Universidade de Aveiro
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HUGO RAFAEL SOARES FERREIRA

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DEMOGRAPHIC PROCESSES OF A LONG–DISTANT MIGRATORY WATERBIRD FACING GLOBAL CHANGES

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Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia e Ecologia das Alterações Globais, realizada sob a orientação científica do Doutor José Augusto Belchior Alves, Investigador Principal do CESAM da Universidade de Aveiro.

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“Learning things is one of the fundamental joys of being human grasping the world's wonders, discovering how to make and build things, understanding the past, the future, oneself, others, I simply wish to learn all I can!”

Tatsuya Endo, Spy Family
(Translation: Casey Loe)

“Et si j`avais l`opportunité de reprendre cette aventure depuis le début ? Je ferais la même chose…en redoublant d`énergie et d`opiniâtreté !”

Luc Hoffmann

Dedico este trabalho ao meu vagalume, padrinho, pai e mãe, sem vocês a curiosidade, mãos e paixão que escreveram este trabalho não existiriam...

Hugo Ferreira

o júri

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	Doutor José Augusto Belchior Alves Investigador Principal da Universidade de Aveiro (orientador)

agradecimentos

A few years ago, I found myself defeated on the warm shores of southern Portugal. Outside, the scenario was sunny and beautiful, but inside my mind, it was dark and gloomy. My youthful passion for science was fading, and I was on the verge of giving up, confirming some of my biology teacher's dire warnings... there is no point in pursuing a life in ecology...However, my stubbornness would not let me give up, and fortunately, I also had family and friends who helped me keep going…Out of desperation, I quit my job and flew into the unknown. I arrived in a place where I had little knowledge or interest in the language, food, or nature, but it felt like my only chance to get a glimpse of what it might be like to be one of the people in the science documentaries that had captivated and inspired me as a child. What was supposed to be a nine-month volunteering experience turned into this thesis. This thesis was born out of a new passion for the Camargue and the Spoonies that reignited the same flame that drove me as a child, the curiosity to know more and the will to give something back to a place and people that allowed me to live my dream. I would therefore like to thank the Tour du Valat and what makes it so special, its people. Thank you for this incredible journey!

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agradecimentos (continuação)

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palavras-chave

Áreas protegidas; Captura-Recaptura; Comportamentos migratórios; Desempenho reprodutor; Fenologia reprodutora; Impactos antropogénicos; Monitorização de longa-duração; Ontogenia; *Platalea leucorodia*.

resumo

Devido ao desenvolvimento humano contínuo e crescente, as alterações globais estão a ocorrer a um ritmo alarmante. As atividades antropogénicas têm não só um impacto direto significativo na perda contínua de habitats e, consequentemente, na biodiversidade, mas também efeitos indiretos, como a redução da capacidade de resposta das espécies às alterações globais. As aves migratórias, que atualmente estão a sofrer declínios globais rápidos e acentuados, estão entre as taxas mais afetadas pelas alterações climáticas globais e pela perda de habitats. No entanto, nem todas as espécies deste grupo estão em declínio e algumas parecem estar a recuperar, pelo menos a nível local, como é o caso de várias espécies de aves aquáticas na Europa. Compreender como estas espécies em recuperação são capazes de lidar com as alterações ambientais em curso, tanto em termos de clima como de habitat, pode fornecer informações valiosas sobre a sua resiliência.

Um exemplo notável de aumento da população após anos de declínio é o Colhereiro-europeu, uma espécie parcialmente migratória que se distribui desde a costa atlântica oriental até ao sudeste asiático. Nesta tese, investiguei o papel das condições ambientais, do comportamento e da experiência na resposta desta ave aquática às alterações globais e locais causadas por fatores antropogénicos diretos e/ou indiretos. Especificamente, esta tese é composta por seis capítulos empíricos que têm como objetivo de (i) explorar como o desempenho reprodutor está associado às condições ambientais locais; (ii) avaliar o impacto dos fatores antropogénicos ao longo do ciclo anual e entre diferentes grupos etários; e (iii) compreender o efeito do comportamento migratório na sobrevivência e produtividade da espécie.

