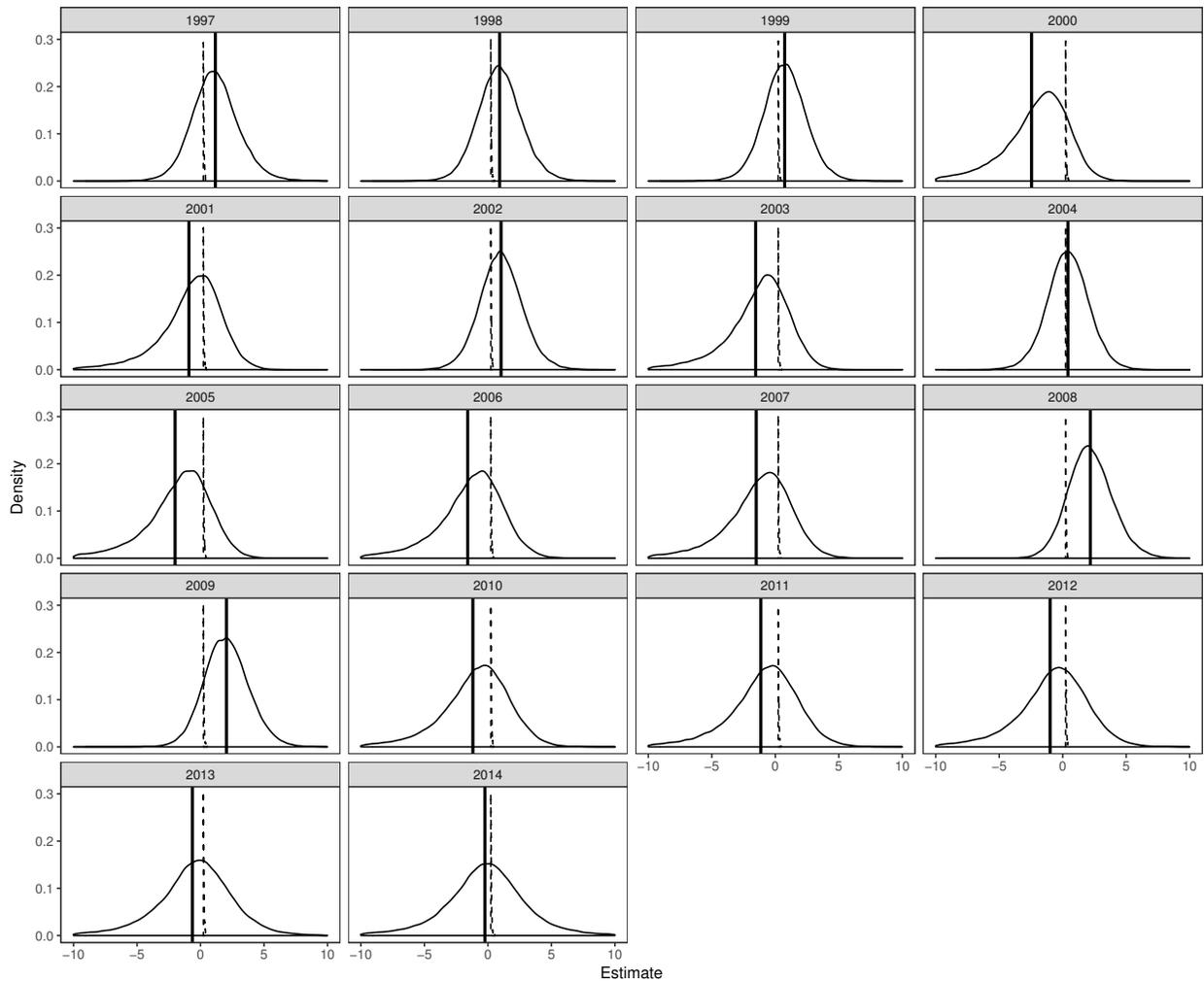


Figure B.18: **Posterior distribution of the age effect on transition probability from successful breeding state inside Brittany for resident.** Mean value is indicated with a vertical line and prior distribution in dashed line.

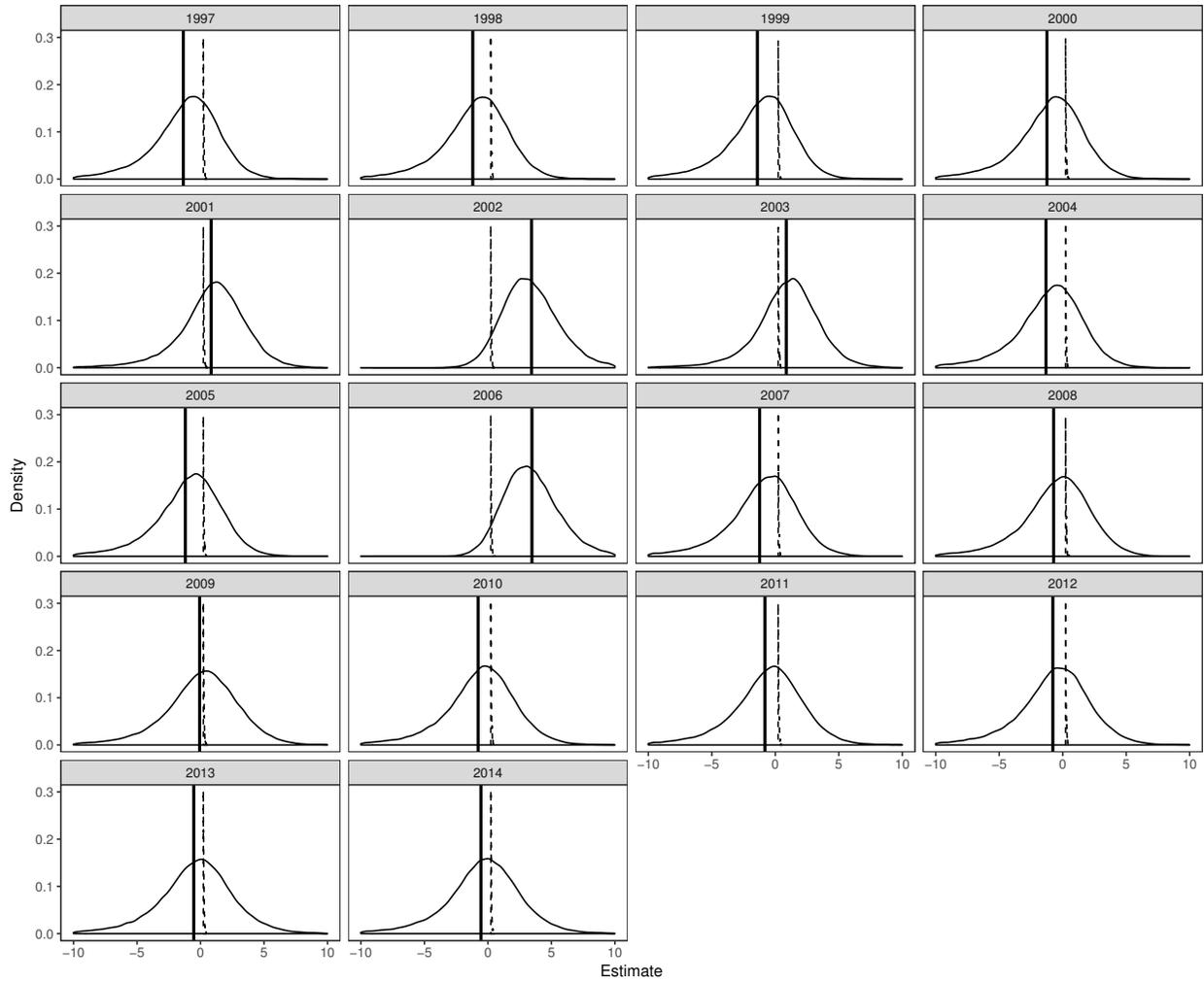


Figure B.19: **Posterior distribution of the age effect on transition probability from successful breeding state inside Brittany for migrant.** Mean value is indicated with a vertical line and prior distribution in dashed line.

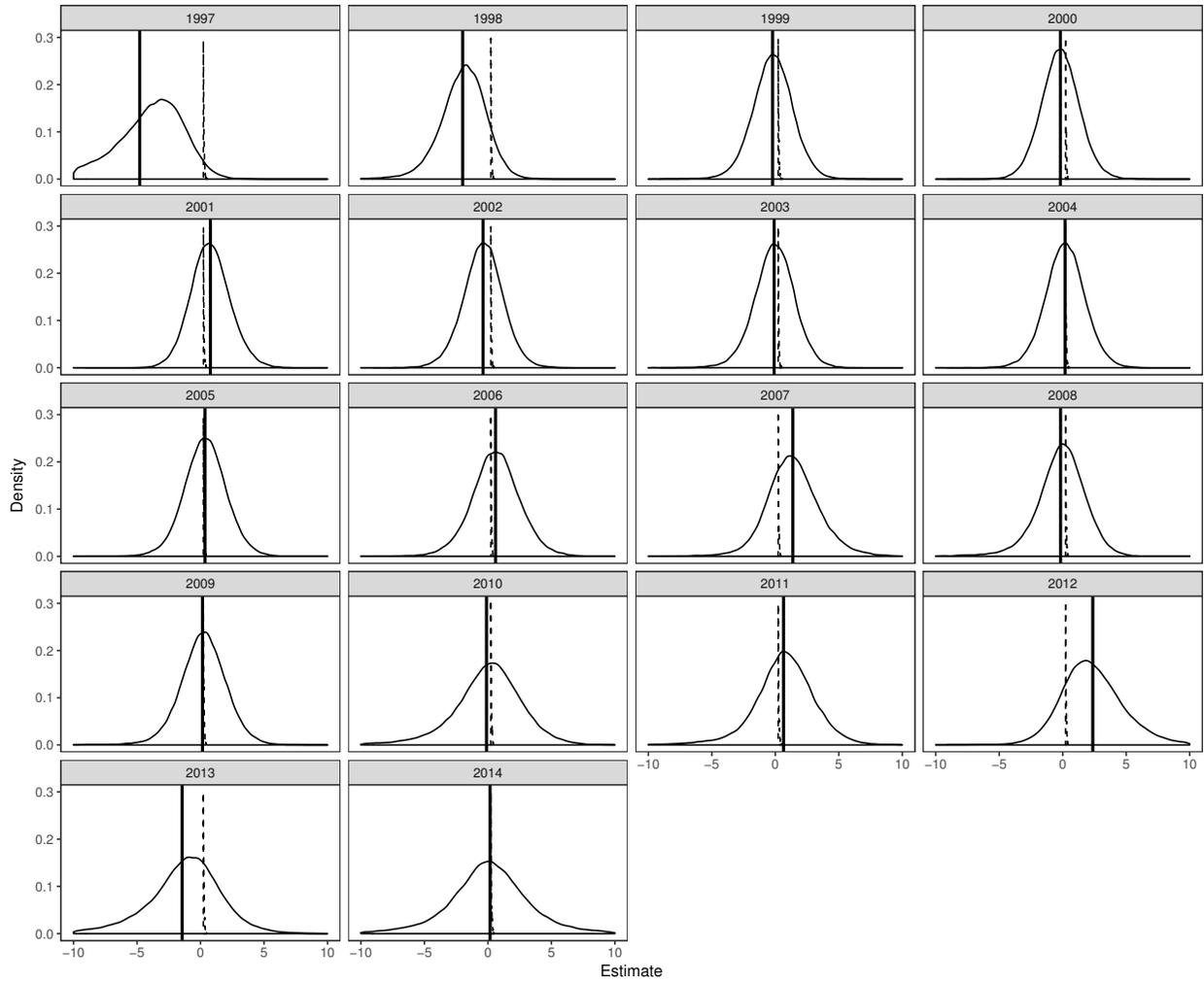


Figure B.20: **Posterior distribution of the age effect on transition probability from non-breeding state outside Brittany for resident.** Mean value is indicated with a vertical line and prior distribution in dashed line.

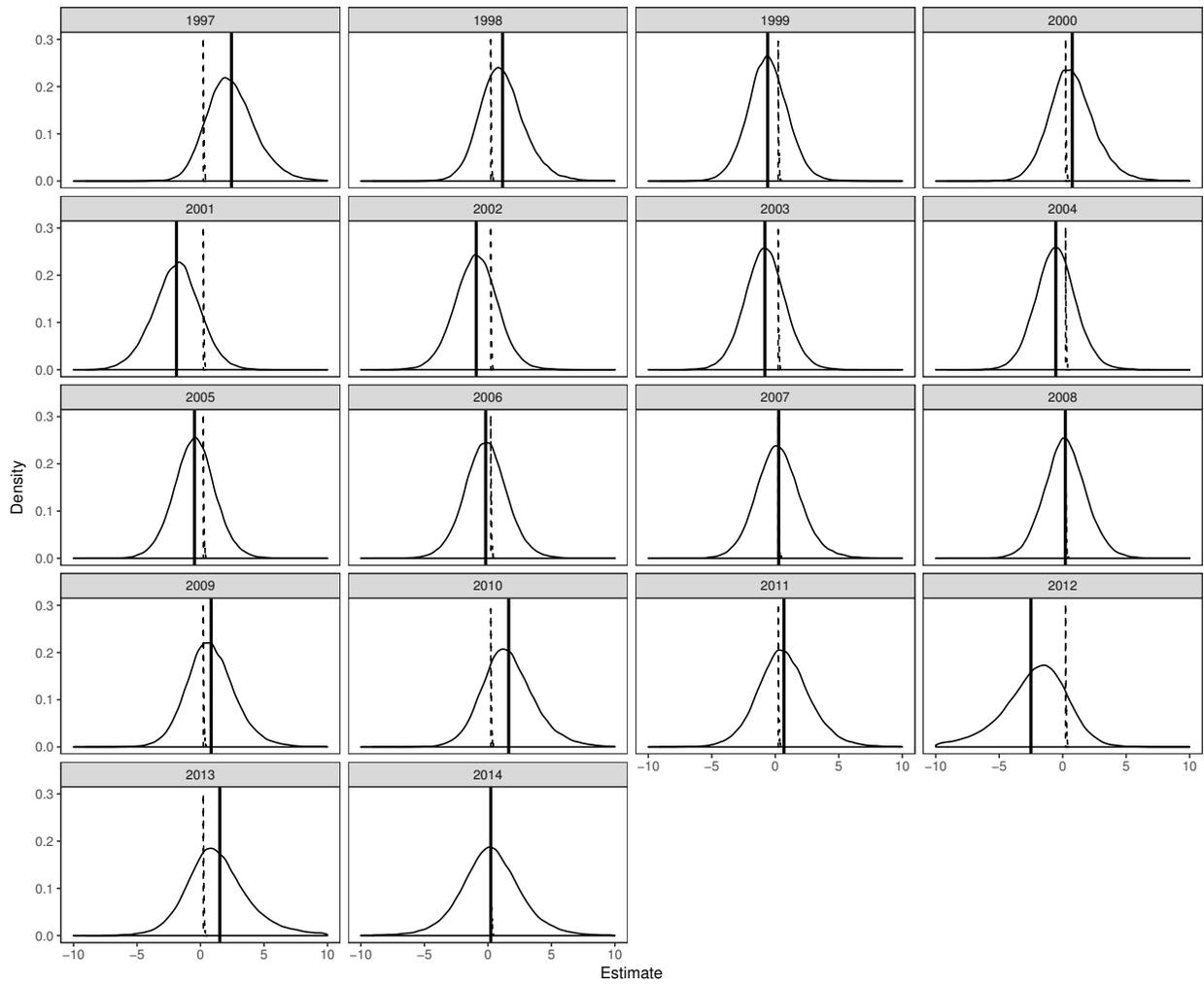


Figure B.21: **Posterior distribution of the age effect on transition probability from non-breeding state outside Brittany for migrant.** Mean value is indicated with a vertical line and prior distribution in dashed line.

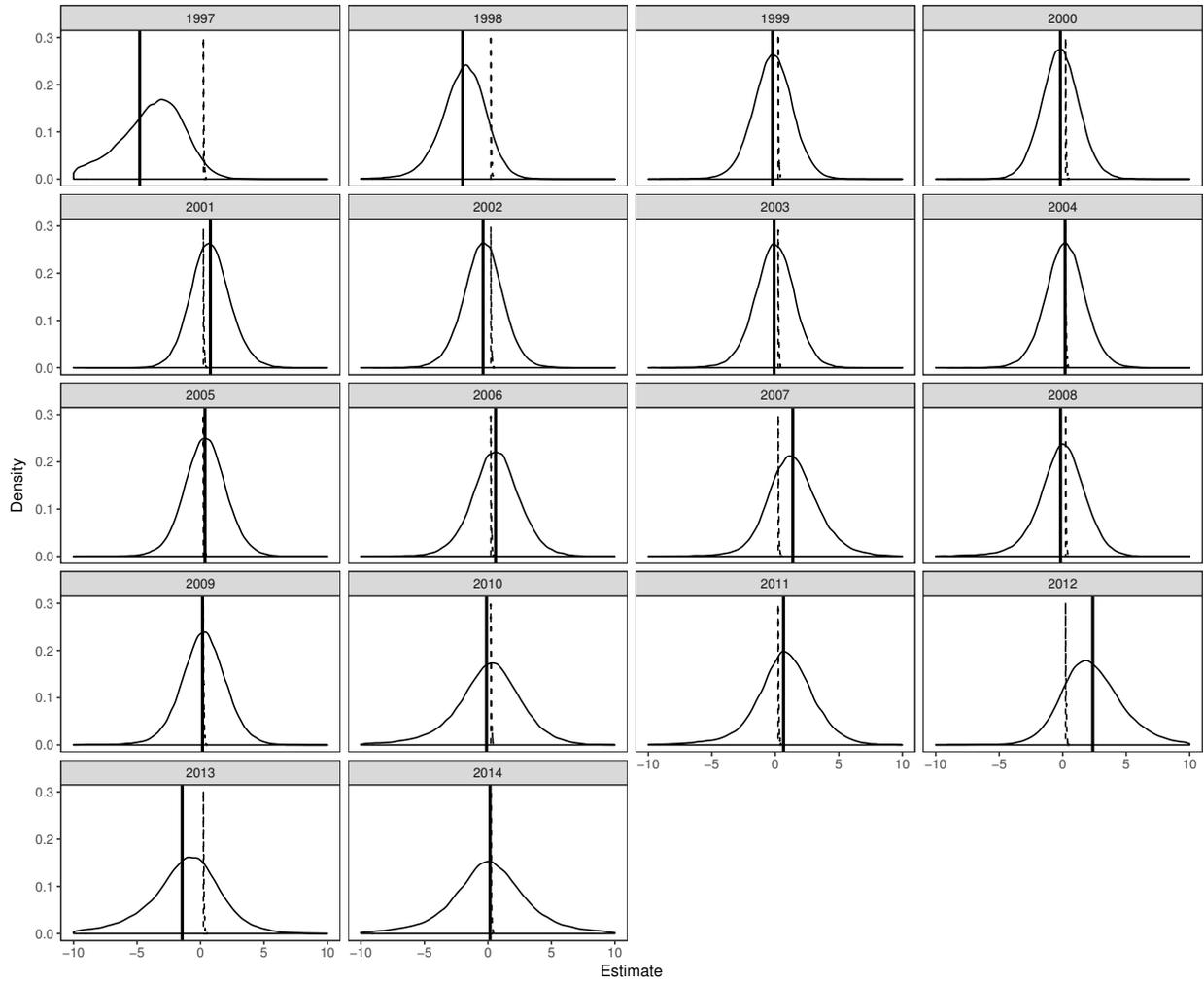


Figure B.22: **Posterior distribution of the age effect on transition probability from unsuccessful breeding state outside Brittany for resident.** Mean value is indicated with a vertical line and prior distribution in dashed line.

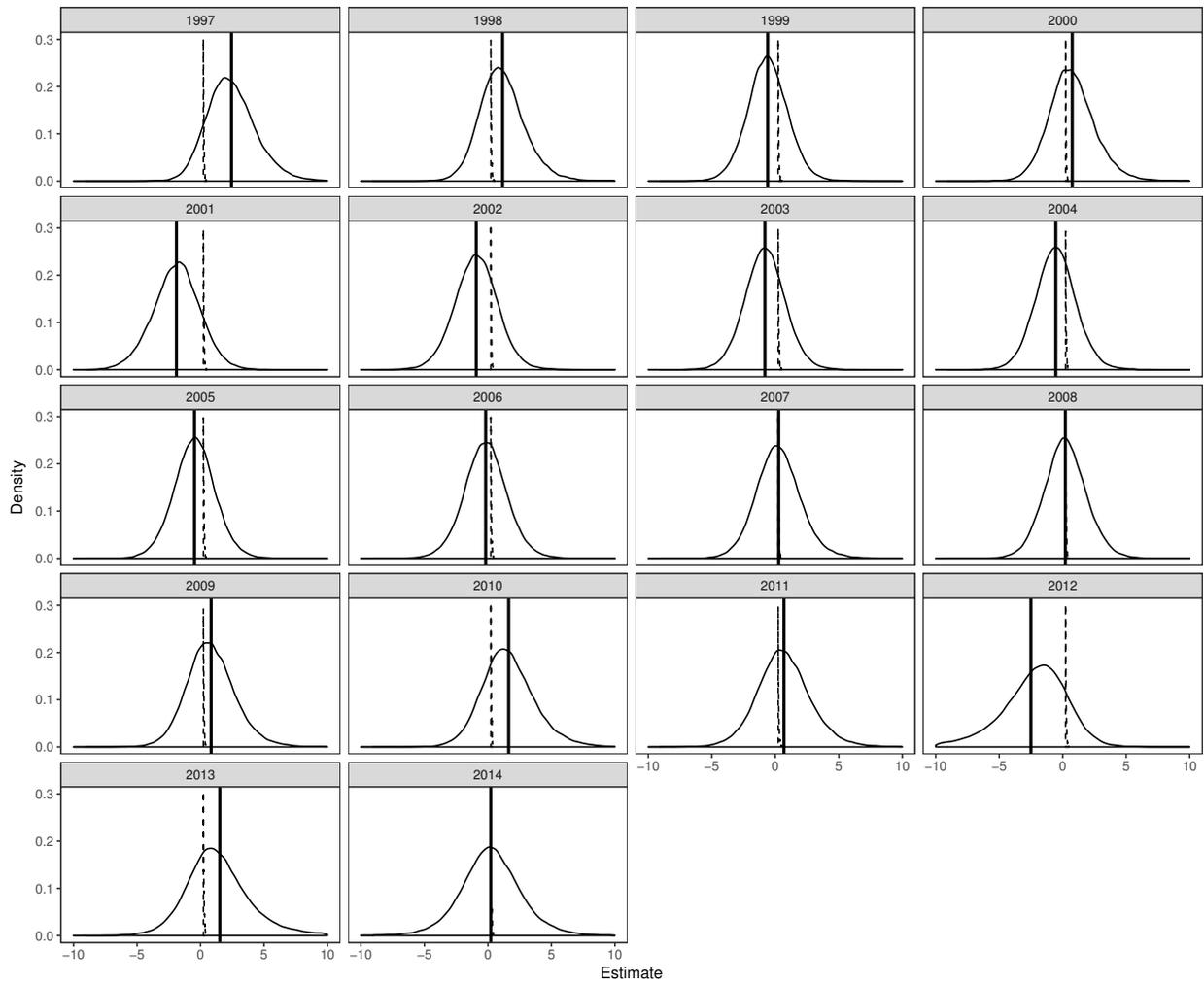


Figure B.23: **Posterior distribution of the age effect on transition probability from unsuccessful breeding state outside Brittany for migrant.** Mean value is indicated with a vertical line and prior distribution in dashed line.

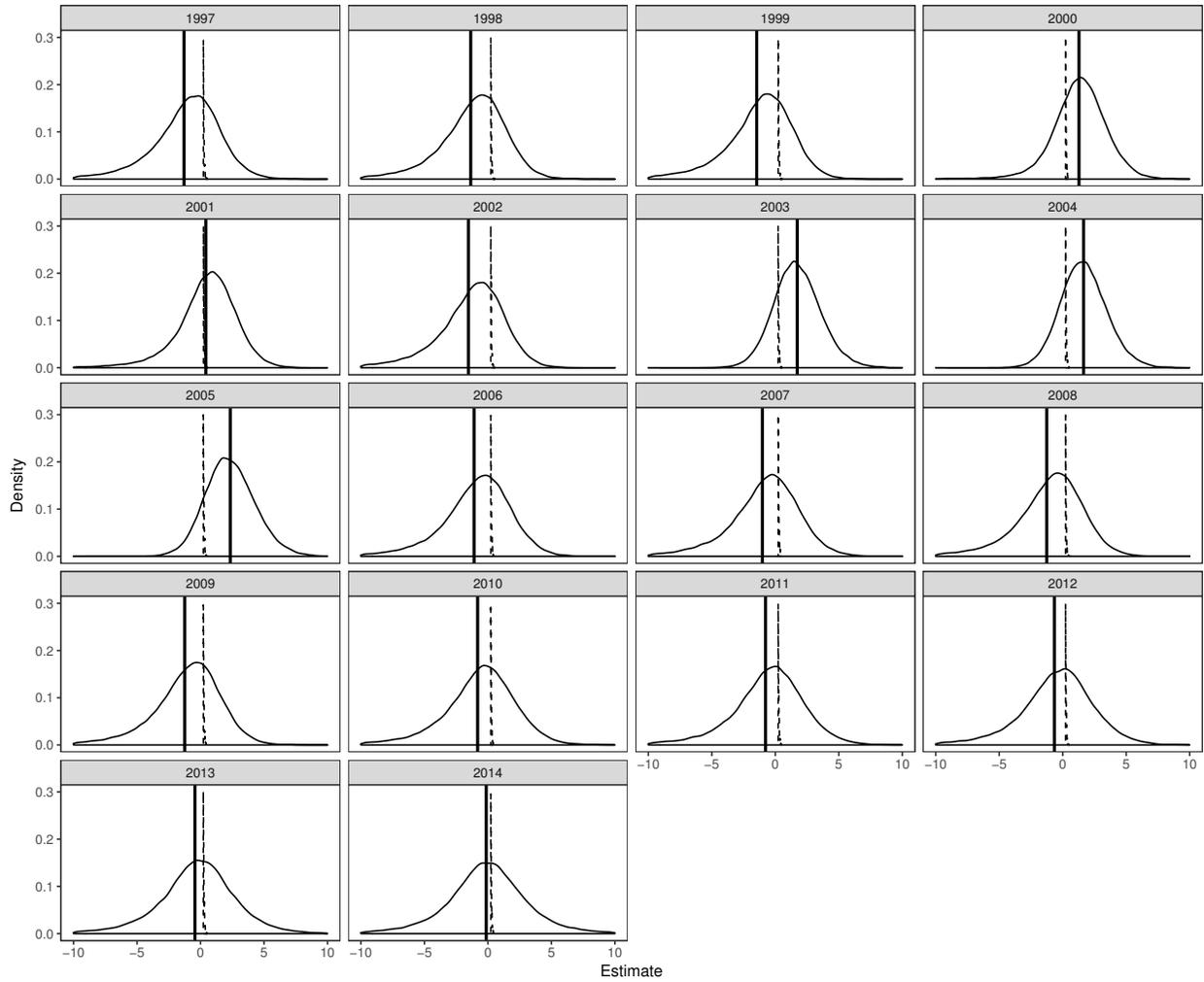


Figure B.24: **Posterior distribution of the age effect on transition probability from successful breeding state outside Brittany for resident.** Mean value is indicated with a vertical line and prior distribution in dashed line.

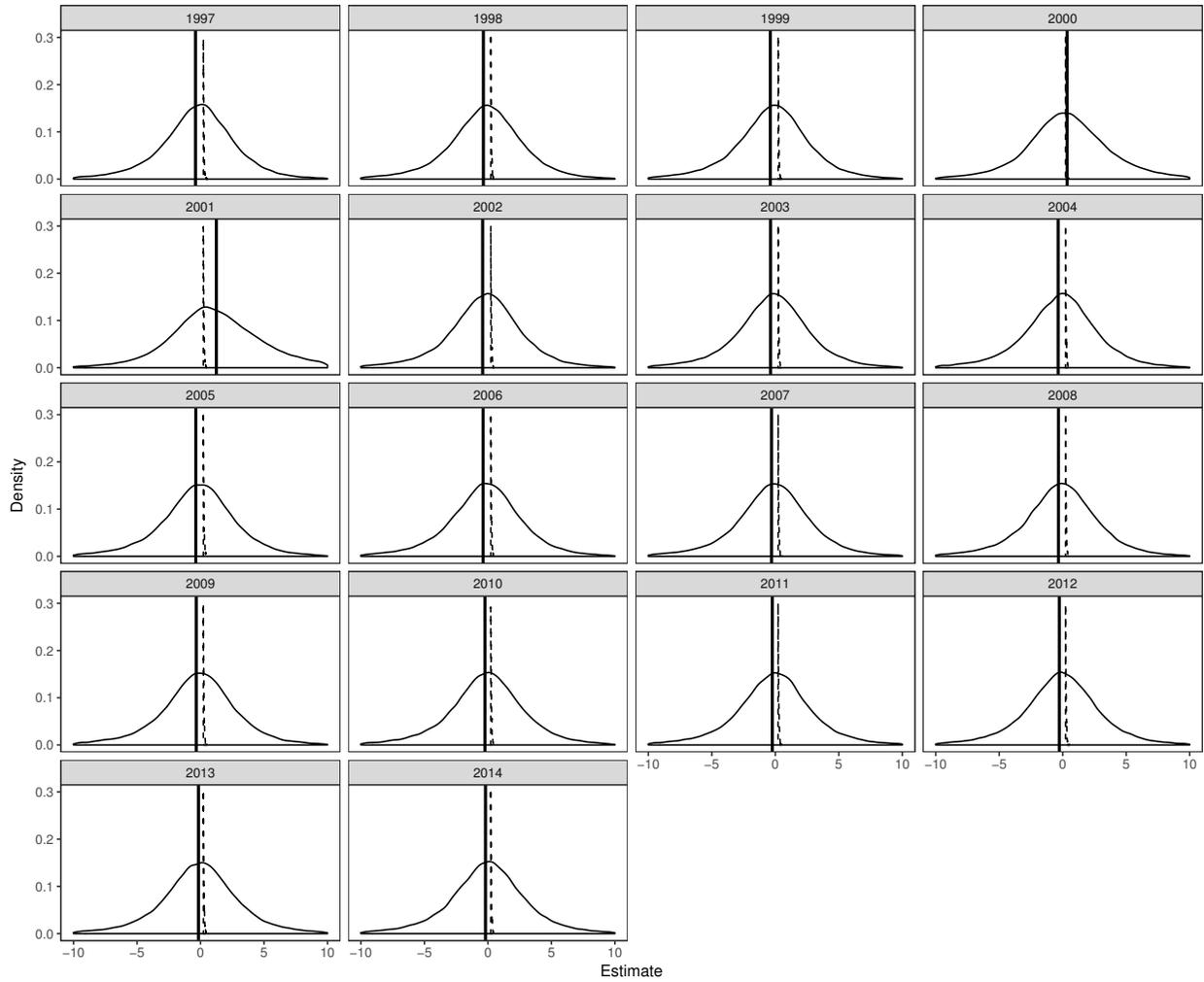


Figure B.25: **Posterior distribution of the age effect on transition probability from successful breeding state outside Brittany for migrant.** Mean value is indicated with a vertical line and prior distribution in dashed line.

Appendix C

Supporting information to chapter IV

C.1 Bayesian IPM parametrisation

C.1.1 Demographic stochasticity

In the main text of chapter IV, we specified the deterministic relationships between population age classes with the equations 4.1 (p. 76). In order to include demographic stochasticity in our model we used statistical distributions which linked age-specific segments of the population from year t to $t + 1$. We specially use Binomial and Poisson distributions and we specified the following relationships:

$$\begin{aligned} N_{1,t+1} &\sim \text{Poisson}(N_{tot_t} \times \phi_{1,t} \times f_t \times 0.44), \\ N_{2,t+1} &\sim \text{Binomial}(\phi_{1,t}, N_{1,t}) \\ &\quad \vdots \\ N_{14,t+1} &\sim \text{Binomial}(\phi_{13,t}, N_{13,t}) \\ N_{15+,t+1} &\sim \text{Binomial}(\phi_{14,t}, N_{14,t}) + \text{Binomial}(\phi_{15,t}, N_{15+,t}), \end{aligned} \tag{C.1}$$

where $N_{i,t}$ is the number of females in age class i in year t , N_{tot_t} is the number of pairs in year in year t , $\phi_{i,t}$ is the survival probability of age class i in year t and f_t the fecundity in year t . Poisson distribution is appropriate for first year old stage, because the number of these individuals can vary between 0 (no juvenile survived or was product the year before) to the maximum number of juveniles that the population can produce, i.e. a wide range of positive values. For the other population age classes, the number of individuals in one class is bounded by 0 (all individuals from the lower age class died the year before) and a

maximum equal to the number of individuals in the lower age class the year before (if all individuals survived). thus, the Binomial distribution is more appropriate.

For each population age class, we can derived four sub-populations as a product with transition probabilities, except for age class one when juveniles can only by recruited in Brittany or outside Brittany. Then equation C.1 become:

$$\begin{aligned}
 N_{1,t+1} &\sim Poisson(N_{1,t}\psi_{1,I,I}) + Poisson(N_{1,t}\psi_{1,I,O}) = NB_{1,t+1} \\
 N_{2,t+1} &\sim Binomial(\phi_{1,t}, N_{1,t}\psi_{t,I,I} + N_{1,t}\psi_{t,O,I}) + Binomial(\phi_{1,t}, N_{1,t}\psi_{t,O,O} + N_{1,t}\psi_{t,I,O}) \\
 &= NB_{2,t+1} + Nem_{2,t+1} \\
 &\quad \vdots \\
 N_{14,t+1} &\sim Binomial(\phi_{13,t}, N_{13,t}\psi_{t,I,I} + N_{13,t}\psi_{t,O,I}) + Binomial(\phi_{13,t}, N_{13,t}\psi_{t,O,O} + N_{13,t}\psi_{t,I,O}) \\
 &= NB_{14,t+1} + Nem_{14,t+1} \\
 N_{15+,t+1} &\sim (Binomial(\phi_{14,t}, N_{14,t}\psi_{t,I,I} + N_{14,t}\psi_{t,O,I}) + Binomial(\phi_{14,t}, N_{14,t}\psi_{t,O,O} + N_{14,t}\psi_{t,I,O})) + \\
 & (Binomial(\phi_{15+,t}, N_{15+,t}\psi_{t,I,I} + N_{15+,t}\psi_{t,O,I}) + Binomial(\phi_{15+,t}, N_{15+,t}\psi_{t,O,O} + N_{15+,t}\psi_{t,I,O})) \\
 &= NB_{15+,t+1} + Nem_{15+,t+1}
 \end{aligned}$$

where $NB_{i,t}$ is the number of philopatric females of age class i , $Nem_{i,t}$ is the number of emigrated females of age class i and ψ_t the transition probability between breeding colonies in Brittany (I) and outside Brittany (O).

C.1.2 Likelihoods for the available data

As explain in the main text, the likelihood of the IMP is the product of the likelihoods for the separated dataset (population counts, CR data and productivity data). The dependence between likelihood and model formulation is resumed in Fig. C.1.

Likelihoods for count data

The formal relationships that link the different stages of the population for the count dataset is described above as a series of equations (see C.1.1). Here, we describe the likelihood of the state-space model that link the true process to the observation process (de Valpine &

Hastings, 2002), i.e. the population size fluctuations taking into account of females (pairs) detection error. The observation process of the annual count data (C_t) was assumed to follow a Poisson distribution :

$$C_t \sim \text{Poisson}(NB_t)$$

This parametrisation is in accordance with the fact that variance in the observation process increase with the number of individuals monitored. As observation time is finite, when population size increase observation time per individuals decreased and observation error increase in the same time. In any case, the true population size is rarely known in such study with multiple sites and large monitoring area. The count of breeding pairs is here an estimate from census of all colonies around the Morbihan Gulf, which is subject to imperfect detection.

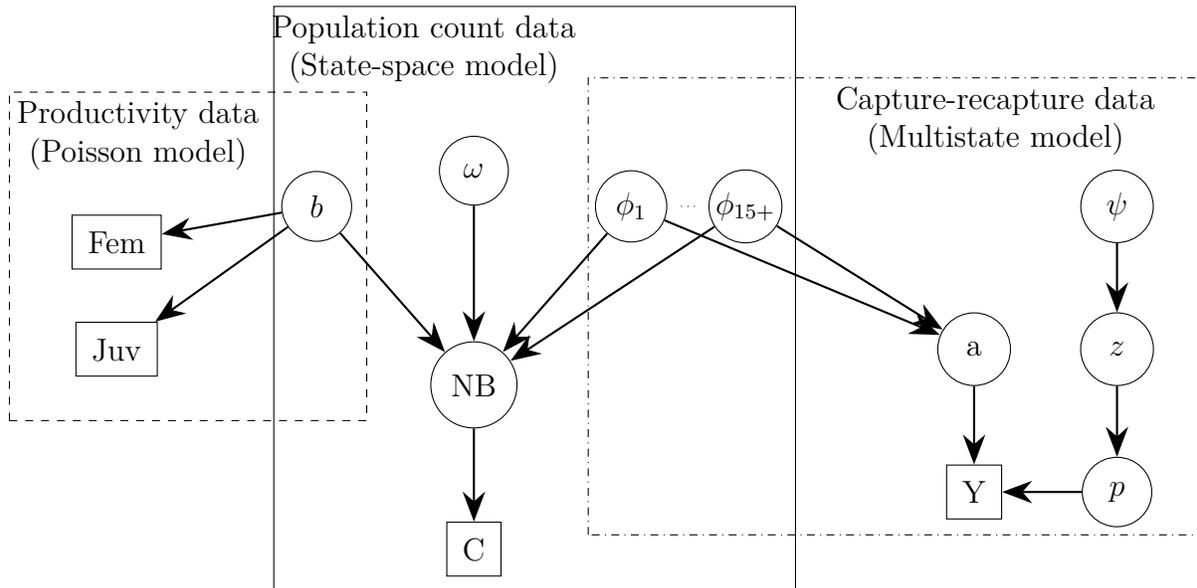


Figure C.1: **Directed acyclic graph of the IPM.** Circles represent estimated parameters and the data are represented by rectangles. Dependence between nodes are represented by arrows. Node notation: Y =capture-recapture data; C =count data; Fem =number of reproductive females; Juv =number of fledglings; b =fecundity; ϕ_1 =apparent survival of one year old individuals; ϕ_{15+} apparent survival of ten and more years old individuals; ω immigration rate; p recapture probability; ψ =annual transition probability between breeding states; z =observed states. Only two age-stages survival are represented for the seek of clarity, but the model contains 15 age-stages. Share parameters between component of the IPM are at the intersection of the rectangles.

Likelihoods for CR data

The second likelihood, concerning the CR data, was specified as a multistate CR model (Fig C.1). The approach is similar as the CDL approach (Schofield & Barker, 2008; Schofield, Barker & MacKenzie, 2009) already described in chapter II (see Appendix A.2.1, p. 128). More specifically, we used an individual-based state-space formulation with partially observed state (z), *i.e.* the area where individuals bred (inside or outside Brittany). Partially observed state was implemented as an individual random covariate with a categorical distribution (Eqn. C.3). The first state for all individuals corresponded to the birth colony, in Brittany, and the following state results in transitions (ψ) that depend on the initial state. We tested a fix year effect or a constant term for the first transition. For the subsequent transitions we tested a constant term or a linear time trend with a random time effect (see bellow, section C.2). In the CR data likelihood, the detection process is condition on reproductive state but not survival (results from preliminary explorations and previous analysis chapter II and III). Observation process is assumed to follow a Bernoulli distribution (Eqn. C.2) with a detection probability varying with state (γ_z) and a random time \times state parameter ($\eta_{z,t}^p$), see Eqn. C.4. Survival probability (ϕ) is formulated as a logistic regression with a linear age trend and individual heterogeneity for adult (age > 1 year) and with a year effect and individual heterogeneity for juvenile (Eqn. C.5). We tested a random time effect on survival, see model selection (see bellow, section C.2). This formulation was shown to be appropriate for Brittany's breeding Pied Avocet in chapter II and III. Then we can formulated the state-space likelihood for individual i in time t as:

$$[Y_{i,t}|p_{z_{i,t},t}, a_{i,t}, z_{i,t}] = \text{Bernoulli}(a_{i,t}p_{z_{i,t}}), \quad (\text{C.2})$$

$$[z_{i,t}|\psi_{z_{i,t-1},t}] = \text{Categorical}(\psi_{z_{i,t-1}}) \text{ with} \quad (\text{C.3})$$

$$\begin{cases} \psi_{z_{i,2}} \sim \text{Dirichlet}(1, 1), \text{ recruitment (first breeding season),} \\ \text{logit}(\psi_{z_{i,t}}) = \beta_3 + \alpha_3 * ((t - 10)/10) + \epsilon_t^\lambda, \text{ for } t \in \{3, \dots, 19\}, \end{cases}$$

$$\text{logit}(p_{z,t}) = \beta_2 + \gamma_z + \eta_{z,t}^p, \text{ with } \eta_{z,t}^p \sim \text{Normal}(0, \sigma_{p_z}^2), \quad (\text{C.4})$$

$$[a_{i,t}|\phi_{i,t}] = \text{Bernoulli}(a_{i,t-1}\phi_{i,t}) \text{ with} \tag{C.5}$$

$$\begin{cases} \text{logit}(\phi_{i,1}) = \beta_1 + \alpha_2[t] + \eta_i^\phi, \\ \text{logit}(\phi_{i,t}) = \beta_1 + \alpha_1 \times \text{Age}_i + \eta_i^\phi, \text{ with } \eta_i^\phi \sim \text{Normal}(0, \sigma_\phi^2). \end{cases}$$

We also added a wintering state covariate (zh) which describe wintering states, a two stages categorical covariate, in order to estimate the proportion of North and South wintering birds.

We followed previous results in chapter II and used a categorical distribution for zh as :

$$\begin{cases} [zh_{i,t}|zhp_{i,t}] = \text{Categorical}(zhp_{i,t}) \text{ for first winter, with } zhp_{i,t} \sim \text{Dirichlet}(1, 1) \\ [zh_{i,t}|\psi_{zh_{i,t-1}}] = \text{Categorical}(\psi_{zh_{i,t-1}}) \text{ for subsequent winters, with } \psi_{zh_{i,t-1}} \sim \text{Dirichlet}(1, 1), \end{cases}$$

where zhp was the annual dispersion probability of juveniles to wintering area and ψ_{zh} corresponded to the subsequent transitions but was time-independent and depended only the previous state. However, zh did not contribute to the likelihood but was used to derive fitness concerning the two wintering strategies, *i.e.* the annual population growth rates of North and South wintering individuals.