Embora se esperasse que padrões geográficos ou climáticos em escala continental influenciassem a fenologia da reprodução, a condição corporal das crias e o volume dos ovos, apenas foi detetada uma tendência latitudinal geral na altura da reprodução, com os colhereiros das latitudes mais baixas a começarem a postura mais cedo do que os das latitudes mais altas (Capítulo 2). Além disso, os resultados sugerem que adultos experientes se reproduzem mais cedo e provavelmente produzem crias de melhor qualidade do que os inexperientes (Capítulo 3). Os colhereiros respondem ativamente à poluição na Camargue (Sul de França), evidenciado pelo uso crescente de materiais artificiais no revestimento dos seus ninhos (Capítulo 4). Apesar de a Camargue ser uma área fragmentada, com várias perturbações antropogénicas e níveis de proteção variáveis (Capítulo 5), os colhereiros beneficiam das zonas geridas para aves aquáticas, seja para fins de conservação ou de caça.

resumo (continuação)

Por fim, demonstro como a migração de longa distância, que inclui a travessia de grandes barreiras ecológicas, pode ser dispendiosa para a sobrevivência e produtividade dos colhereiros e como estes se tornam mais capazes de enfrentar esses desafios com a idade (Capítulo 3, 6 e 7). Também exploro o impacto da degradação das zonas húmidas nas taxas demográficas e discuto o potencial recrutamento de colhereiros para regiões de reprodução ao longo das rotas migratórias, o que pode explicar a aparente baixa filopatria desta espécie (Capítulo 7).

Esta tese explora a forma como uma espécie de ave aquática moderadamente especializada pode beneficiar das atuais alterações globais, explorando novas oportunidades, tais como a utilização de espécies invasoras como novas fontes de alimento e a utilização de zonas húmidas geridas para atividades económicas e recreativas. Destaca também como a melhoria do desempenho (e.g., reprodução e migração), impulsionada pela idade e pelas sugestões sociais de conspecíficos mais velhos, aumenta ainda mais a capacidade do colhereiro para prosperar em ambientes em mudança. Por fim, questiona a rapidez com que um cenário atualmente positivo pode mudar face a uma degradação significativa das zonas húmidas ou da falta de flexibilidade de adaptação às alterações globais em curso.

keywords

Anthropogenic impacts; Breeding performance; Breeding phenology; Capture-Recapture; Long-term monitoring; Migratory behaviours; Ontogeny; *Platalea leucorodia*; Protected areas.

abstract

Global changes are occurring at an alarming rate due to continued and increasing human development. Anthropogenic activities not only have a profound direct impact on the ongoing loss of habitats and thus biodiversity, but also have indirect effect, for example on the ability of species to respond to global changes. Migratory birds, which are currently experiencing high and fast global declines, are among the taxa most affected by both climate global changes and habitat loss. However, not every species in this group is declining and some appear to be recovering, at least locally, such as several waterbird species in Europe. Understanding how these recovering species are able to cope with ongoing environmental changes, both in terms of climate and habitat, can provide insights into their resilience.

A notable example of population increase after years of decline is the Eurasian spoonbill, a partial-migratory species that ranges from the East-Atlantic Coast to the Southeast Asia. In this thesis, I investigated the role of environmental conditions, behaviour and experience in influencing the response of this waterbird to global and local changes driven by direct and/or indirect anthropogenic factors. Specifically, this thesis is comprised of six empirical chapters aiming at (i) exploring how breeding performance is associated with environmental conditions experienced locally; (ii) assessing the impact of anthropogenic factors throughout the annual cycle and across age groups; and (iii) understanding the effect of migratory behaviour on survival and productivity.