Likelihoods for productivity data

The total number of fledglings was recorded annually and supposed to be unbiased. No particular protocol was applied to estimate possible bias in this parameter. Then, annual number of newborn individuals observed (Juv) was modelled with a Poisson distribution $[Juv_t, Fem_t|b_t] = \text{Poisson}(Fem_t b_t)$, where b_t is the annual fecundity and Fem_t is the annual breeding females census, assuming they bred one brood per season.

C.1.3 Prior distributions

We used the following prior distribution for each parameters:

- Intercept of survival logistic regression : $\beta_1 \sim \text{Student}(0, 0.16, 3)$.
- Linear age effect on survival : $\alpha_1 \sim \text{Student}(0, 0.16, 3)$.
- Individual variability of survival (priors on the standard deviation, on the logit scale) : $\sigma_\phi^2 \sim \text{Student}(0, 0.04, 3)$.
- Intercept of detection logistic regression : $\beta_2 \sim \text{Student}_3(0, 0.16)$.
- State effect on detection : $\gamma_1 \sim \text{Student}(0, 0.16, 3)$ and $\gamma_2 = 0$.

- Temporal variability of survival (priors on the standard deviation, on the logit scale) : $\sigma_p^2 \sim Student(0, 0.04, 3)$.
- First transition probability between breeding states : $zp_{1:2} \sim Dirichlet(1, 1)$.
- Transition probability between breeding states : $\psi_{1:2,1:2}^z \sim Dirichlet(1, 1, 1, 1)$.
- First transition probability between wintering states : $zhp_{1:2} \sim Dirichlet(1, 1)$.
- Transition probability between wintering states : $\psi_{1:2,1:2}^{zh} \sim Dirichlet(1, 1, 1, 1)$.
- Number of individuals in first year old class during first occasion (priors were truncated and rounded to integer) : $NI_{1,t} \sim Normal^+(50, 100)$ and $NO_{1,t} \sim Normal^+(50, 100)$.
- Number of individuals in each state (priors were truncated and rounded to integer) :
 $NI_{i,t} \sim Normal^+(50, 100)$ and $NO_{i,t} \sim Normal^+(50, 100)$, for $i \in \{2, \dots, 5\}$;
 $NI_{i,t} \sim Normal^+(30, 100)$ and $NO_{i,t} \sim Normal^+(30, 100)$, for $i \in \{6, \dots, 9\}$;
 $NI_{i,t} \sim Normal^+(20, 100)$ and $NO_{i,t} \sim Normal^+(20, 100)$, for $i \in \{10, 11, 12\}$;
 $NI_{i,t} \sim Normal^+(10, 100)$ and $NO_{i,t} \sim Normal^+(10, 100)$, for $i \in \{13, 14, 15+\}$;
- Number of immigrants in each year (prior rounded to integer): $Nim \sim Uniform(-5, 100)$.
- Mean annual fecundity: $b_t \sim Uniform(0, 5)$.

C.1.4 Emigration and immigration, estimations and assumptions

Using resighting localisations we estimated movements from and to Brittany for the marked individuals and we made the assumption that these rates were share by the unmarked native individuals. We were able to estimate emigration from marked individual, which correspond to breeding dispersal. Return in Brittany, from previously emigrated individual, and philopatry inside and outside Brittany were also estimated. However, the return rate was estimated apart from immigration, the latter corresponding to individuals that were not born in Brittany. Emigration rate and return rate to Brittany after dispersal were used to derive the size of the sub-population of emigrants and philopatric individuals.

The annual number of immigrants (non native individuals entering in the population) was not directly observable in our study as a consequence we have no data collected that could help to estimate neither their number, their age-stage structure or their survival rate.

In this context, as described in the plain text (see Eqn. 4.2), immigration can nevertheless be estimated by integration as the extra number of individuals present in the population not explain by all other demographic processes (*e.g.* survival, fecundity, emigration). However, in absence of specific data on immigration, we made the assumption that the survival rate was the same for immigrants and for the rest of the population. Indeed, when recruited immigrants are incorporated the following year in the different age-stage population and then considered in the model as having the same survival as their conspecifics. It is unlikely that survival rate differ substantially between immigrant and resident individuals because we shown in chapter II and III that life-histories (wintering or breeding strategies) did not affected significantly survival of the Pied Avocets from Brittany. It seems plausible that Pied Avocets, born outside Brittany but sharing similar life experiences have very similar survival. We also suspected that immigrant individuals, even if they differ in survival rate at their arrival, reach rapidly similar survival rate after entering the population.

Following recommendations from Schaub & Fletcher (2015), we used a prior distribution on the number of immigrants not on the rate and derived immigration rate from population size (see 4.2), for the seek of accuracy in parameter estimation. We used as prior for the annual number of immigrants a Uniform distribution bounded to -5 in case of null immigration or uncertainty in the estimation Schaub & Fletcher (2015).

C.2 Model selection

Model	ϕ	ψ_{z_1}	$\psi_{z_t > 2}$	DIC	pD
Model 1	linear time trend, random individual effect	constant	linear time trend, random time effect	8609.0	2832.5
Model 2	linear time trend, random individual effect	constant	constant	8825.8	3043.9
Model 3	linear time trend, random individual effect	fix year effect	linear time trend, random time effect	9581.3	3818.7
Model 4	linear time trend, random individual effect, random time effect	constant	linear time trend, random time effect	8848.6	3064.6

Table C.1: **Model description and model selection.** Cells in grey indicated parametrisation changes from model 1. Model 1 is the best fitted model (lowest DIC). ϕ is adult survival, ψ_{z_1} is the recruitment probability for first year old individuals, $\psi_{z_t \geq 2}$ is the transition probability between breeding states from two years old. DIC is the deviance information criterion and pD is the effective number of parameters.

C.3 IPM code

Jags code for the best fitted model (mod2).

```

model{

  for(i in 1:m) {
    for(j in 1:(since[i]-1)){
      a[i,j] <- 0
      ad[i,j] <- 1
    }

    for(j in since[i]:until[i]){
      # DEATH
      ad[i,j] ~ dbern(piad[i,j]) # latente death matrix
      # ALIVE
    }
  }
}

```

```

    a[i,j] <- ab[i,j]*ad[i,j] # alive matrix
  }

# Observation process
for(j in (since[i]+1):until[i]){
  Y[i,j] ~ dbern(pdet[i,j])
  pdet[i,j] <- a[i,j]*pdt[i,j]
}

# MODEL FOR COVARIATE
z[i,(since[i]+1)] ~ dcat(zp[1:2]) # first breeding state

for(j in (since[i]+2):until[i]){
  z[i,j] ~ dcat(psi[j,z[i,j-1],1:2]) # breeding states transitions
}

# Prob for death
piad[i,since[i]] <- 1
for(j in (since[i]+1):until[i]){
  piad[i,j] <- ad[i,j-1]*(ab[i,j-1]*sv[i,j-1] + (1-ab[i,j-1]))
}

# Death
for(j in 1:(until[i]-1)){
  d[i,j] <- equals(a[i,j],1)*equals(a[i,j+1],0)
}

# Survival prob
logit(sv[i,since[i]]) <- beta[1] + alpha1[since[i]] + etas[i]

```

```
for(j in (since[i]+1):(until[i]-1)){
  logit(sv[i,j]) <- beta[1] + alpha2*age[i,j] + etas[i]
}

for(j in (since[i]+1):until[i]){
  pdt[i,j] <- p[z[i,j],j]
}
}

p[1,1] <- 0
p[2,1] <- 0

for(j in 2:n_occ){
  logit(p[1,j]) <- beta[2] + gamma + etap[1,j-1]
  logit(p[2,j]) <- beta[2] + etap[2,j-1]
}

# Death rate
for(j in 1:(n_occ-1)){
  dr[j] <- sum(d[,j])/sum(a[,j])
}

for(i in 1:n) {
  for(j in since[i):(until[i]-1)){
    # Observation process
    Y2[i,j] ~ dbern(pd2[i,j])
    pd2[i,j] <- a[i,j+1]*pdt2[i,j]
  }
}
```

```

zh[i,since[i]] ~ dcat(zp2[since[i],1:2]) # first Wintering state

for(j in (since[i]+1):(until[i]-1)){
  zh[i,j] ~ dcat(psi2[zh[i,j-1],1:2]) # Wintering states transitions in winter
}

for(j in 1:(since[i]-1)){
  a1[i,j] <- 0
  a2[i,j] <- 0
}

for(j in since[i):(until[i]-1)){
  a1[i,j] <- a[i,j]*(2-zh[i,j]) # alive matrix in for individuals in the North
  a2[i,j] <- a[i,j]*(zh[i,j]-1) # alive matrix in state for individuals in the So
}

for(j in since[i):(until[i]-1)){
  pdt2[i,j] <- p[(zh[i,j]+2),j]
}
}

for(j in 1:(n_occ-1)){
  logit(p[3,j]) <- beta[4] + etaph[1,j]
}

for(j in 1:3){
  logit(p[4,j]) <- beta[5] + etaph[2,j]
}

```

```
for(j in 4:9){
  p[4,j] <- 0
}

for(j in 10:(n_occ-1)){
  logit(p[4,j]) <- beta[5] + etaph[2,j]
}

p[3,19] <- 0
p[4,19] <- 0

for(h in 1:5){
  beta[h] ~ dt(0,0.16,3)
}

for(h in 1:2){
  taup[h] <- 1/sdp[h]/sdp[h]
  sdp[h] ~ dt(0,0.04,3)T(0,)
  tauph[h] <- 1/sdph[h]/sdph[h]
  sdph[h] ~ dt(0,0.04,3)T(0,)
}

alpha2 ~ dt(0,0.16,3)
gamma ~ dt(0,0.16,3)T(-20,20)
taus <- 1/sds/sds
sds ~ dt(0,0.04,3)T(0,)

for(j in 1:(n_occ-1)){
  alpha1[j] ~ dt(0,0.16,3)
```

```
}

for(j in 1:(n_occ-1)){
  for(h in 1:2){
    etap[h,j] ~ dnorm(0,taup[h])
  }
}

for(j in 1:(n_occ-1)){
  for(h in 1:2){
    etaph[h,j] ~ dnorm(0,tauph[h])
  }
}

for(i in 1:m){
  etas[i] ~ dnorm(0,taus)T(-20,20)
}

for(h in 1:2){
  # prior the values for alphas
  alpha[h] <- 1
}

for(i in 1:2){
  for(h in 1:2){
    psi[1,i,h] <- 0
    psi[2,i,h] <- 0
  }
}
}
```

```
alpha3 ~ dt(0,0.16,3)

for(j in 3:n_occ){
  psi[j,1,1] <- ilogit(beta[3] + alpha3*((j-10)/10) + etapsi[j-2])
  psi[j,1,2] <- 1 - psi[j,1,1]
  psi[j,2,1:2] ~ ddirch(alpha[])
}

zp[1:2] ~ ddirch(alpha[])
taupsi <- 1/sdpsi/sdpsi
sdpsi ~ dt(0,0.04,3)T(0,)

for(j in 3:n_occ){
  etapsi[j-2] ~ dnorm(0,taupsi)
}

for(h in 1:2){
  psi2[h,1:2] ~ ddirch(alpha[])
}

for(j in 1:(n_occ-1)){
  zp2[j,1:2] ~ ddirch(alpha[])
}

# demographic processes
for(i in 1:2){
  n1[i,1] ~ dnorm(50,0.01)T(0,) # Adults = 1 years
```

```
N1[i,1] <- round(n1[i,1])
for(j in 1:2){
  n2[i,j] ~ dnorm(50, 0.01)T(0,) # Adults = 2 years
  N2[i,j] <- round(n2[i,j])
  n3[i,j] ~ dnorm(50, 0.01)T(0,) # Adults = 3 years
  N3[i,j] <- round(n3[i,j])
  n4[i,j] ~ dnorm(50,0.01)T(0,) # Adults = 4 years
  N4[i,j] <- round(n4[i,j])
  n5[i,j] ~ dnorm(50, 0.01)T(0,) # Adults = 5 years
  N5[i,j] <- round(n5[i,j])
  n6[i,j] ~ dnorm(30, 0.01)T(0,) # Adults = 6 years
  N6[i,j] <- round(n6[i,j])
  n7[i,j] ~ dnorm(30,0.01)T(0,) # Adults = 7 years
  N7[i,j] <- round(n7[i,j])
  n8[i,j] ~ dnorm(30, 0.01)T(0,) # Adults = 8 years
  N8[i,j] <- round(n8[i,j])
  n9[i,j] ~ dnorm(30, 0.01)T(0,) # Adults = 9 years
  N9[i,j] <- round(n9[i,j])
  n10[i,j] ~ dnorm(20, 0.01)T(0,) # Adults = 10 years
  N10[i,j] <- round(n10[i,j])
  n11[i,j] ~ dnorm(20, 0.01)T(0,) # Adults = 11 years
  N11[i,j] <- round(n11[i,j])
  n12[i,j] ~ dnorm(20, 0.01)T(0,) # Adults = 12 years
  N12[i,j] <- round(n12[i,j])
  n13[i,j] ~ dnorm(10, 0.01)T(0,) # Adults = 13 years
  N13[i,j] <- round(n13[i,j])
  n14[i,j] ~ dnorm(10, 0.01)T(0,) # Adults = 14 years
  N14[i,j] <- round(n14[i,j])
  n15[i,j] ~ dnorm(10, 0.01)T(0,) # Adults >= 15 years
```

```
      N15[i,j] <- round(n15[i,j])
    }
}

for(j in 1:n_occ){
  nim[j] ~ dunif(-5,100) # Immigrants
  Nim[j] <- round(nim[j])
}

for(j in 1:(n_occ-1)){
  f[j] ~ dunif(0,5) # fecundity
}

# productivity process
for (j in 1:(n_occ-1)){
  Juv[j] ~ dpois(rho[j])
  rho[j] <- Fem[j]*b[j]
}

# population structure
for(j in 2:n_occ){
  for(h in 1:2){
    n1[h,j] <- b[j-1] * 0.44 * svj[j-1] * Ntot[j-1] * zp[h]
    N1[h,j] ~ dpois(n1[h,j])
  }
}

NB[1] <- N1[1,1]+ N2[1,1] + N3[1,1] + N4[1,1] + N5[1,1] + N6[1,1] + N7[1,1] + N8[1,1]
Ntot[1] <- NB[1] + N1[2,1] + N2[2,1] + N3[2,1] + N4[2,1] + N5[2,1] + N6[2,1] + N7[2,1]
```

```

popcount[1] ~ dpois(NB[1])

for(j in 2:n_occ){
  NB[j] <- N1[1,j] + N2[1,j] + N3[1,j] + N4[1,j] + N5[1,j] + N6[1,j] + N7[1,j] + N8[1,
  Ntot[j] <- NB[j] + N1[2,j] + N2[2,j] + N3[2,j] + N4[2,j] + N5[2,j] + N6[2,j] + N7[2,
  popcount[j] ~ dpois(NB[j])
}

for(j in 3:n_occ){
  N2[1,j] ~ dbin(sva[1],round(N1[1,j-1]*psi[j,1,1]+N1[2,j-1]*psi[j,2,1]))
  N2[2,j] ~ dbin(sva[1],round(N1[1,j-1]*psi[j,1,2]+N1[2,j-1]*psi[j,2,2]))
  N3[1,j] ~ dbin(sva[2],round(N2[1,j-1]*psi[j,1,1]+N2[2,j-1]*psi[j,2,1]))
  N3[2,j] ~ dbin(sva[2],round(N2[1,j-1]*psi[j,1,2]+N2[2,j-1]*psi[j,2,2]))
  N4[1,j] ~ dbin(sva[3],round(N3[1,j-1]*psi[j,1,1]+N3[2,j-1]*psi[j,2,1]))
  N4[2,j] ~ dbin(sva[3],round(N3[1,j-1]*psi[j,1,2]+N3[2,j-1]*psi[j,2,2]))
  N5[1,j] ~ dbin(sva[4],round(N4[1,j-1]*psi[j,1,1]+N4[2,j-1]*psi[j,2,1]))
  N5[2,j] ~ dbin(sva[4],round(N4[1,j-1]*psi[j,1,2]+N4[2,j-1]*psi[j,2,2]))
  N6[1,j] ~ dbin(sva[5],round(N5[1,j-1]*psi[j,1,1]+N5[2,j-1]*psi[j,2,1]))
  N6[2,j] ~ dbin(sva[5],round(N5[1,j-1]*psi[j,1,2]+N5[2,j-1]*psi[j,2,2]))
  N7[1,j] ~ dbin(sva[6],round(N6[1,j-1]*psi[j,1,1]+N6[2,j-1]*psi[j,2,1]))
  N7[2,j] ~ dbin(sva[6],round(N6[1,j-1]*psi[j,1,2]+N6[2,j-1]*psi[j,2,2]))
  N8[1,j] ~ dbin(sva[7],round(N7[1,j-1]*psi[j,1,1]+N7[2,j-1]*psi[j,2,1]))
  N8[2,j] ~ dbin(sva[7],round(N7[1,j-1]*psi[j,1,2]+N7[2,j-1]*psi[j,2,2]))
  N9[1,j] ~ dbin(sva[8],round(N8[1,j-1]*psi[j,1,1]+N8[2,j-1]*psi[j,2,1]))
  N9[2,j] ~ dbin(sva[8],round(N8[1,j-1]*psi[j,1,2]+N8[2,j-1]*psi[j,2,2]))
  N10[1,j] ~ dbin(sva[9],round(N9[1,j-1]*psi[j,1,1]+N9[2,j-1]*psi[j,2,1]))
  N10[2,j] ~ dbin(sva[9],round(N9[1,j-1]*psi[j,1,2]+N9[2,j-1]*psi[j,2,2]))
  N11[1,j] ~ dbin(sva[10],round(N10[1,j-1]*psi[j,1,1]+N10[2,j-1]*psi[j,2,1]))
  N11[2,j] ~ dbin(sva[10],round(N10[1,j-1]*psi[j,1,2]+N10[2,j-1]*psi[j,2,2]))

```

```

N12[1,j] ~ dbin(sva[11],round(N11[1,j-1]*psi[j,1,1]+N11[2,j-1]*psi[j,2,1]))
N12[2,j] ~ dbin(sva[11],round(N11[1,j-1]*psi[j,1,2]+N11[2,j-1]*psi[j,2,2]))
N13[1,j] ~ dbin(sva[12],round(N12[1,j-1]*psi[j,1,1]+N12[2,j-1]*psi[j,2,1]))
N13[2,j] ~ dbin(sva[12],round(N12[1,j-1]*psi[j,1,2]+N12[2,j-1]*psi[j,2,2]))
N14[1,j] ~ dbin(sva[13],round(N13[1,j-1]*psi[j,1,1]+N13[2,j-1]*psi[j,2,1]))
N14[2,j] ~ dbin(sva[13],round(N13[1,j-1]*psi[j,1,2]+N13[2,j-1]*psi[j,2,2]))
N15.1[1,j] ~ dbin(sva[14],round(N14[1,j-1]*psi[j,1,1]+N14[2,j-1]*psi[j,2,1]))
N15.1[2,j] ~ dbin(sva[14],round(N14[1,j-1]*psi[j,1,2]+N14[2,j-1]*psi[j,2,2]))
N15.2[1,j] ~ dbin(sva[15],round(N15[1,j-1]*psi[j,1,1]+N15[2,j-1]*psi[j,2,1]))
N15.2[2,j] ~ dbin(sva[15],round(N15[1,j-1]*psi[j,1,2]+N15[2,j-1]*psi[j,2,2]))
N15[1,j] <- N15.1[1,j] + N15.2[1,j]
N15[2,j] <- N15.1[2,j] + N15.2[2,j]
}

# Survival for each age class
for(j in 1:(n_occ-1)){
  svj[j] <- 1/(1+exp(-beta[1] - alpha1[j]))
}

for(i in 2:16){
  sva[i-1] <- 1/(1+exp(-beta[1] - alpha2*((i-10)/10)))
}

# Immigration rate
for(j in 1:(n_occ-1)){
  omega[j] <- Nim[j+1]/NB[j]
}

for(j in 1:(n_occ-1)){

```

```

Nn[j] <- Ntot[j] * sum(a1[1:n,j])/(sum(a1[1:n,j])+sum(a2[1:n,j]))
Ns[j] <- Ntot[j] * sum(a2[1:n,j])/(sum(a1[1:n,j])+sum(a2[1:n,j]))
}

# posterior predictive checks for count data (Pearson residuals):
for(j in 1:n_occ){
  fitc[j] <- (popcount[j] - NB[j])*(popcount[j] - NB[j]) / NB[j]
  popcountnew[j] ~ dpois(NB[j])
  fitc.new[j] <- (popcountnew[j] - NB[j])*(popcountnew[j] - NB[j]) / NB[j]
}

# posterior predictive checks for fledglings (Pearson residuals):
for(j in 1:(n_occ-1)){
  fitj[j] <- (Juv[j] - rho[j])*(Juv[j] - rho[j]) / rho[j]
  Juvnew[j] ~ dpois(rho[j])
  fitj.new[j] <- (Juvnew[j] - rho[j])*(Juvnew[j] - rho[j]) / rho[j]
}

# posterior predictive checks for detection CR data (Pearson residuals):
for(i in 1:m){
  for(j in 1:since[i]){
    p.resy[i,j] <- 0
    p.resynew[i,j] <- 0
  }
  for(j in (since[i]+1):until[i]){
    p.resy[i,j] <- Y[i,j]-pdt[i,j] # Pearson resi
    # Replicate data sets
    Ynew[i,j]~dbern(pdet[i,j])
    p.resynew[i,j] <- Ynew[i,j]-pdt[i,j] # Pearson resi
  }
}

```

```
    }  
  }  
  
  for(j in 1:n_occ){  
    fity[j] <- sum(p.resy[,j])  
    fity.new[j] <- sum(p.resynew[,j])  
  }  
}
```

C.4 Population growth regression framework

In order to estimate regression coefficients corresponding to the effects of age class numbers on population growth (see main text), we fitted the following model using JAGS:

```
model{  
  
  for(j in 1:16){  
    for(i in 1:n){  
      loglam[i,j] ~ dnorm(mu[i,j],tau[j])  
      mu[i,j] <- alpha + beta[1]*N1[i,j] + beta[2]*N2[i,j] + beta[3]*N3[i,j] +  
        beta[4]*N4[i,j] + beta[5]*N5[i,j] + beta[6]*N6[i,j] + beta[7]*N7[i,j] +  
        beta[8]*N8[i,j] + beta[9]*N9[i,j] + beta[10]*N10[i,j] + beta[11]*N11[i,j] +  
        beta[12]*N12[i,j] + beta[13]*N13[i,j] + beta[14]*N14[i,j] + beta[15]*N15[i,j]  
    }  
  }  
  
  alpha ~ dnorm(0,0.001)  
  
  for(i in 1:15){
```

```

beta[i] ~ dnorm(0,0.001)
}

tau <- 1/sd/sd
sd ~ dunif(0,5)

}

```

We used vague Normal priors on regression coefficients ($\beta_i \sim Normal(0,0.001)$ and $\alpha \sim Normal(0,0.001)$) and a unifor prior on the standard deviation of the random time effect ($\sigma_\lambda \sim Uniform(0,5)$). Results from the estimations of regression coefficients β_i and the probability that they were inferior to zero are shown in Table C.2. Standard deviation of random time effects on log scale was 0.072.

Parameter	$P(\beta_i < 0)$	Mean	2.5%	97.5%
β_1	0	0.000	0.000	0.000
β_2	1	-0.001	-0.001	-0.001
β_3	1	-0.001	-0.001	-0.001
β_4	1	-0.001	-0.001	-0.001
β_5	1	0.000	0.000	0.000
β_6	1	0.000	0.000	0.000
β_7	1	-0.001	-0.001	-0.001
β_8	0	0.000	0.000	0.000
β_9	1	-0.002	-0.002	-0.002
β_{10}	0	0.002	0.002	0.002
β_{11}	1	-0.002	-0.002	-0.001
β_{12}	1	0.000	0.000	0.000
β_{13}	0.42	0.000	0.000	0.000
β_{14}	1	-0.001	-0.001	-0.001
β_{15}	0	0.000	0.000	0.000

Table C.2: Effects (β_i) of the number of the number of individuals (N_i) in the age class i on population growth rate. Means and associated 95% BCI are displayed and the probability that $\beta_i < 0$.

C.5 Posterior predictive checks

The χ^2 discrepancy measure Gelman *et al.* (2003) is the sum of squared Pearson residuals and can be used as an overall goodness of fit test. This summary of fit, for an univariate response y , can be written:

$$T(y^{obs}|\theta) = \sum_i^n \frac{(y_i^{obs} - E(y_i|\theta))^2}{var(y_i|\theta)} ; \quad T(y^{rep}|\theta) = \sum_i^n \frac{(y_i^{rep} - E(y_i|\theta))^2}{var(y_i|\theta)},$$

where y^{obs} is the observed data and y^{rep} is the replicated data using the model estimates, θ is the model parameters, $E(y_i|\theta)$ is the expectation, var is the variance and n is the number of posterior samples of variable y . The χ^2 discrepancy metric measure distance of data and replicated data to the model.

The posterior predictive p-value or Bayesian p-value is the probability that distance of observed data to the model is higher than replicated data and was used to quantify the discrepancy of the model:

$$B_{p-value} = p(T(y^{obs}|\theta) > T(y^{rep}|\theta))$$

A model is suspect to lack of fit if the $B_{p-value}$ is close to 0 or 1. We computed these values overall years and each year for the observed data of the three sub-models, the Bernoulli observation process in the CR data, the Poisson observation processes in the count and in the productivity data. The results are shown on Fig. C.2 to C.5.

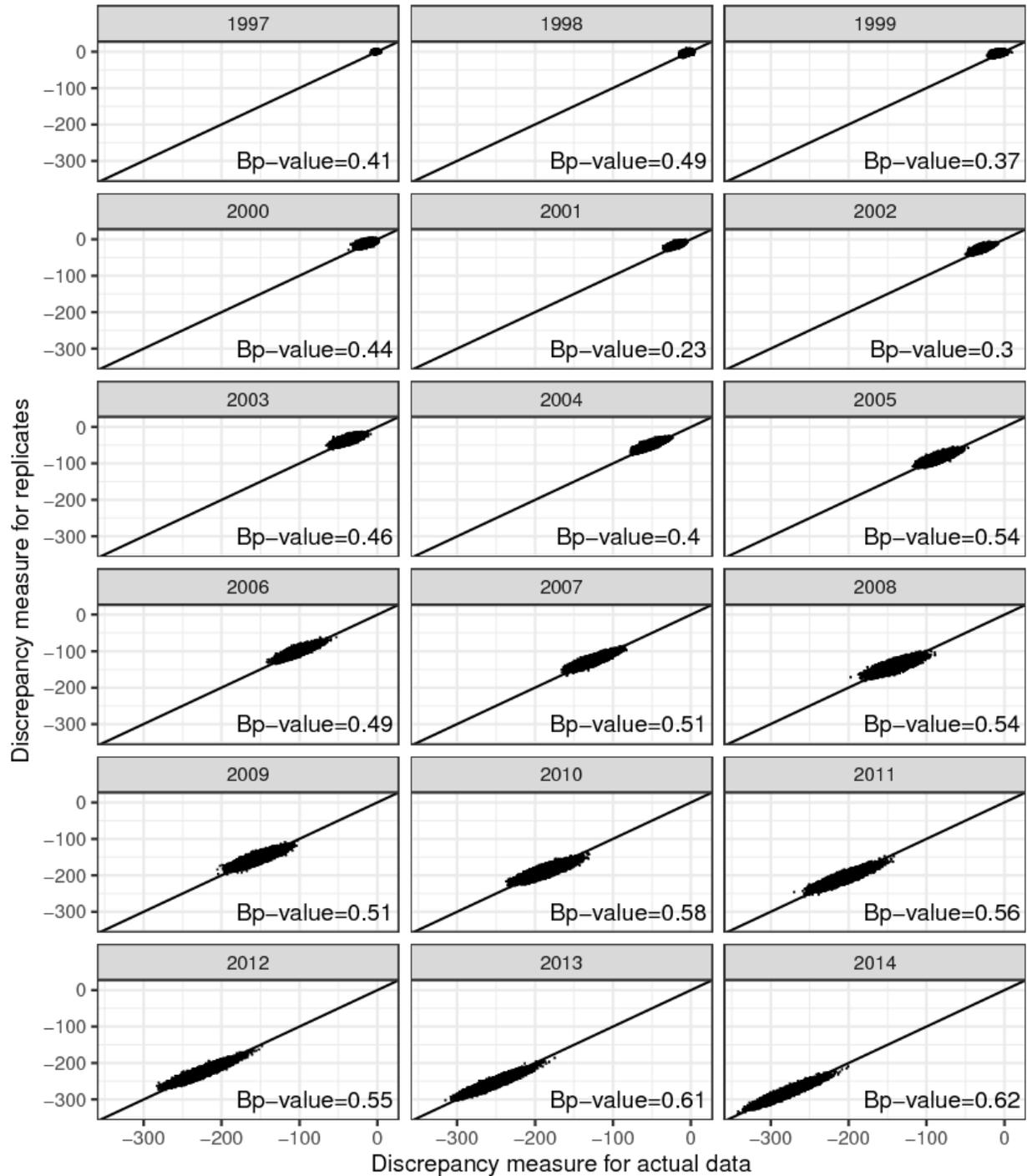


Figure C.2: χ^2 discrepancy plot for CR data. Annual discrepancy measures for replicates data against observations data for all posterior samples. Panel are classified per study occasion (year). Only year 1996 showed a lack of fit.

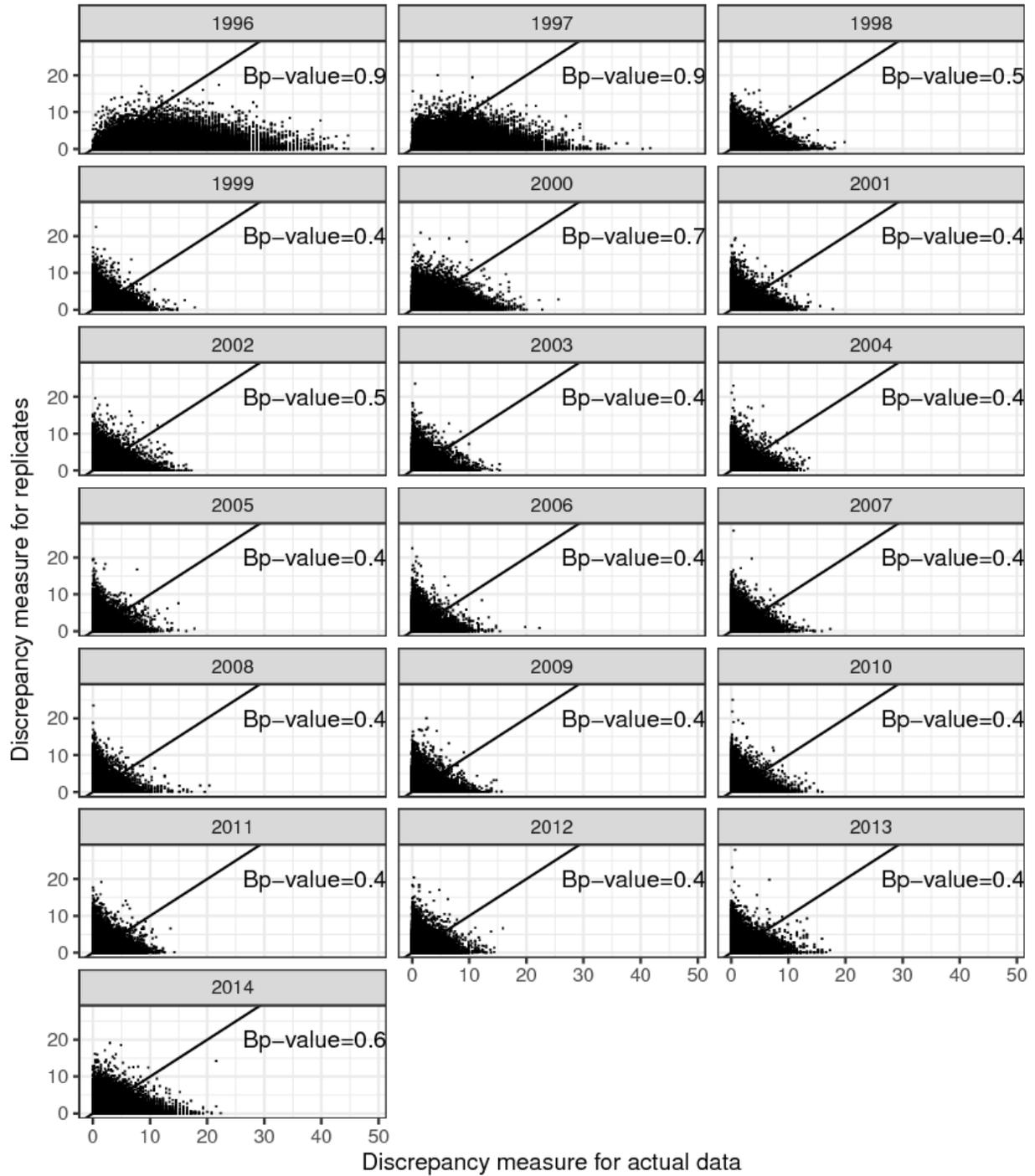


Figure C.3: χ^2 discrepancy plot for count data. Annual discrepancy measures for replicates data against observations data for all posterior samples. Panel are classified per study occasion (year). Only year 1996 and 1997 showed lack of fit.

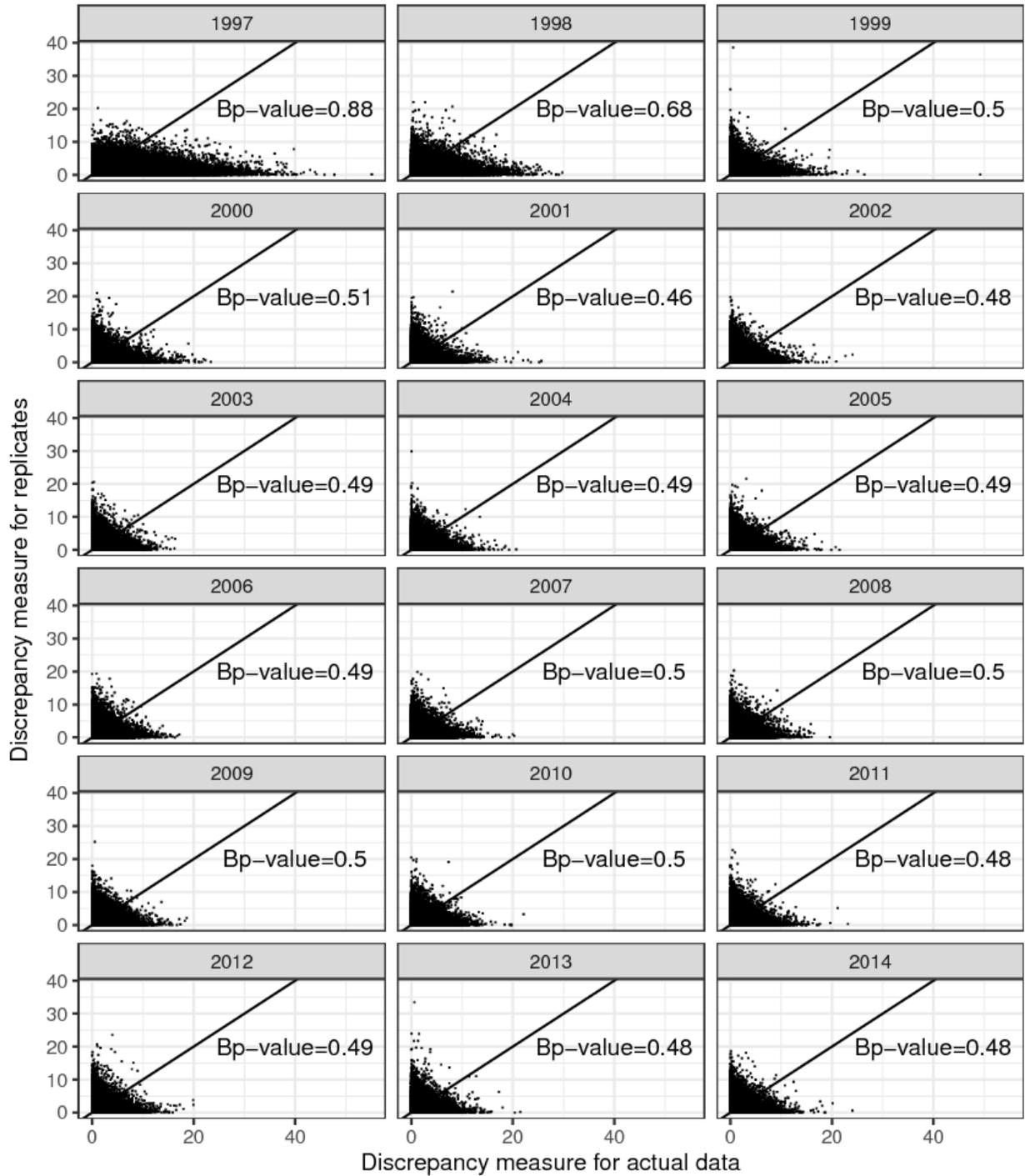


Figure C.4: χ^2 discrepancy plot for fecundity data. Annual discrepancy measures for replicates data against observations data for all posterior samples. Panel are classified per study occasion (year). No lack of fit appeared.

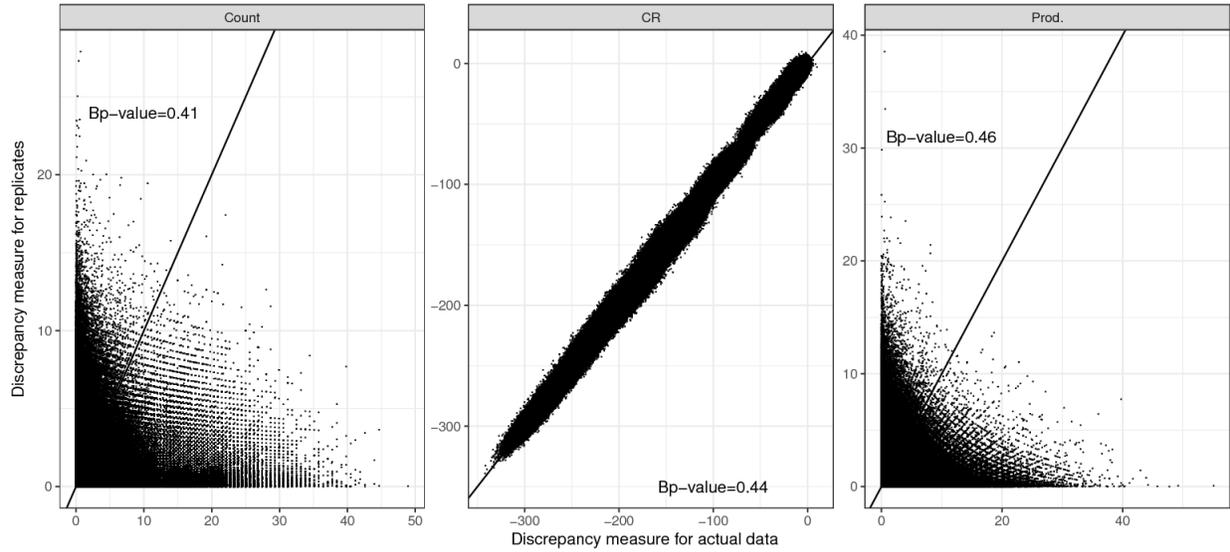


Figure C.5: χ^2 discrepancy plot for all observation processes. Discrepancy measures for replicates data against observations data for all posterior samples overall years. Panel are classified per data sources: Count, CR and productivity (Prod.) data, from left to right respectively. Global fit of the three sub-models was good.

C.6 Complements and results from the derived quantities

C.6.1 Variations in annual demographic rates

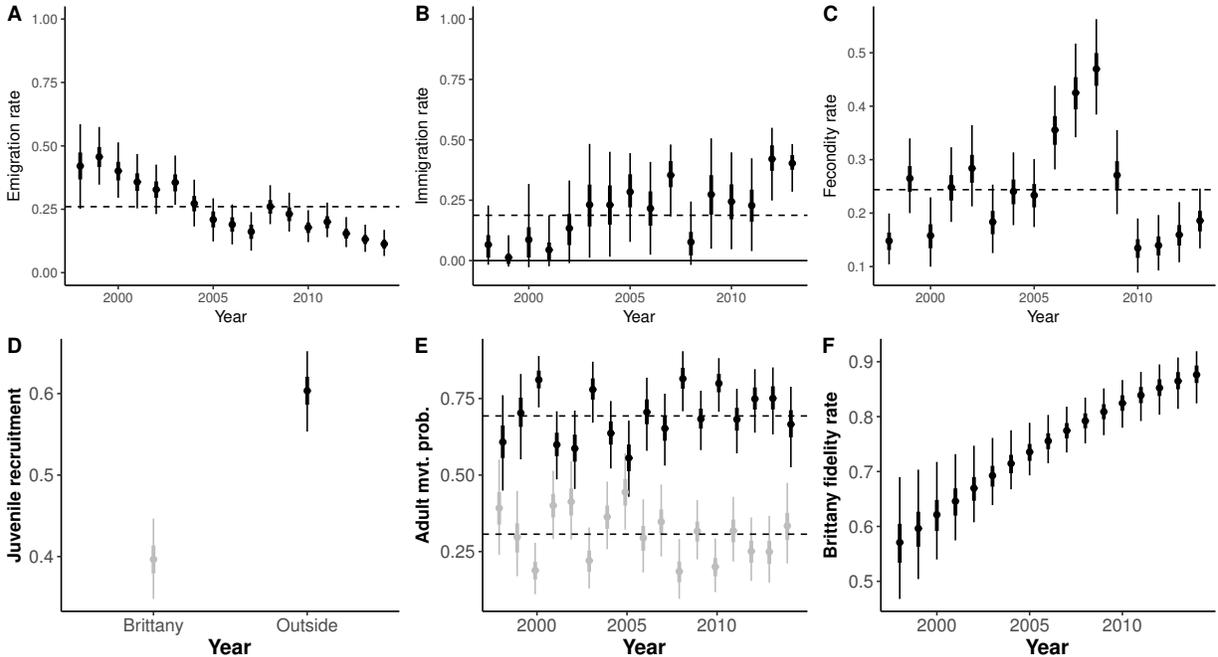


Figure C.6: **Annual fluctuation of demographic rates.** Pannel (A) shows annual emigration rate from Brittany’s breeding colonies, mean value 0.26 (BCI 0.1, 0.5). Pannel (B) shows annual immigration rate of non native individuals into Brittany’s breeding colonies, mean 0.2 (BCI: -0.02,0.48). Pannel (C) shows annual fecundity rate of the overall population, mean 0.27 (BCI: 0.11, 0.53). horizontal dashed line is the mean value during the study. Pannel (D) shows annual juvenile recruitment probability. In grey, recruitment in Brittany with mean value 0.40 (BCI: 0.35, 0.45) and in black, the complement, *i.e.* recruitment outside Brittany. Pannel (E) shows subsequent annual transition probabilities from outside Brittany for individuals born in Brittany. In black, probability to remain outside Brittany with mean 0.62 (BCI: 0, 0.86). In grey, the complement, *i.e.* the probability to return in Brittany after dispersal, with mean 0.45 (BCI: 0.13, 0.87). Panel (F) show time trend (α_3) in colony fidelity rate for Brittany’s breeders.