While geographical or climatic patterns across a continental scale were expected to influence breeding phenology, body condition of chicks, and egg volume, only an overall latitudinal trend in the timing of breeding was detected; with spoonbills at lower latitudes generally starting to lay earlier than those at higher latitudes (Chapter 2). In addition, the results suggest that experienced adults breed earlier and likely produce better quality chicks than inexperienced ones (Chapter 3). Spoonbills do respond to existing pollution in Camargue (South France), as shown by the increasing use of artificial materials in their nest lining (Chapter 4). Although Camargue is a fragmented area with several anthropogenic disturbances and varying levels of protection (Chapter 5), spoonbills benefit from areas managed for waterbirds, whether for conservation or hunting purposes. Finally, I show how long-distance migration, involving the crossing of major ecological barriers, can be costly for the survival and productivity of spoonbills and how they are better able to cope with such challenges as they age (Chapter 3, 6, and 7).

abstract (continued)

I also explore the impact of wetland degradation on demographic rates and discuss the potential recruitment of spoonbills to breeding regions along migratory routes, which may explain the apparently low philopatry in this species (Chapter 7).

This thesis explores how a moderately specialised waterbird species can benefit from current global changes by exploiting new opportunities, such as using invasive species as new food sources and using wetlands managed for economic and recreational activities. It also highlights how improved performance (e.g., breeding and migration), driven by age and social cues from older conspecifics, further enhances spoonbill's ability to thrive in changing environments. Finally, it discusses how quickly a currently positive scenario displayed by waterbirds may change in the face of severe wetland degradation or of a lack of adaptive flexibility to ongoing global changes.

mots-clés

Capture-Recapture; Comportements migratoires; Impacts anthropogéniques; Ontogénie; Phénologie de reproduction; *Platalea leucorodia*; Succès reproducteur; Suivi à long terme; Zones protégées.

résumé

Les changements globaux se produisent à un rythme alarmant en raison du développement humain continu et croissant. Les activités anthropiques entraînent non seulement une perte directe et significative des habitats, et donc de la biodiversité, mais elles influencent également, de manière indirecte, la capacité des espèces à répondre aux changements globaux. Les oiseaux migrateurs, qui connaissent actuellement un déclin important et rapide à l'échelle mondiale, font partie des taxons les plus touchés par les changements climatiques mondiaux et la perte d'habitat. Cependant, toutes les espèces de ce groupe ne sont pas en déclin et certaines semblent se rétablir, au moins localement, comme l’atteste plusieurs espèces d'oiseaux d'eau en Europe. Étudier la manière dont ces espèces en voie de rétablissement s’adaptent aux changements actuels, que ce soit au niveau du climat ou de leur habitat, peut fournir des indications sur la capacité de résilience des espèces d’oiseaux migrateurs.

Un exemple notable d'une croissance de la population après des années de déclin est celui de la Spatule blanche, une espèce partiellement migratrice qui s'étend de la côte est de l'Atlantique à l'Asie du Sud-Est. Dans cette thèse, j'ai étudié le rôle des conditions environnementales, du comportement et de l'expérience dans l'influence de la réponse de cet oiseau d'eau aux changements globaux et locaux induits par des facteurs anthropiques directs et/ou indirects. Plus précisément, cette thèse comprend six chapitres visant à (i) explorer la façon dont le succès de reproduction est associé aux conditions environnementales rencontrées localement ; (ii) évaluer l'impact des facteurs anthropiques tout au long du cycle annuel et selon l'âge ; et (iii) comprendre l'effet du comportement migratoire sur la survie et la productivité.

Alors que l'on s'attendait à ce que la phénologie de la reproduction, la condition corporelle des poussins et le volume des œufs soit influencés par des patrons géographiques ou climatiques à l'échelle continentale, seule une tendance latitudinale globale dans la phénologie de la reproduction a été détectée, les spatules des latitudes plus basses commençant généralement à pondre plus tôt que celles des latitudes plus élevées (Chapitre 2). En outre, les résultats suggèrent que les adultes expérimentés se reproduisent plus tôt et produisent probablement des poussins de meilleure qualité que les adultes inexpérimentés (Chapitre 3).

résumé (continuation)

Les spatules répondent à la pollution existante en Camargue (Midi de la France) par l'utilisation croissante de matériels artificiels dans les nids (chapitre 4). Bien que la Camargue présente un paysage fragmenté avec plusieurs perturbations d’origine anthropiques et différents niveaux de protection, les spatules bénéficient des zones gérées pour les oiseaux d'eau, que ce soit à des fins de conservation ou de chasse (chapitre 5). Enfin, je montre comment la migration sur de longues distances, impliquant le franchissement de barrières écologiques importantes, peut être coûteuse pour la survie et la productivité des spatules et comment elles sont plus à même de faire face à ces défis en vieillissant (chapitres 3, 6 et 7). J'explore également l'impact de la dégradation des zones humides sur les taux démographiques je questione le recrutement potentiel des spatules dans les régions de reproduction le long des routes migratoires, ce qui pourrait expliquer la philopatrie apparemment faible chez cette espèce (chapitre 7).