C.6.2 Temporal variation in the composition of age classes

Appendix C. Supporting information to chapter IV

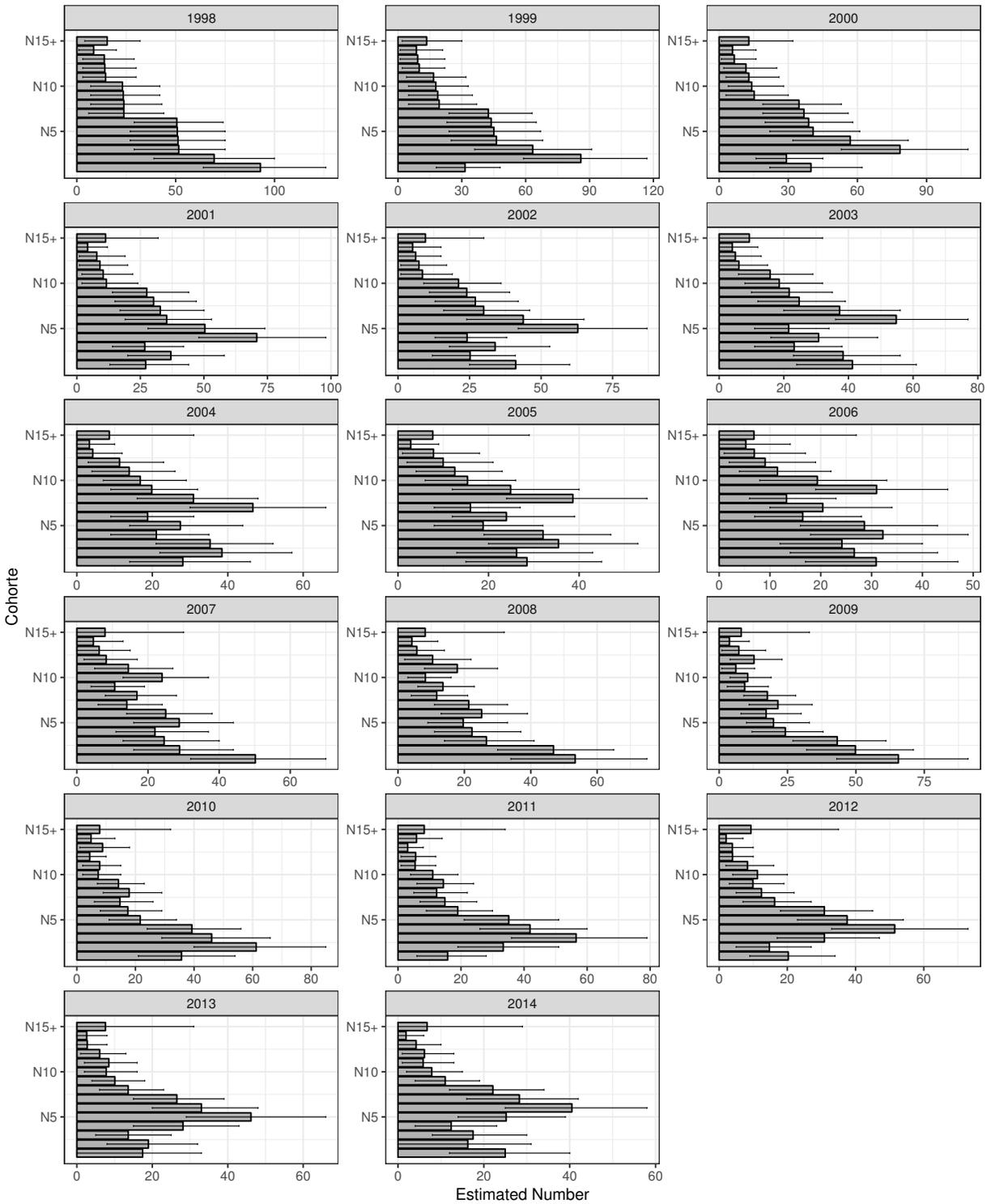


Figure C.7: **Age structure of the population of Pied Avocet.** Estimated number of individuals in each age stage. N_x indicates the cohort of age x . 95% BCI is indicated with a horizontal line. N_{15+} gathers all the individual older than 14 years.

Appendix C. Supporting information to chapter IV

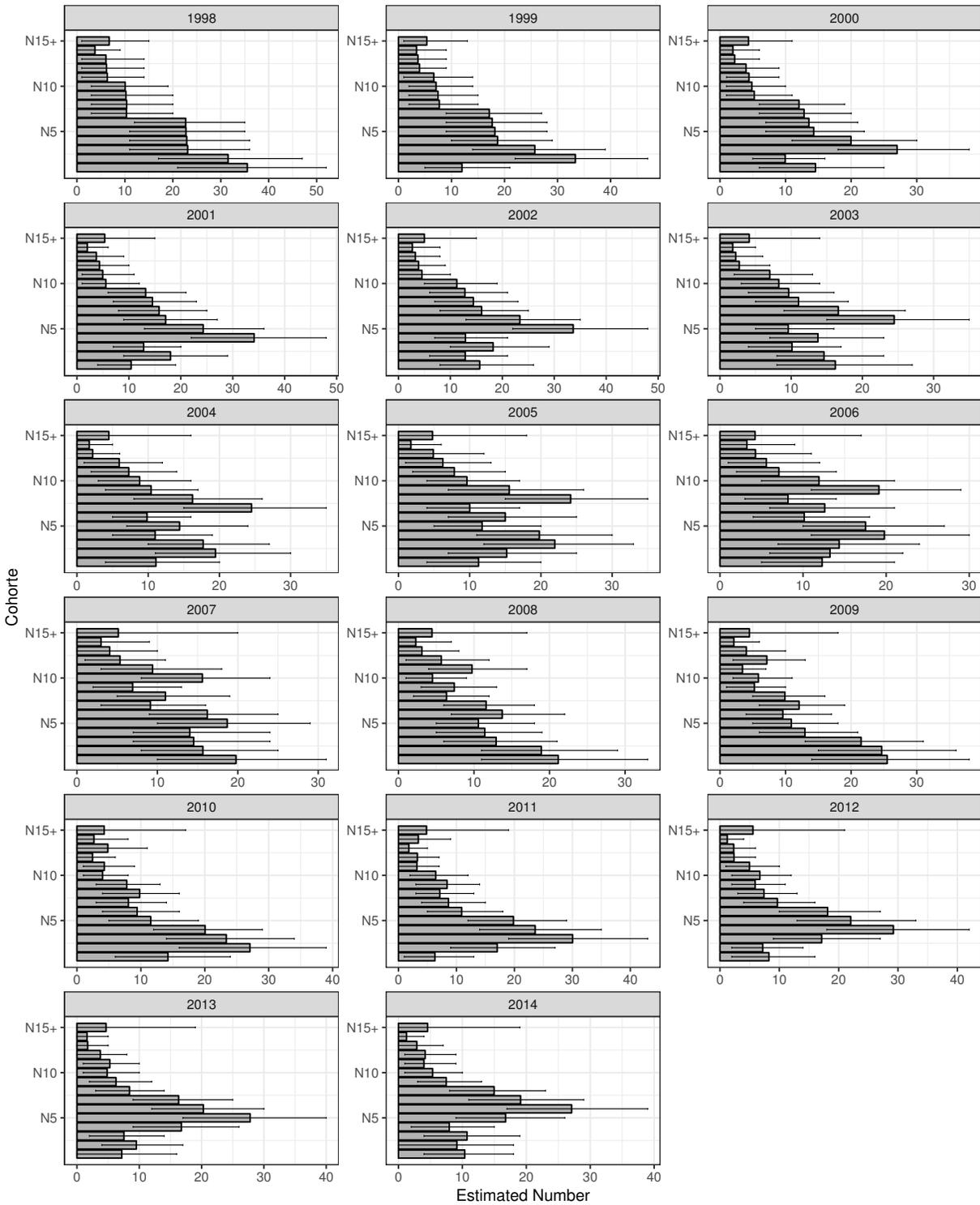


Figure C.8: Age structure of the population of Pied Avocet in Brittany. Estimated number of individuals in each age stage. N_x indicates the cohort of age x . 95% BCI is indicated with a horizontal line. N_{15+} gathers all the individual older than 14 years.

Appendix C. Supporting information to chapter IV

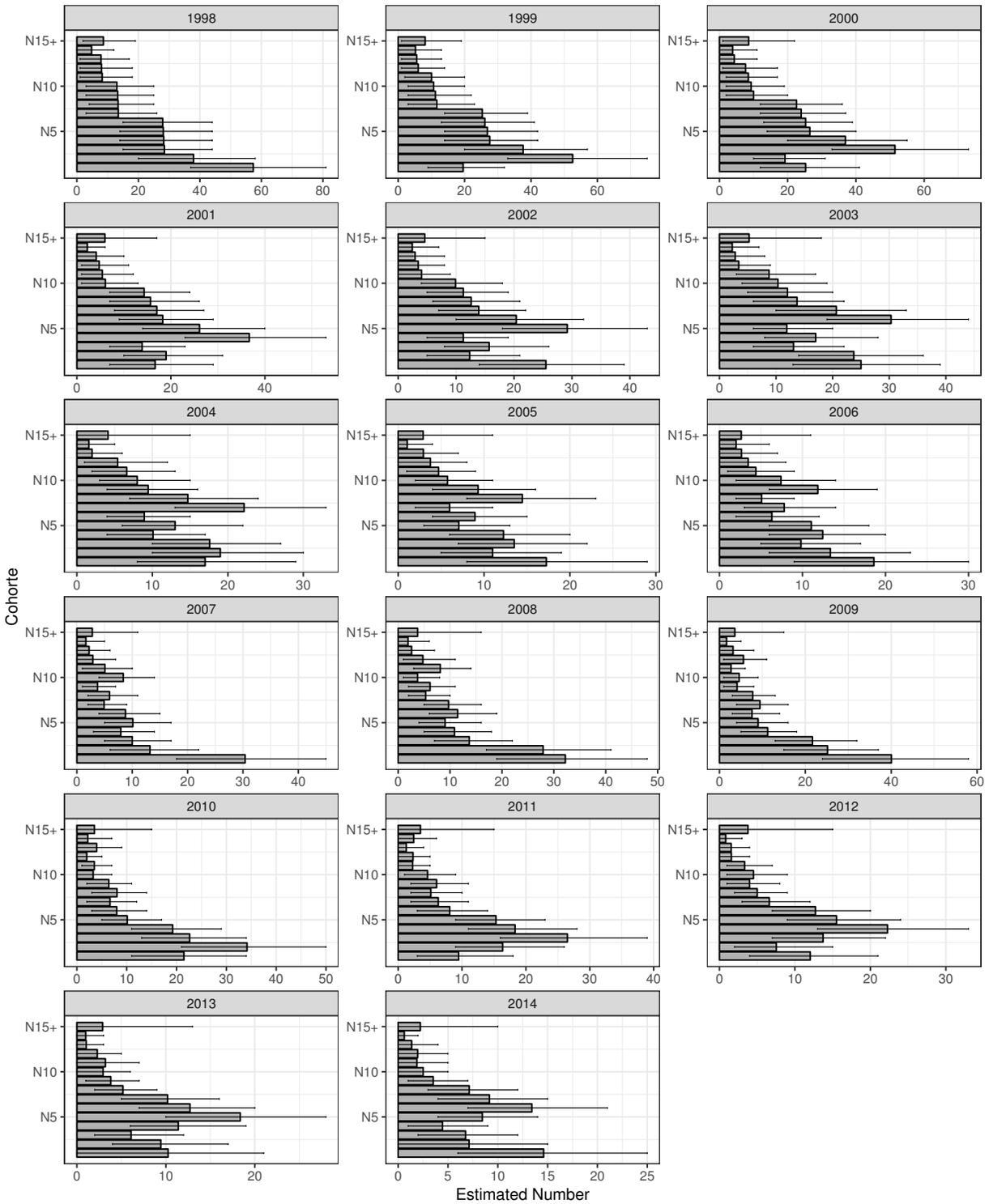


Figure C.9: Age structure of the population of Pied Avocet outside Brittany (emigrants). Estimated number of individuals in each age stage. N_x indicates the cohort of age x . 95% BCI is indicated with a horizontal line. N_{15+} gathers all the individual older than 14 years.

C.6.3 Population growth and age classes effect

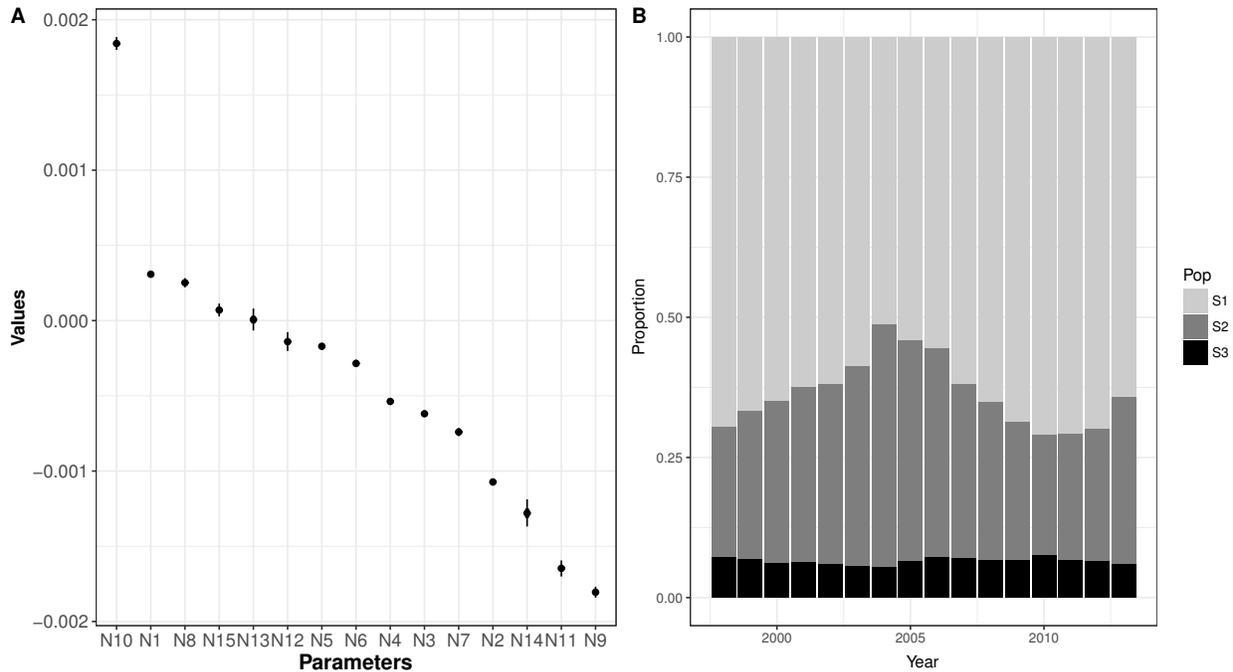


Figure C.10: **Age class effect on population growth.** Panel A, the points indicates the mean value of the regression coefficient. Values are ranked in decreasing order. N_x indicates the cohort of age x . 95% BCI is indicated with an vertical line. Panel B, proportions of individuals in three stages of the population: S1: proportion of individuals in age classes one to six; S2 proportion of individuals in age classes seven to twelve; S3 proportion of individuals older than twelve years.

C.6.4 Correlation between population growth rates and demographic rates

Additional figures showing estimates of the correlations between annual population growth rates and annual estimates of demographic rates.

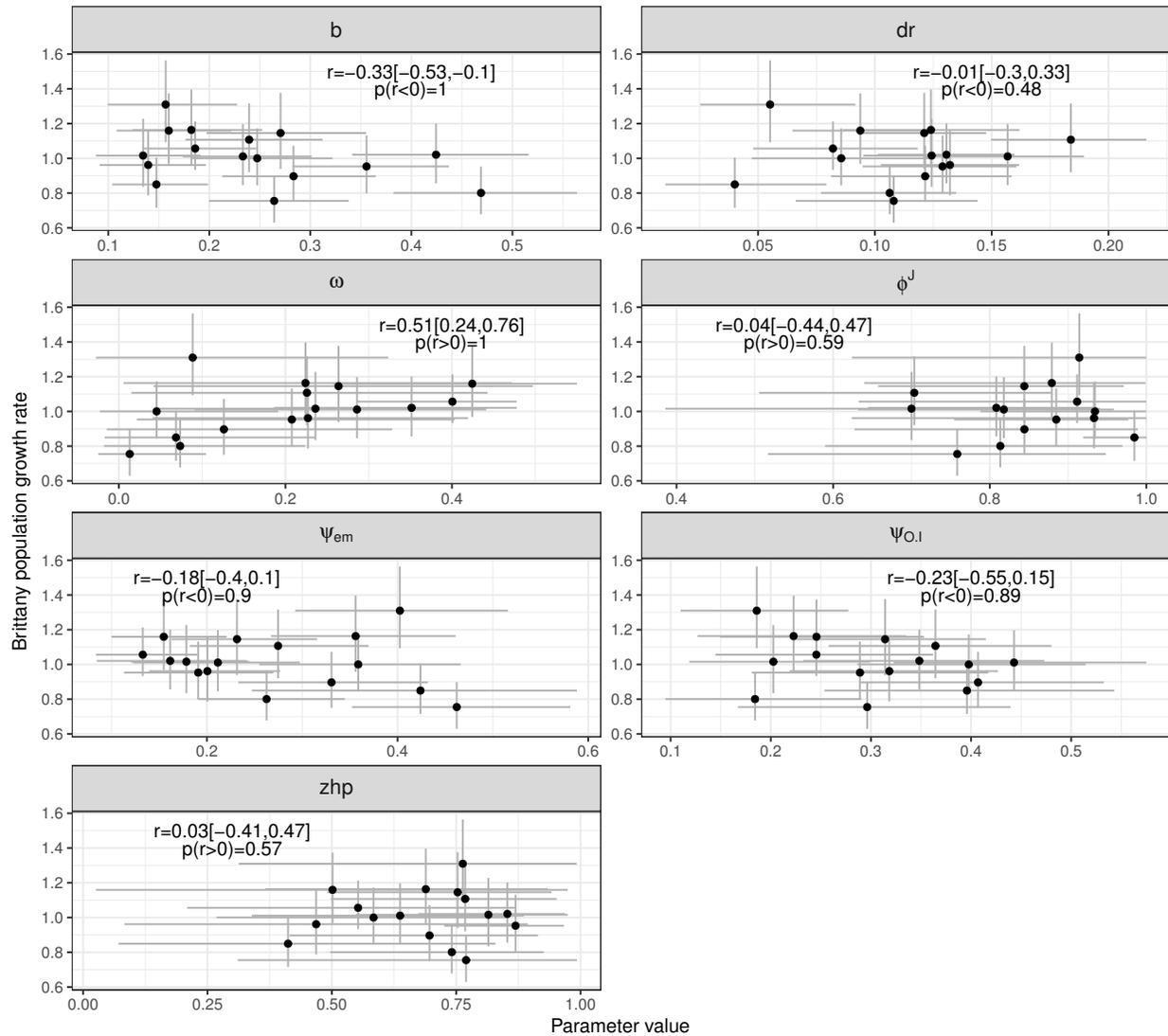


Figure C.11: **Correlation between annual population growth rates in Brittany and annual estimates of demographic rates.** b = annual fecundity rate, dr = annual death rate, ω = annual immigration rate, ϕ^J = annual juveniles survival probability, ψ_{em} = annual emigration rate, $\psi_{O,I}$ = annual rate of return in Brittany if previously emigrated, zhp = annual probability to be resident the first winter. The vertical and horizontal lines show the limits of the 95% BCI, points indicate the posterior means. The mode of the correlation coefficient (r) and the 95% BCI (parentheses) are also indicated. The probabilities that the correlation coefficient was positive ($p(r > 0)$) or negative ($p(r < 0)$) are also given.

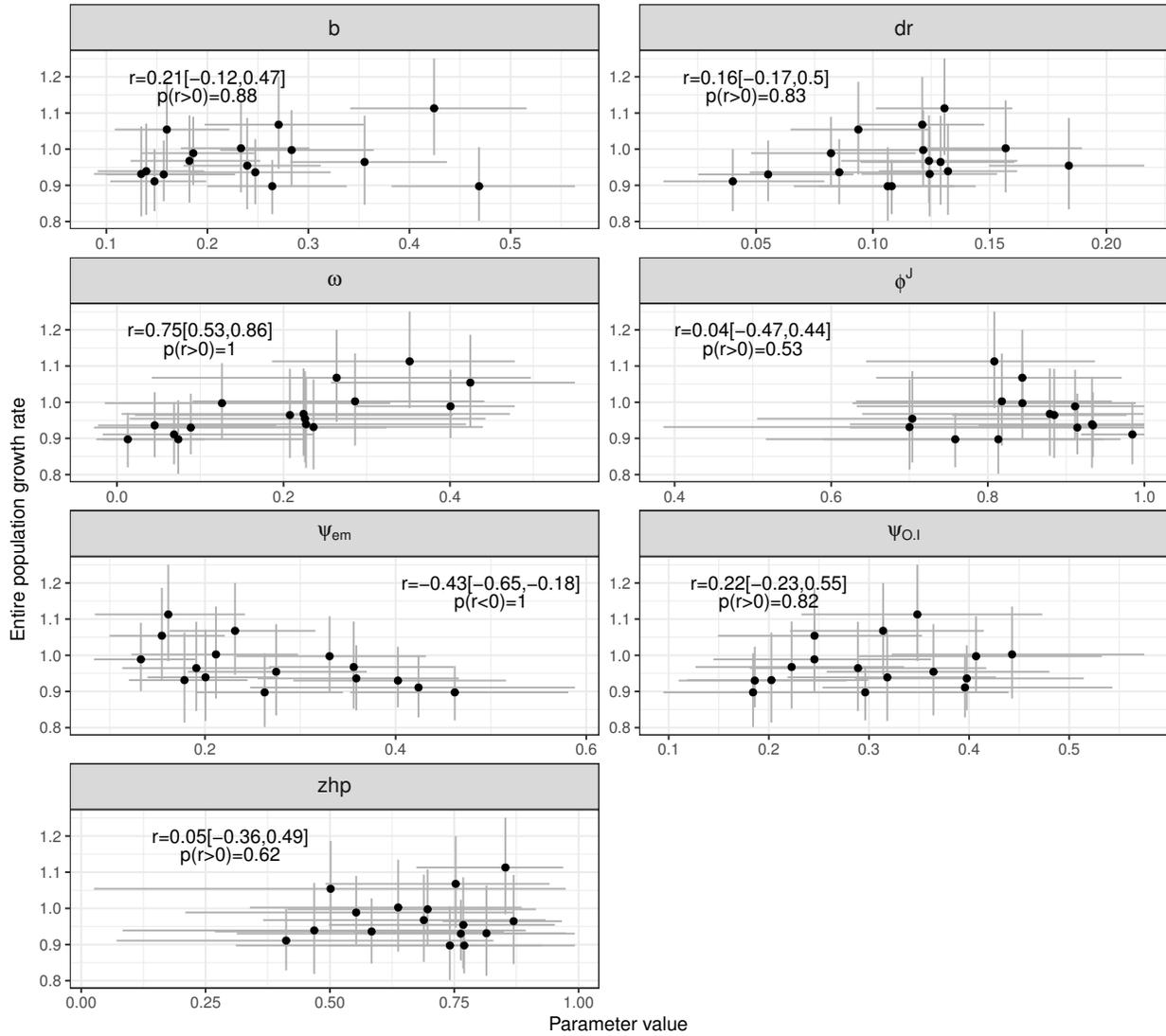


Figure C.12: **Correlation between annual growth rates of the entire population and annual estimates of demographic rates.** b = annual fecundity rate, dr = annual death rate, ω = annual immigration rate, ϕ^J = annual juveniles survival probability, ψ_{em} = annual emigration rate, $\psi_{O,I}$ = annual rate of return in Brittany if previously emigrated, zhp = annual probability to be resident the first winter. The vertical and horizontal lines show the limits of the 95% BCI, points indicate the posterior means. The mode of the correlation coefficient (r) and the 95% BCI (parentheses) are also indicated. The probabilities that the correlation coefficient was positive ($p(r > 0)$) or negative ($p(r < 0)$) are also given.

C.6.5 Correlation of different population sizes with demographic rates

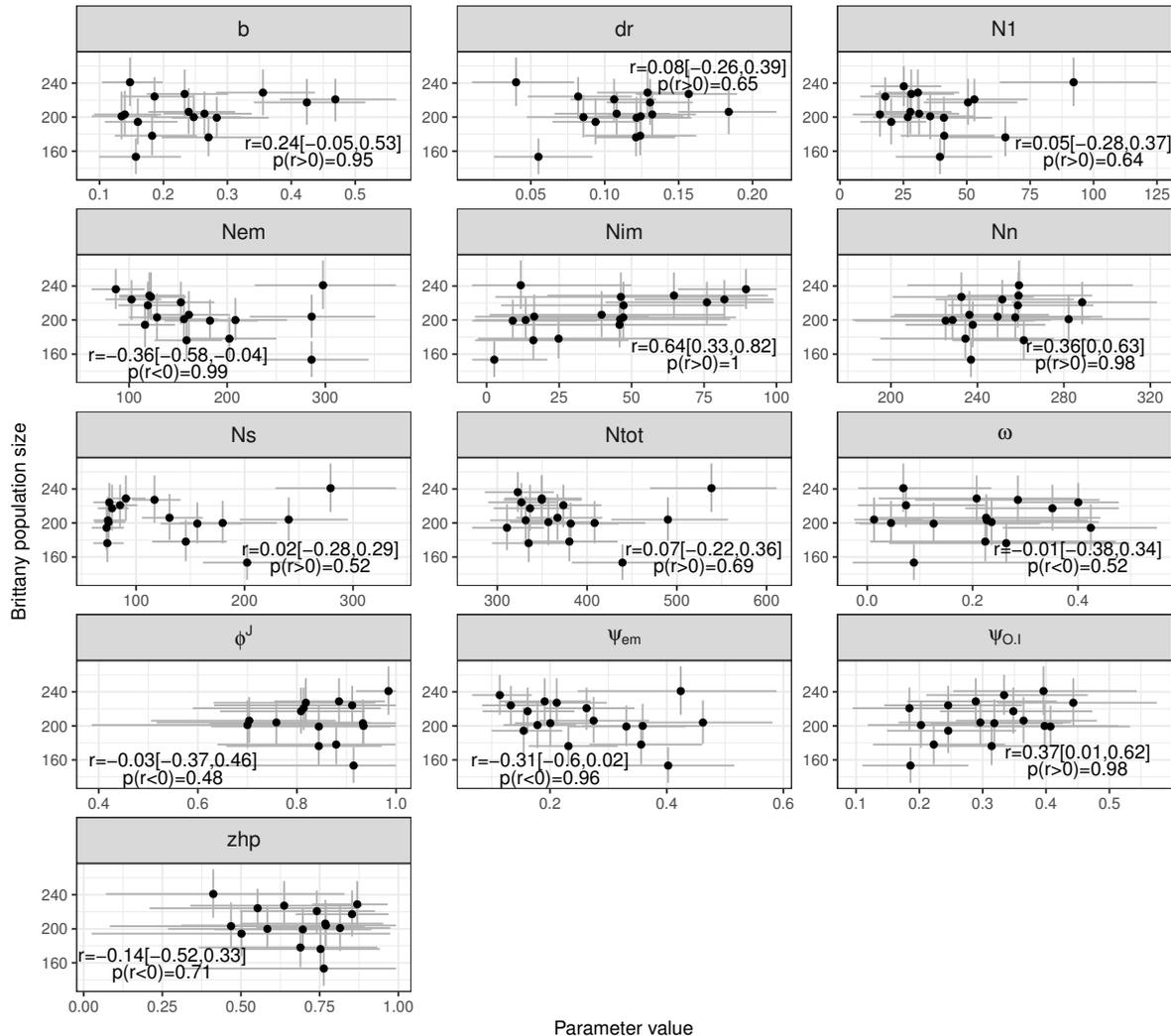


Figure C.13: **Correlation between annual Brittany population size and different annual demographic metrics.** b = annual fecundity rate, dr = annual death rate, N1 = annual number of 1 year old cohort, Nem = annual number of emigrants, Nim = annual number of immigrant, Nn = annual number of North wintering sub-population, Ns = annual number of South wintering sub-population, Ntot = annual size of Brittany's population + emigrants, ω = immigration rate, ϕ^J = juveniles survival probability, ψ_{em} = annual emigration rate, $\psi_{O,I}$ = annual rate of return to in Brittany if previously emigrated, zhp = annual probability to be resident the first winter. The vertical and horizontal lines show the limits of the 95% BCI, points indicate the posterior means. Correlation coefficient (r) and the 95% BCI (parentheses) are also indicated. The probabilities that the correlation coefficient was positive ($p(r > 0)$) or negative ($p(r < 0)$) are also given.

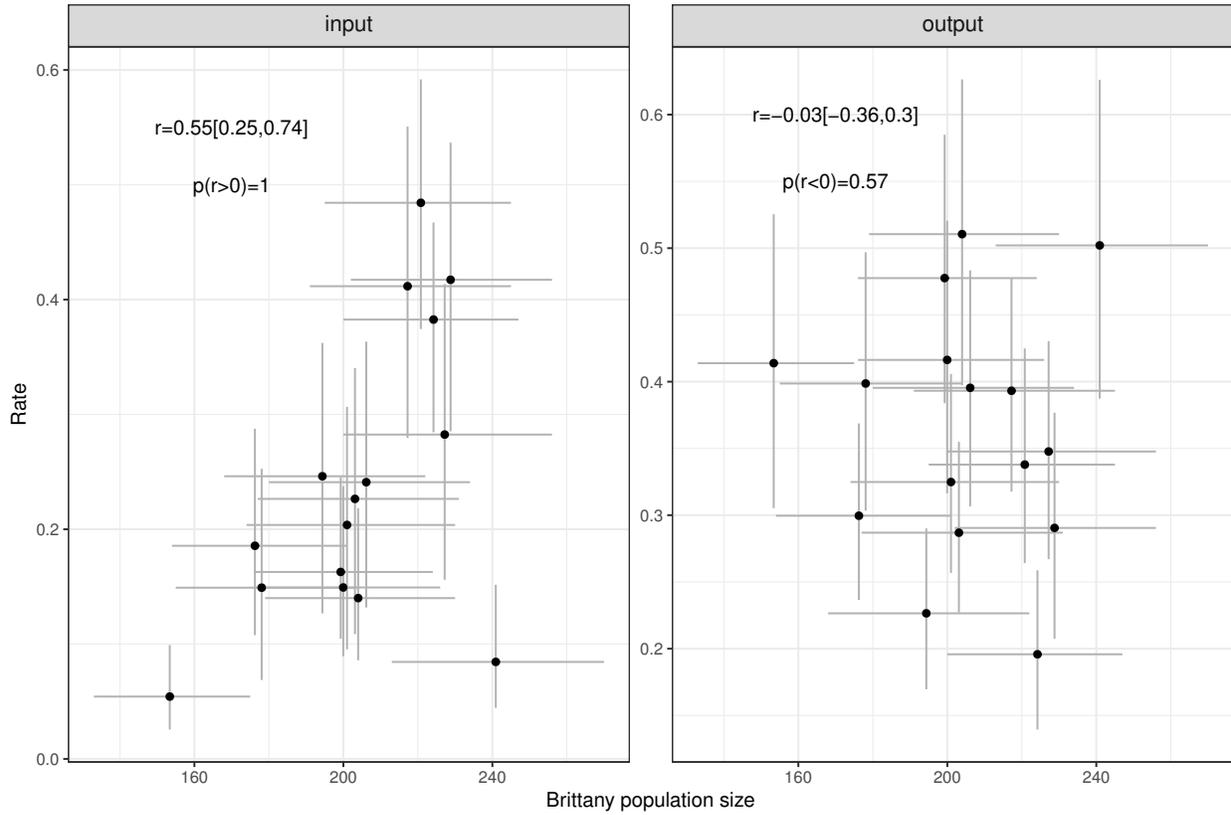


Figure C.14: **Correlation between annual Brittany population size and annual input and output rates.** Input = annual proportion of natality + immigration, output = annual proportion of mortality + emigration. The vertical and horizontal lines show the limits of the 95% BCI, points indicate the posterior means. Correlation coefficient (r) and the 95% BCI (parentheses) are also indicated. The probabilities that the correlation coefficient was positive ($p(r > 0)$) or negative ($p(r < 0)$) are also given.

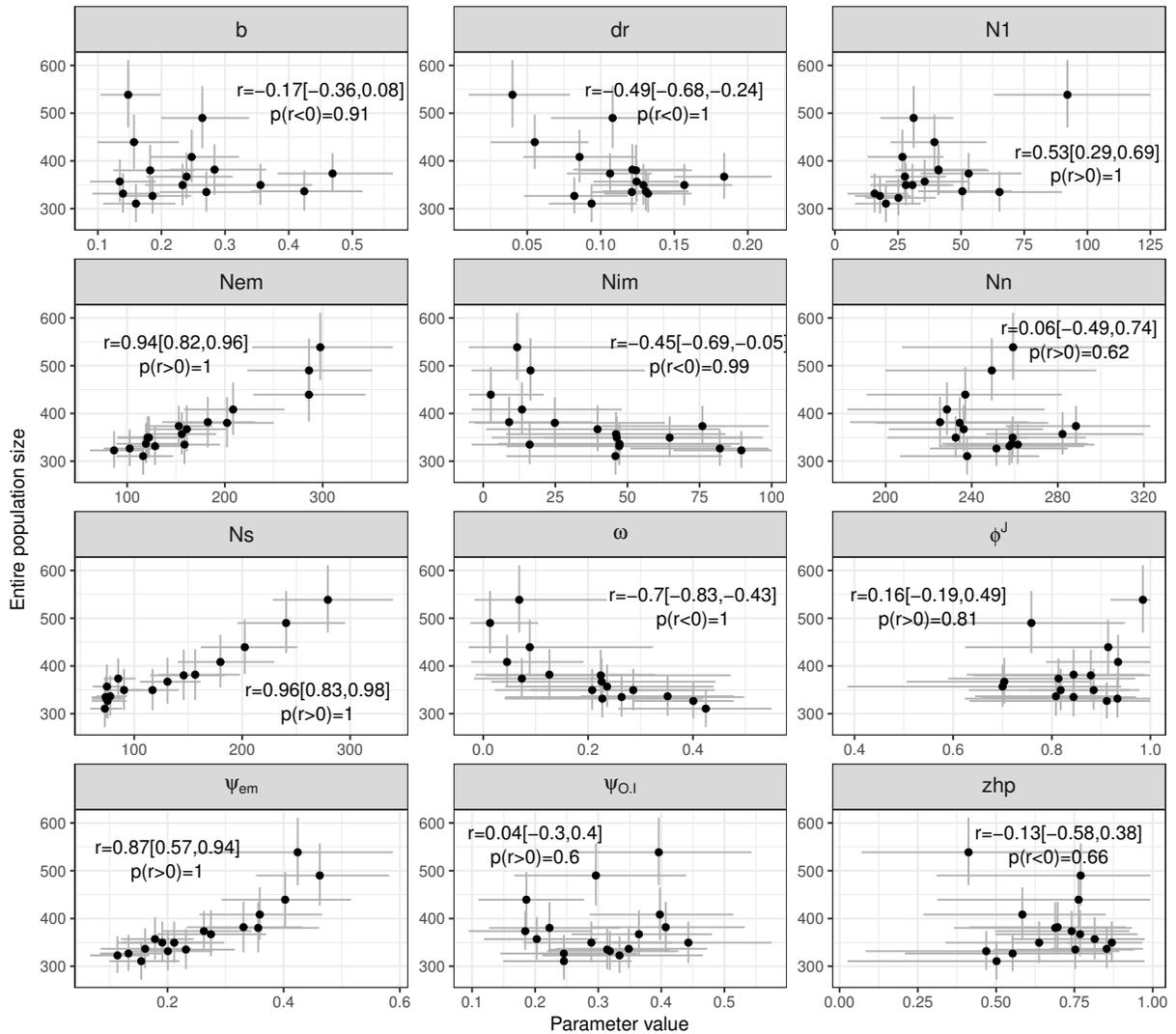


Figure C.15: **Correlation between annual entire population size and different annual demographic metrics.** b = annual fecundity rate, dr = annual death rate, $N1$ = annual number of 1 year old cohort, Nem = annual number of emigrants, Nim = annual number of immigrant, Ns = annual number of South wintering sub-population, ω = immigration rate, ϕ^J = juveniles survival probability, ψ_{em} = annual emigration rate, $\psi_{O,I}$ = annual rate of return to in Brittany if previously emigrated, zhp = annual probability to be resident the first winter. The vertical and horizontal lines show the limits of the 95% BCI, points indicate the posterior means. Correlation coefficient (r) and the 95% BCI (parentheses) are also indicated. The probabilities that the correlation coefficient was positive ($p(r > 0)$) or negative ($p(r < 0)$) are also given.

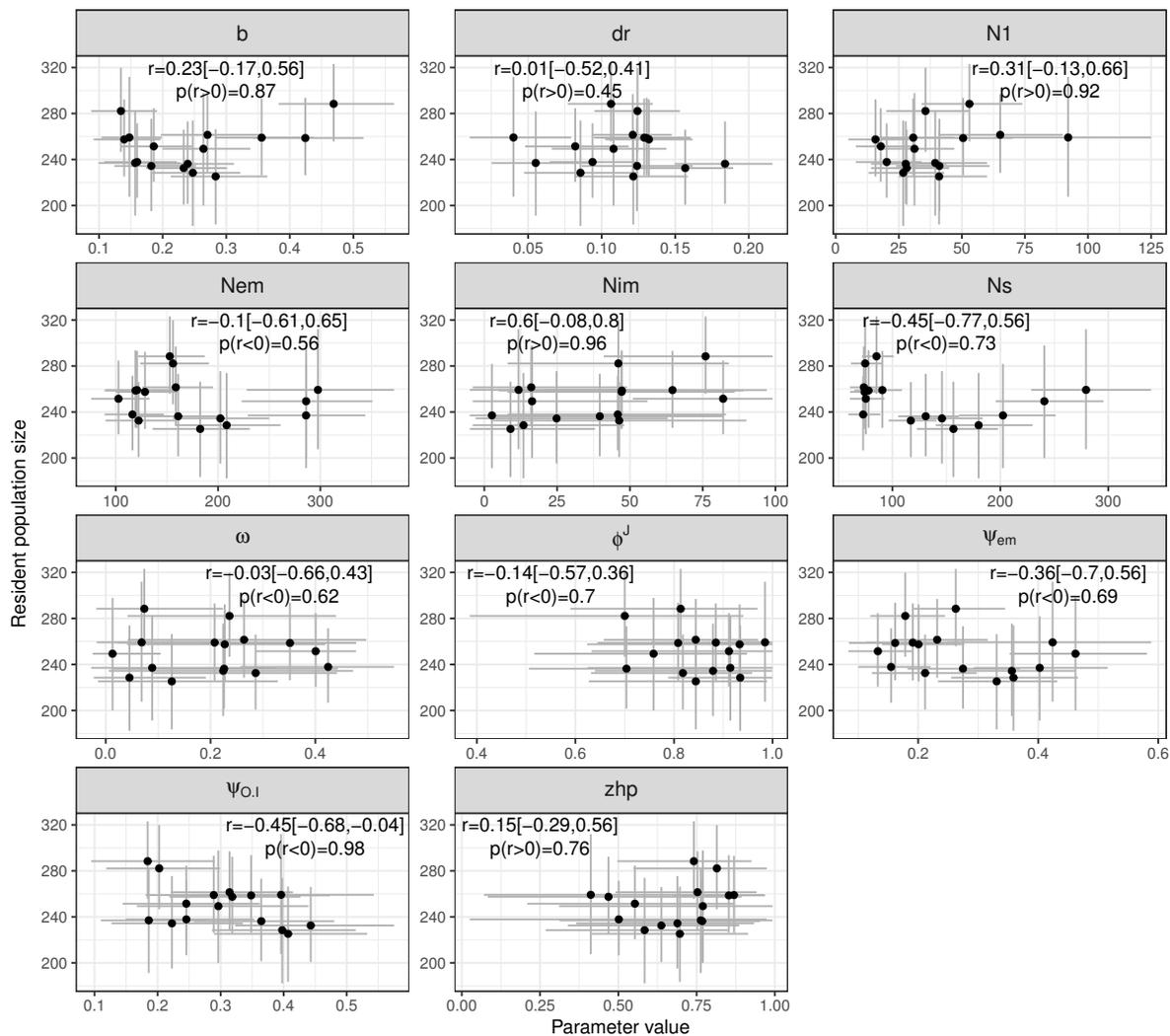


Figure C.16: **Correlation between annual resident population size and different annual demographic metrics.** b = annual fecundity rate, dr = annual death rate, $N1$ = annual number of 1 year old cohort, Nem = annual number of emigrants, Nim = annual number of immigrant, Nn = annual number of North wintering sub-population, Ns = annual number of South wintering sub-population, NB = annual size of Brittany's population, ω = immigration rate, ϕ^J = juveniles survival probability, ψ_{em} = annual emigration rate, $\psi_{O,I}$ = annual rate of return to in Brittany if previously emigrated, zhp = annual probability to be resident the first winter. The vertical and horizontal lines show the limits of the 95% BCI, points indicate the posterior means. Correlation coefficient (r) and the 95% BCI (parentheses) are also indicated. The probabilities that the correlation coefficient was positive ($p(r > 0)$) or negative ($p(r < 0)$) are also given.