Cette thèse explore comment une espèce d'oiseau d'eau modérément spécialisée peut bénéficier des changements globaux actuels en exploitant de nouvelles opportunités, telles que l'utilisation d'espèces envahissantes comme nouvelles sources de nourriture et l'utilisation de zones humides gérées pour des activités économiques et récréatives. Elle souligne également comment l'amélioration des performances (par exemple, la reproduction et la migration), avec l'âge et grâce aux signaux sociaux des congénères plus âgés, renforce la capacité de la spatule à prospérer dans des environnements changeants. Enfin, cette thèse examine la rapidité avec laquelle un scénario actuellement positif (affichés par les oiseaux d'eau) peut changer face à une grave dégradation des zones humides ou à un manque de souplesse d’adaptation aux changements mondiaux en cours.

reconhecimento do uso de ferramentas IA

Reconhecimento do uso de tecnologias e ferramentas de Inteligência Artificial (IA) generativa, softwares e outras ferramentas de apoio.

Reconheço a utilização do Office365 (Microsoft, https://www.office.com) para a escrita do texto. Reconheço a utilização a utilização do DeepL (DeepL, https://www.deepl.com) para revisão linguística do rascunho final.

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CHAPTER 1

General introduction

Eurasian spoonbill in the nest, Camargue, 2021.
The genus name *Platela* is the Latin word for "broad" and the word *leucorodia* is derived from the ancient Greek words *leukos* (white) and *erodios* (heron).

General introduction

1. Anthropogenic global environmental change

The natural world has been undergoing constant change throughout time, but it is now widely apparent that the current rate of global changes originates from anthropogenic sources (Foley et al., 2013; Lindstrom et al., 2014). Anthropogenic activities can have a profound impact on the general environment, in particular through direct (e.g., deforestation, food production, infrastructure development, pollution, and recreational disturbance) and indirect (e.g., changes in atmospheric composition, rising temperatures, and sea level rise) influences on the ongoing loss of habitats and biodiversity (Alerstam and Lindström, 1990; Foley et al., 2013; Newton et al., 2020; Pausas and Bond, 2019; Wulf, 2015). It is therefore currently impossible to dissociate global environmental changes from human activity.

Global changes such as climate and habitat change, are known to be increasingly threatening the natural world and therefore inextricably linked to biodiversity loss (IPBES, 2019). Biodiversity is defined as the variety of life, which encompasses multiple levels, from genes, to functional traits and species (Cardinale et al., 2012). Thus, while biodiversity loss is more commonly known as species extinction, the loss of certain populations may severely reduce the genetic pool and resilience of even widespread of species (May, 1994; Pauls et al., 2013). At the beginning of the 21st century, the estimated rate of biodiversity loss was up to 1,000 times higher than the background rate observed in the fossil record (Baillie et al., 2004; Barnosky et al., 2011; Ceballos et al., 2020; Wilson, 2003), and this has not improved since. In fact, several anthropogenic threats have worsened or accelerated (Ripple et al., 2017; Rockström et al., 2009), with the concomitant and alarming rates of habitat loss (Cushman, 2006; Flockhart et al., 2015; Reif et al., 2010) and species declines (Dirzo et al., 2014; WWF, 2022). An example of habitat loss particularly relevant for this thesis is the loss of wetland ecosystems. Wetlands are among the most biodiverse ecosystems on the planet, providing food, habitat and refuge for up to 40% of the world's biodiversity, including vulnerable and endangered flora and fauna (Gardner and Finlayson, 2018), as well as essential services (e.g., source of freshwater, food, and protection) for human populations (Corcoran, 2010; Keddy, 2010; Lévêque et al., 2005; MEA, 2005; Tiner, 1989). Nevertheless, it is estimated that 87% of the world’s wetlands have been lost since the 1700s, and many of the remaining wetlands are either degraded or currently under severe anthropogenic pressure (Davidson, 2014; Gardner and Finlayson, 2018). Therefore, wetland loss is often associated with substantial declines in biodiversity (Bunn and Arthington, 2002; Lehtinen et al., 1999).