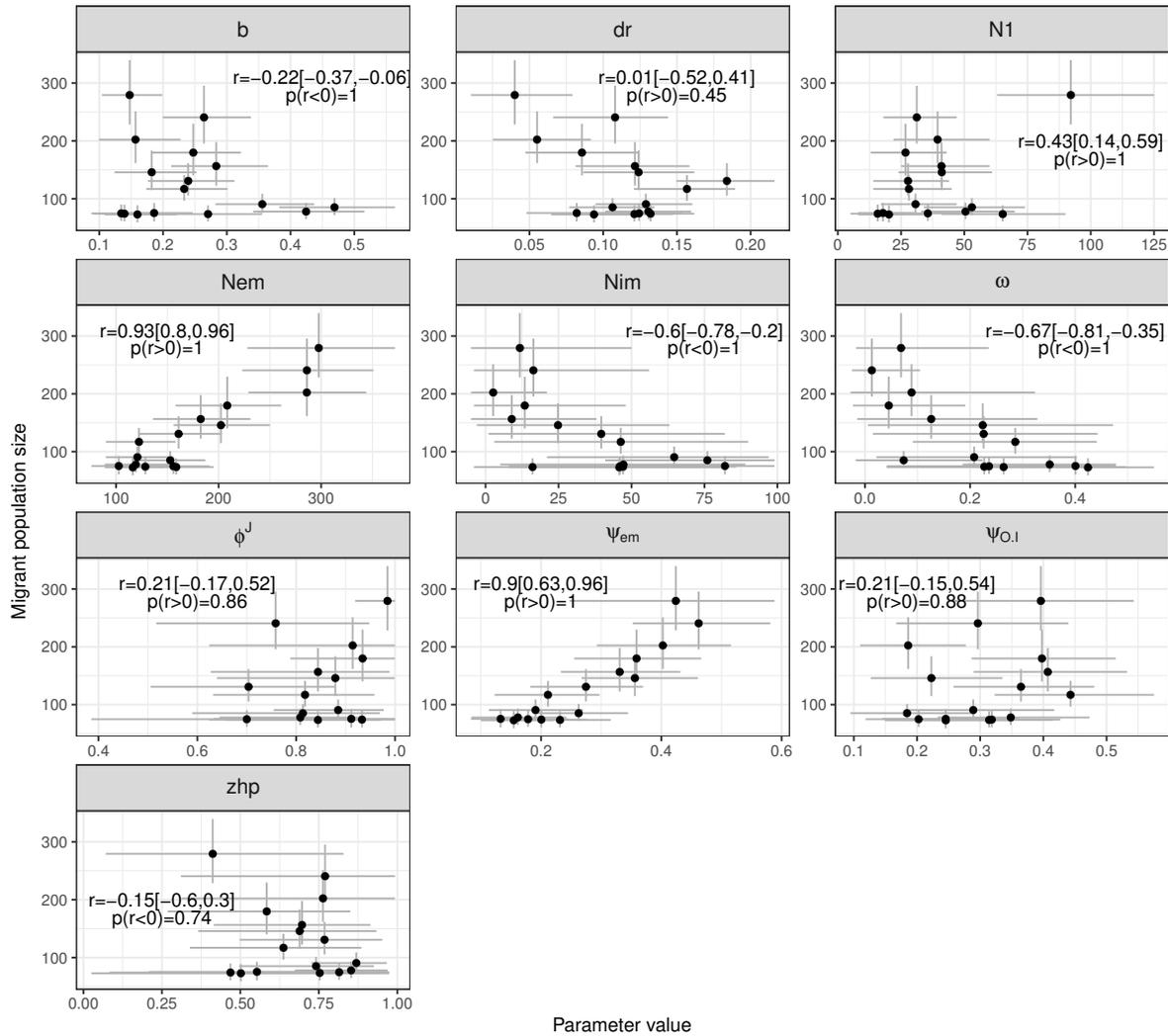


Figure C.17: **Correlation between annual migrant population size and different annual demographic metrics.** b = annual fecundity rate, dr = annual death rate, $N1$ = annual number of 1 year old cohort, Nem = annual number of emigrants, Nim = annual number of immigrant, Nn = annual number of North wintering sub-population, Ns = annual number of South wintering sub-population, NB = annual size of Brittany’s population, ω = immigration rate, ϕ^J = juveniles survival probability, ψ_{em} = annual emigration rate, $\psi_{O,I}$ = annual rate of return to in Brittany if previously emigrated, zhp = annual probability to be resident the first winter. The vertical and horizontal lines show the limits of the 95% BCI, points indicate the posterior means. Correlation coefficient (r) and the 95% BCI (parentheses) are also indicated. The probabilities that the correlation coefficient was positive ($p(r > 0)$) or negative ($p(r < 0)$) are also given.

C.6.6 Correlation of residents and migrants population growth rate with demographic metrics

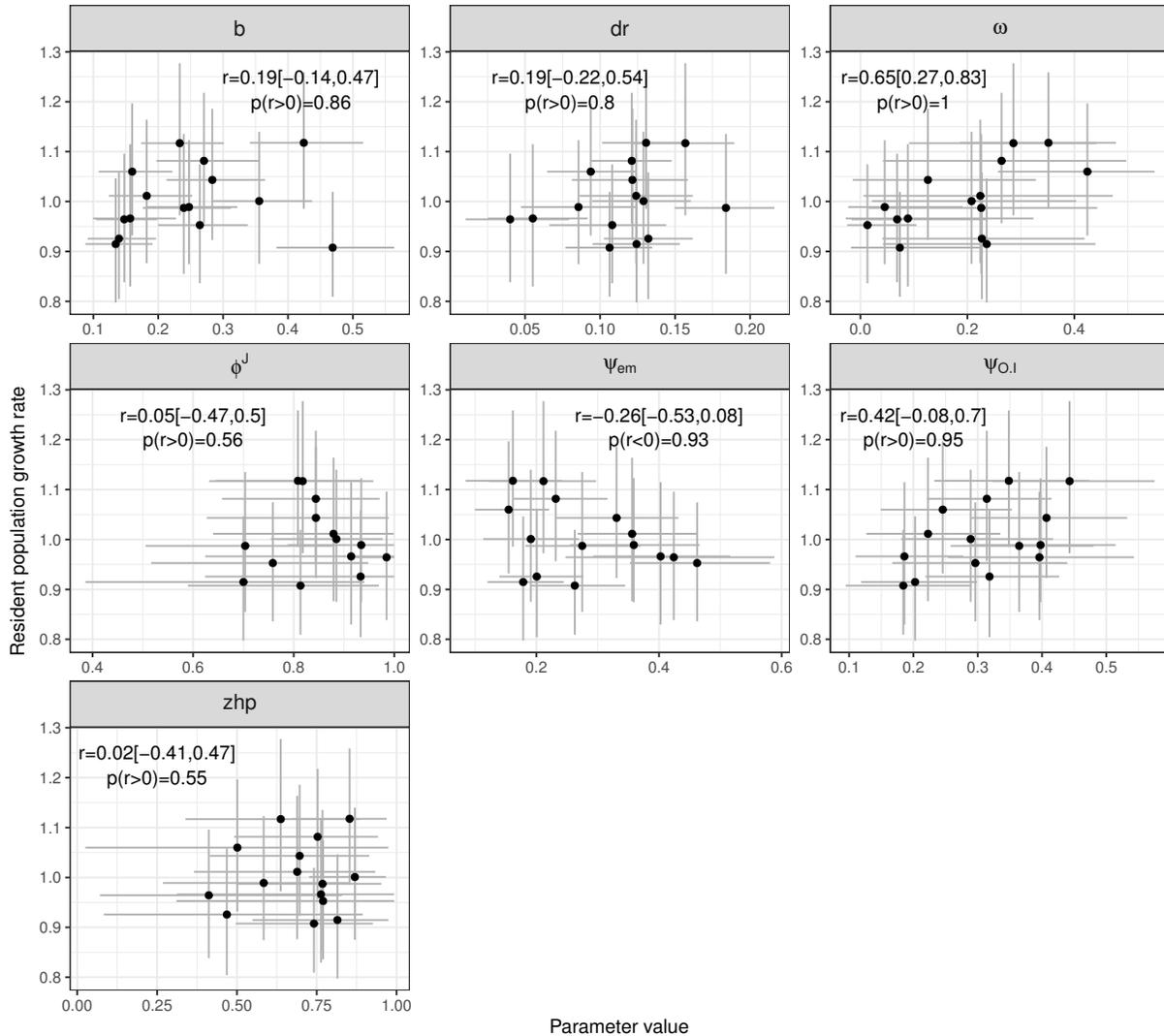


Figure C.18: **Correlation between annual resident population growth rate and different annual demographic metrics.** b = annual fecundity rate, dr = annual death rate, ω = immigration rate, ϕ^J = juveniles survival probability, ψ_{em} = annual emigration rate, $\psi_{O,I}$ = annual rate of return to in Brittany if previously emigrated, zhp = annual probability to be resident the first winter. The vertical and horizontal lines show the limits of the 95% BCI, points indicate the posterior means. Correlation coefficient (r) and the 95% BCI (parentheses) are also indicated. The probabilities that the correlation coefficient was positive ($p(r > 0)$) or negative ($p(r < 0)$) are also given.

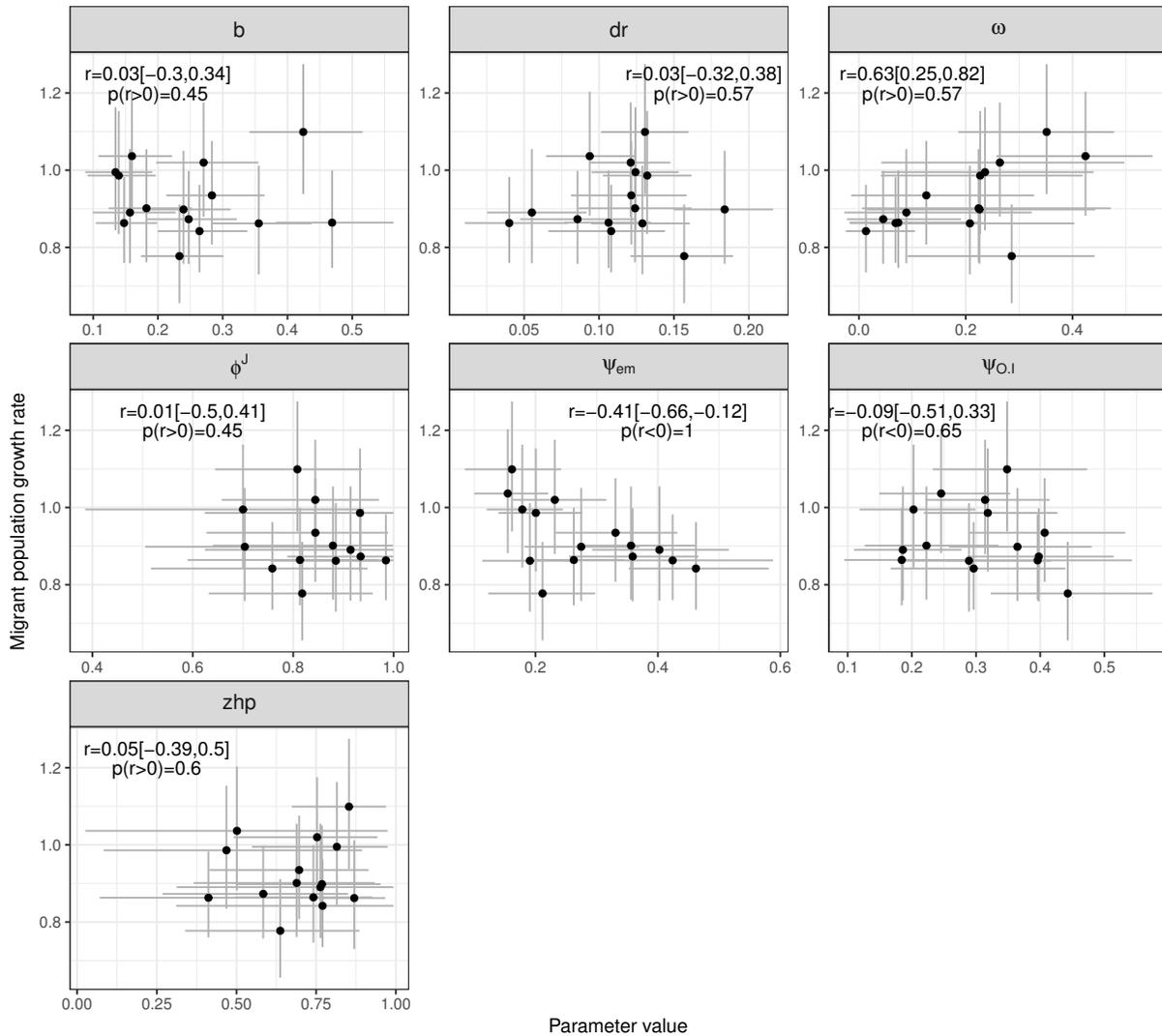


Figure C.19: **Correlation between annual entire population size and different annual demographic metrics.** b = annual fecundity rate, dr = annual death rate, ω = immigration rate, ϕ^J = juveniles survival probability, ψ_{em} = annual emigration rate, $\psi_{O,I}$ = annual rate of return to in Brittany if previously emigrated, zhp = annual probability to be resident the first winter. The vertical and horizontal lines show the limits of the 95% BCI, points indicate the posterior means. Correlation coefficient (r) and the 95% BCI (parentheses) are also indicated. The probabilities that the correlation coefficient was positive ($p(r > 0)$) or negative ($p(r < 0)$) are also given.

C.6.7 Correlation between population size and age class

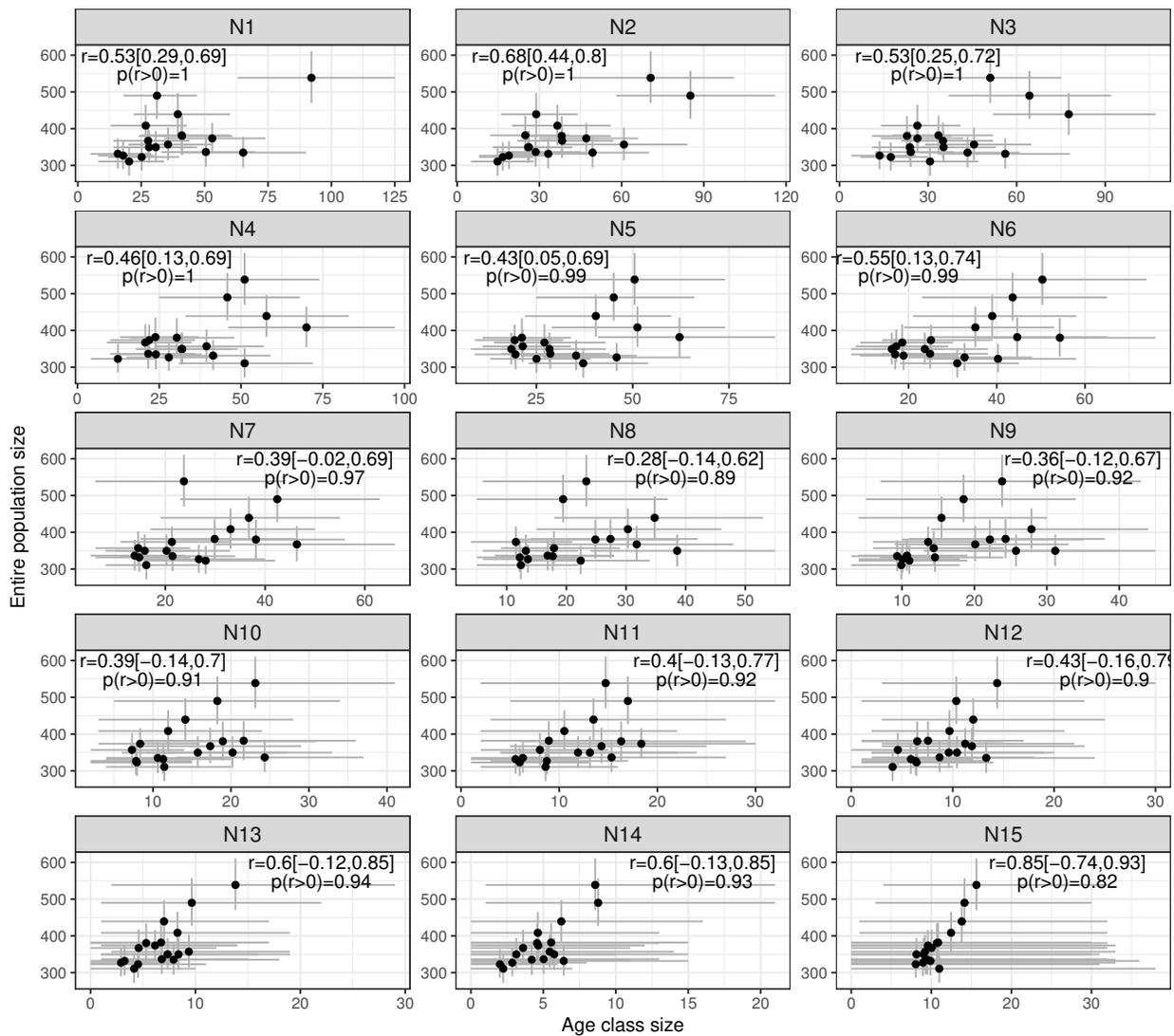


Figure C.20: Correlation between entire population size and age classes size. N_x = number of individuals of age class x . Correlation coefficient (r) and the 95% BCI (parentheses) are also indicated. The probabilities that the correlation coefficient was positive ($p(r > 0)$) or negative ($p(r < 0)$) are also given.

C.6.8 Posterior distribution of model parameters

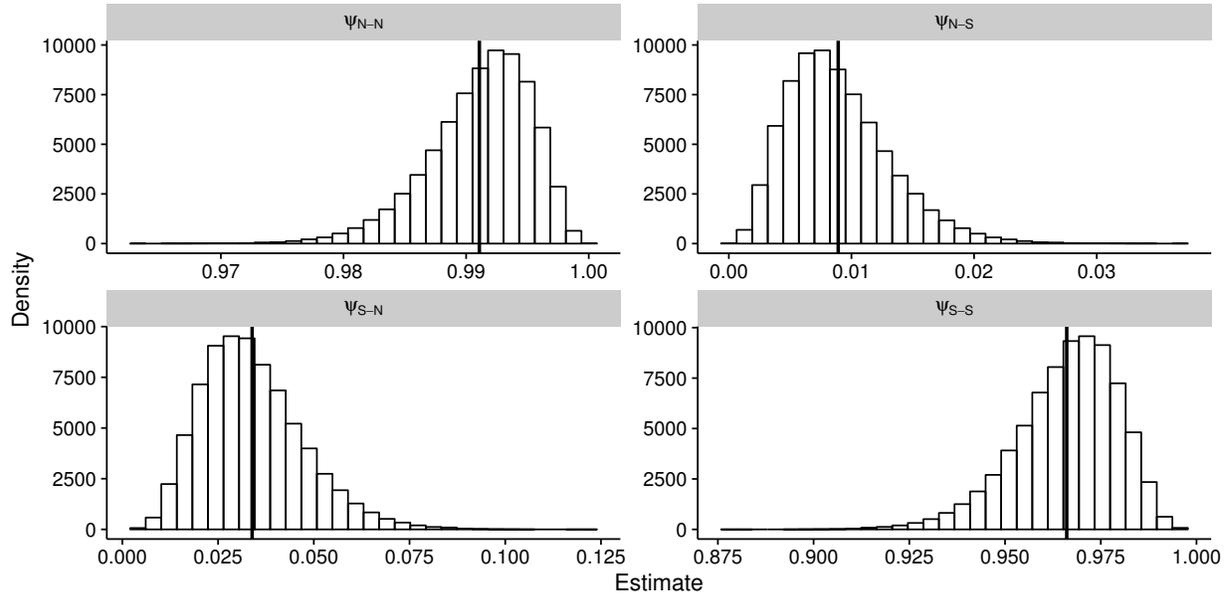


Figure C.21: **State transition of adults during Winter.** Posterior distribution of the transition probability between the North and South of Europe during winter ψ on the logit scale. N: North and S: South. Mean value is indicated with a vertical line.

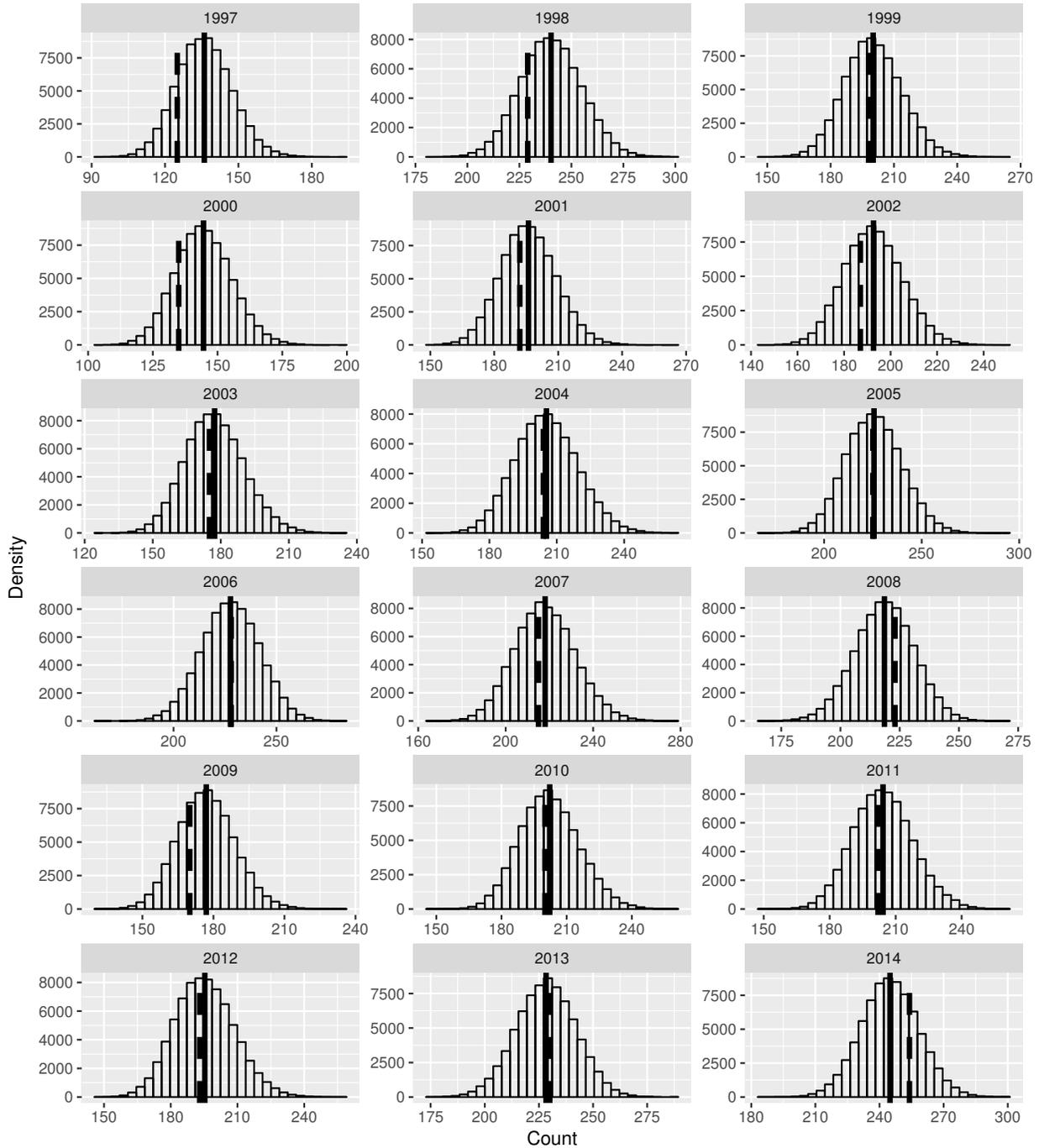


Figure C.22: **Posterior distribution of the estimated number of pairs.** Estimation from the annual count of Females (breeding pairs). The vertical line indicates the mean and the dashed line the observation value.

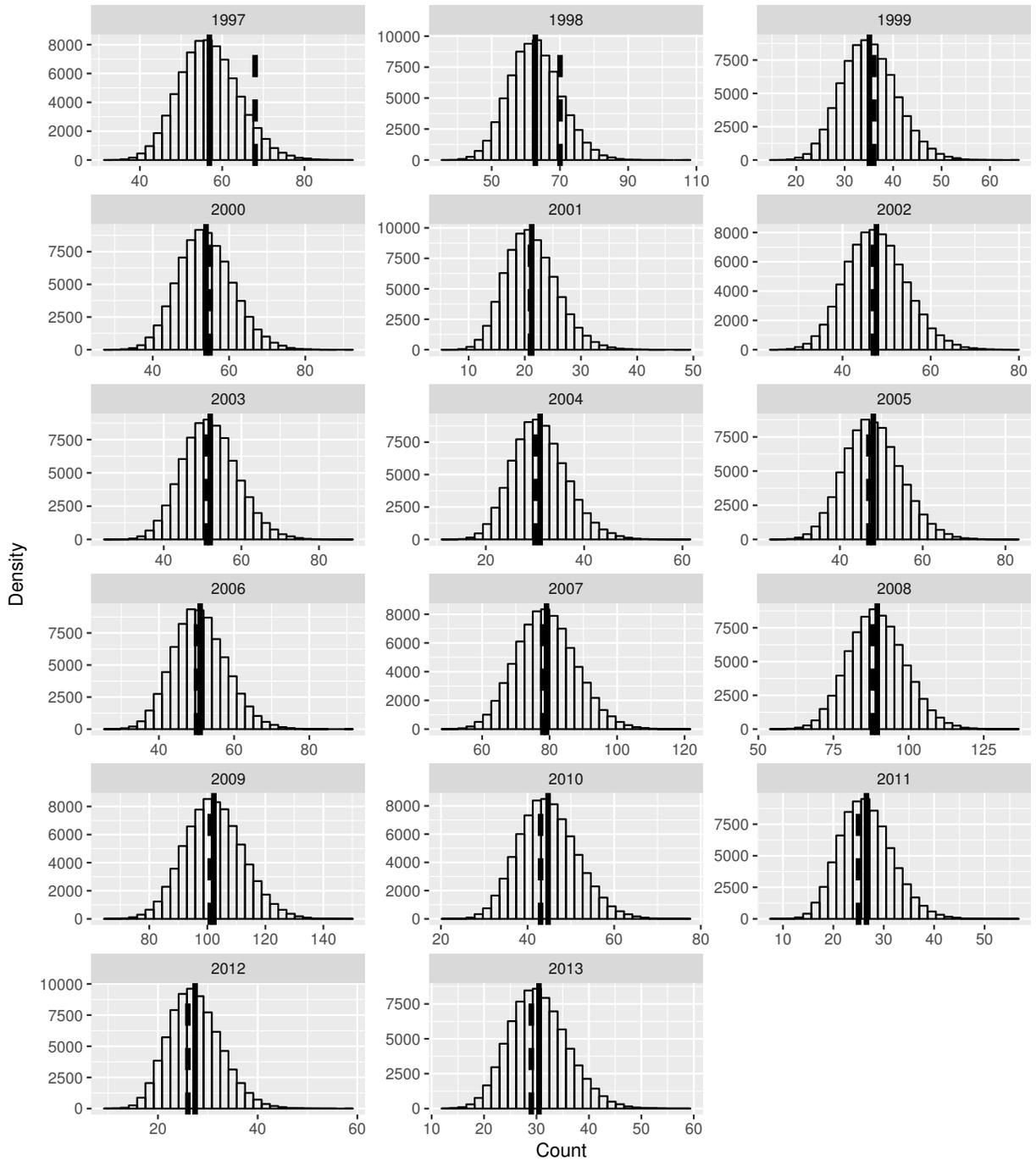


Figure C.23: **Posterior distribution of the estimated number of Juveniles.** Estimation from the annual count of Fledglings. The vertical line indicates the mean and the dashed line the observation value.

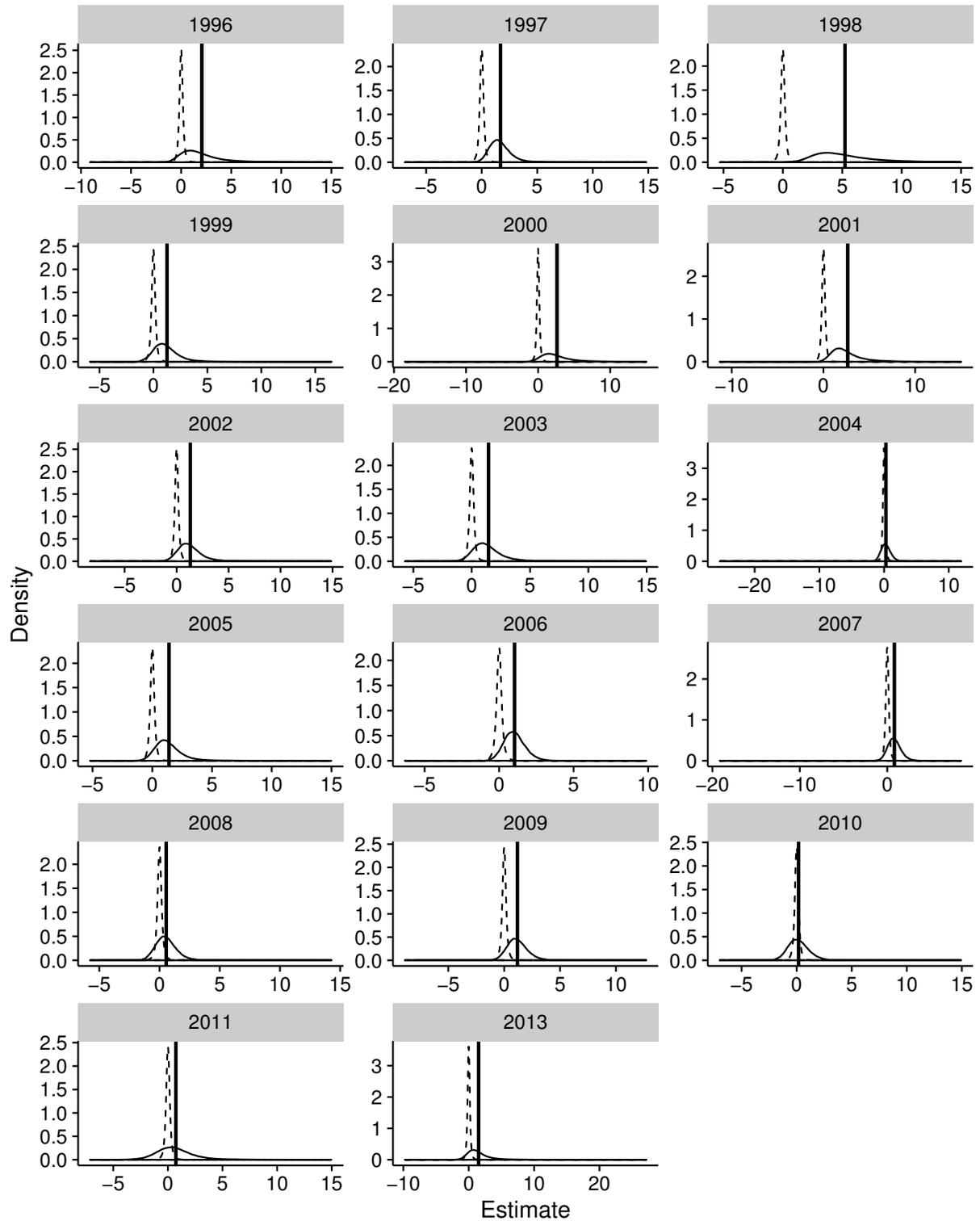


Figure C.24: **Juvenile survival annual effect.** Posterior distribution of parameter α_1 on the logit scale. Mean value is indicated with a vertical line and prior distribution in dashed line.

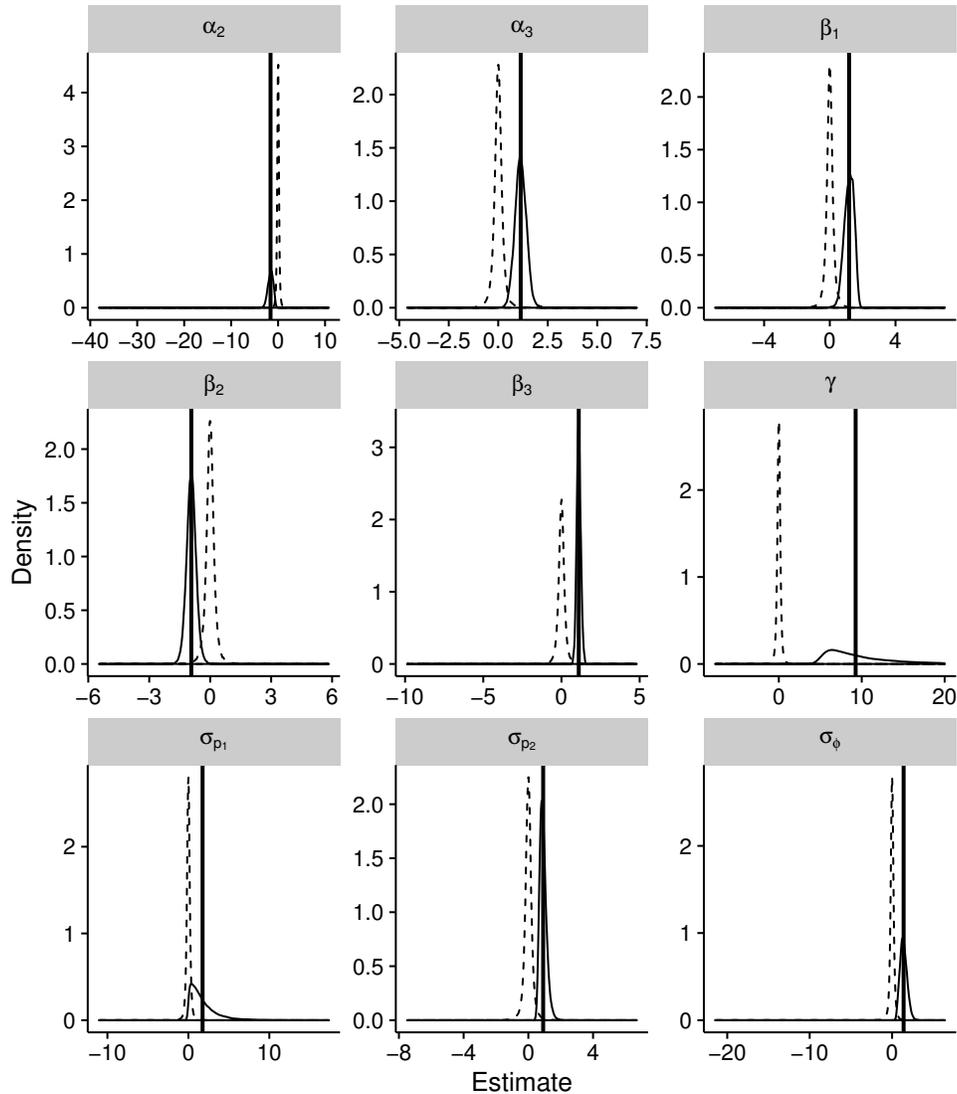


Figure C.25: **Posterior distribution of different parameters.** Density of posterior distribution shown on the logit scale. α_2 is the trend age parameter of adult survival regression with mean -2.05 (BCI: -3.13,-1.07). β_1 is the intercept of the juvenile survival with mean 0.83 (BCI: 0.21,1.42). β_2 is the intercept of the detection probability with mean -0.91 (BCI: -1.39,-0.45). γ is the effect of breeding area on detection probability with mean 11.5 (BCI: 6.68,19.95), this positive value indicate a significant higher detection probability in Brittany. σ_{p_1} is the standard error of the random time effect for the detection probability of breeding birds inside of Brittany with mean 1.84 (BCI: 0.06,5.9). σ_{p_2} is the standard error of the random time effect for the detection probability of breeding birds outside of Brittany with mean 0.91 (BCI: 0.58,1.41). σ_ϕ is the standard error of individual random effect in the survival probability regression with mean 1.75 (BCI: 1,2.59). Mean value is indicated with a vertical line and prior distribution in dashed line.

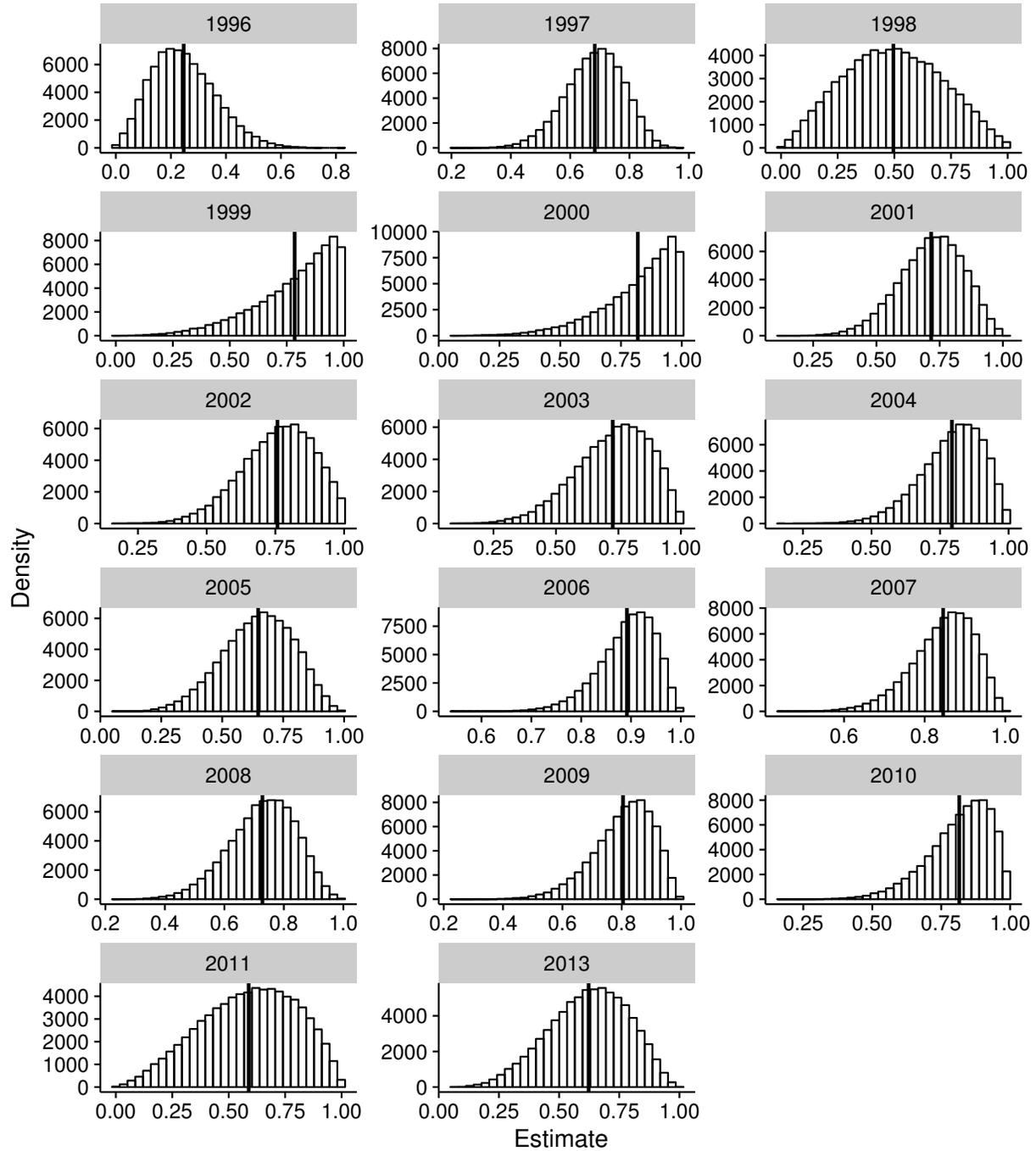


Figure C.26: **Annual juvenile dispersal during Winter.** Posterior distribution of the probability to stay in the North of Europe during winter $\psi_{1,t}$ on the logit scale. Mean value is indicated with a vertical line.

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Title: Evolutionary demography of a partial migrant shorebird species

Thesis supervisor: Emmanuelle CAM

Place and date of defence: Toulouse, 30 October 2017

Abstract: Global warming causes changes in the dynamics and distribution of populations. I used a 19-year study, in Brittany, on a long-lived and partial migrant, the Pied Avocet, to quantify and compare the demographic rates associated with different migration strategies. Survival rates and associated senescence patterns were similar in residents and in migrants, but migrants exhibited a delayed recruitment age. Reproductive investment was higher and senescence was absent in individuals recruited at the age of one year, whereas those who began to reproduce later showed reproductive senescence. The fitness of migrants was lower than the fitness of residents, which explained their decline over the study period, while the resident population remained stable. Low productivity, due to predation, caused the Brittany population to decline despite a high immigration rate, which questions local conservation policies.

Keywords: *Bayesian model, fitness, individual heterogeneity, migration cost, partial migration, population dynamics, population structure, recruitment age, reproductive investment, Recurvirostra avosetta, senescence, survival.*

Administrative discipline: Ecology, biodiversity and evolution

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Titre: Demographie évolutive chez une espèce de limicole migratrice partielle

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Lieu et date de soutenance: Toulouse le 30 octobre 2017

Résumé: Le réchauffement climatique entraîne des changements dans la dynamique et la distribution des populations. J'ai utilisé une étude de 19 ans, en Bretagne, sur un limicole longévif et migrateur partiel, l'Avocette élégante, pour quantifier et comparer les paramètres démographiques associés aux différentes stratégies de migration. Les taux de survie et les manifestations de la sénescence associées étaient similaires chez les résidents et les migrants, mais les migrants montraient un âge de recrutement plus tardif que les résidents. L'investissement reproductif était plus élevé et exempt de sénescence chez les individus recrutés à l'âge d'un an, alors que ceux commençant à se reproduire plus tard subissaient de la sénescence reproductrice. La fitness des migrants était inférieure à celle des résidents, ce qui explique leur déclin pendant la période étudiée, alors que la population résidente est restée stable. La faible productivité, due à la prédation, entraîne le déclin de la population bretonne malgré un taux d'immigration important, ce qui doit absolument être pris en compte lors de la définition des politiques locales de conservation.

Mots-clés: *âge de recrutement, coût de migration, dynamique de population, fitness, hétérogénéité entre individus, investissement dans la reproduction, migration partielle, modèle Bayésien, *Recurvirostra avosetta*, sénescence, structure de population, survie.*

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