Between 1970 and 2014, populations of various wetland species from different taxa such as amphibians, birds, fish, mammals, and reptiles declined by 60%, with a total of 25% of wetland species being currently threatened with extinction (Finlayson et al., 2022; Gardner and Finlayson, 2018; Lefeuvre and Bouchard, 2020). Waterbirds have been particularly affected by wetland loss and have declined sharply in recent decades (MEA, 2005).

In addition to habitat change, such as that occurring in wetlands, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) currently identifies four other major threats to biodiversity: pollution; invasive alien species; nutrient loading; and overexploitation. Pollution, such as the influx of artificial materials into the general environment is occurring at an alarming rate as a direct consequence of anthropogenic actions (Galgani et al., 2013; Hoornweg et al., 2013; Schneider et al., 2018), and is of particular relevance for this thesis. The abundance and slow rate of degradation of artificial materials currently make them one of the main threats to natural ecosystems around the world (Galgani et al., 2013). Plastic pollution in particular has become such a challenge, that the United Nations Environment Programme (UNEP) has classified it as a critical environmental issue (UNEP, 2011, 2014). However, despite global alerts and efforts to reduce societal dependency on (single-use) plastics (UNEP, 2016) or to remove them from the environment (Jain, 2017), their spread and abundance in the environment continues to increase (Borrelle et al., 2020; Geyer et al., 2017). Consequently, interactions between wildlife and artificial materials have been increasingly reported. For example, artificial materials have been found in the digestive tract of several species (Kühn and van Franeker, 2020; Laist, 1997) and in some cases, they have been shown to affect species development and behaviour (Derraik, 2002; Gregory, 2009). It is therefore important to better understand how animals are impacted by adverse and increasing anthropogenic influences (e.g., affecting their physiology and/or survival) as such knowledge is fundamental to establishing a baseline for mitigating their negative impacts in the environment (Avery-Gomm et al., 2018; Jagiello et al., 2019; Sergio et al., 2011).

Further to direct anthropogenic pressures on habitats and species (Burton et al., 2006; Piersma et al., 2016). Climatic changes can also affect species in different ways and are often linked to shifts in population distribution, such as shifts to higher latitudes or altitudes due to rising temperatures (Chen et al., 2011; Hickling et al., 2005; La Sorte and Thompson III, 2007; Parmesan, 2007; Peel et al., 2017; Thomas and Lennon, 1999; Thurman et al., 2020). For example, there is currently a widespread and rapid shrub expansion in the Artic tundra, an area typically dominated by low-growing plants (e.g., mosses) and lichens, which is attributed to regional warming (i.e., arctic surface air temperatures are rising at more than twice the global rate; Pachauri et al., 2014) and associated sea ice reduction (Blok et al., 2011; Swann et al., 2010). However, climate change can also affect species abundance and lead to changes in activity patterns, phenology (e.g., breeding timing), and microhabitat use (Bates et al., 2014; Williams et al., 2008). Migratory animals are particularly susceptible to the effects of environmental change due to their extensive geographical ranges and dependence on seasonal variation in environmental conditions (Wilcove and Wikelski, 2008). For example, due to climate induced changes in resources at different seasonal stages, there could potentially be a temporal mismatch between resources and migration cycles (Lehikoinen et al., 2004; Robinson et al., 2009). In the case of the sympatric (i.e., species with overlapping geographic ranges) Fin (*Balaenoptera physalus*) and Humpback (*Megaptera novaeangliae*) whales in the Gulf of St. Lawrence, earlier ice break-up and rising sea surface temperatures likely triggered earlier availability of their prey (Ramp et al., 2015), with both species advancing their arrival to match. While they displayed phenotypic plasticity in response to past climatic changes, it is uncertain whether these species can sustain the rate of change necessary: their departure dates are currently shifting at different rates, leading to increased spatiotemporal overlap (Ramp et al., 2015) in site use.

2. Seasonal migration and environmental change

One of the animal groups most affected by global environmental change is that of migratory birds, which are currently experiencing high and fast declining rates worldwide (Kirby et al., 2008; Rosenberg et al., 2019; Xu et al., 2019). Each year, a substantial number of birds migrate across diverse spatial and temporal scales to exploit seasonal peaks in resources (Alerstam and Lindström, 1990; Berthold, 2001; Chapman et al., 2011; Dingle, 1980; Lok et al., 2015; Newton, 2008). The migratory phenomenon is a highly energetically demanding process (Alerstam and Lindström, 1990), and different migratory behaviours (e.g., migratory route, distance or wintering site location) may be associated with different fitness outcomes (Acker et al., 2021; Alves et al., 2013; Carneiro et al., 2021; Grist et al., 2017; Lok et al., 2015; Reid et al., 2020).

Migratory behaviour, such as wintering site location, can be highly variable within and between species (Alerstam et al., 2003; Alerstam and Lindström, 1990; Newton, 2008). In some species behavioural differences are so extreme, that some individuals do not migrate at all (residents) while others travel several thousands of kilometres to their witnering sites each year (Chapman et al., 2011; Lundberg, 1988; Newton, 2008). These systems are known as partial migratory species, and such variation between individuals has been suggested to affect demographic parameters such as survival and productivity, via carry-over effects (Acker et al., 2021; Grist et al., 2017; Lok et al., 2015; Méndez et al., 2022; Reid et al., 2020). This might be due to a mixture of geographically and ecologically distinct environments experienced by individuals during the non-breeding season at their wintering site or during migration (Boyle, 2008; Chapman et al., 2011; Gillis et al., 2008; Harrison et al., 2011; Hötker, 2003; Loonstra et al., 2019; Sergio et al., 2014; Swift et al., 2020). To explain differences in migratory behaviour among conspecifics, five hypotheses have been proposed: some individuals have a genetic predisposition to migrate while others do not – *genetic control hypothesis* (Berthold, 1984); the intensity of competition for breeding opportunities may differ among classes or sexes in a population, leading to differential advantages of an early return to the breeding sites – *arrival-time hypothesis* (Ketterson and Nolan, 1976; Myers, 1981); the immune system promotes survival by reducing the probability of disease-related mortality (Roitt et al., 1998), and migratory birds are likely to need a more diverse immune system as they are more likely to encounter more and/or novel pathogens – *immune system hypothesis* (Buehler et al., 2010; Møller and Erritzøe, 1998). Furthermore, regulation of the immune system is costly and requires resource trade-offs with migration, potentially leading to different migratory behaviours (Eikenaar and Hegemann, 2016; Hegemann et al., 2015); The two remaining hypotheses are particularly relevant to this thesis. They suggest that low quality (*body-size hypothesis*, or *foraging-limitation hypothesis* Boyle, 2008) or socially subordinate individuals (*dominance hypothesis*) may be pushed to sub-optimal migration strategies, such as a longer migration, to reduce the negative effects of competition and of harsher environmental conditions during the non-breeding period (Cristol et al., 1999; Hegemann et al., 2015; Ketterson and Nolan, 1983, 1976). Despite being different, some of these hypotheses may complement each other, e.g., an individual in poor condition could be more likely to migrate when resources are scarce or when environmental conditions deteriorate.

The underlying mechanisms linking migratory behaviour to demography (e.g., survival) are often poorly understood, and unravelling such links is further complicated by the difficulty of following individuals throughout their annual cycle (Lok et al., 2015). In fact, while some studies showed benefits of shorter migration distance (Hötker, 2003; Myers, 1981), in other systems, migrating further can be advantageous in terms of survival (Alves et al., 2013; Reneerkens et al., 2020) and/or productivity through carry-over effects (Carneiro et al., 2021; Lourenço et al., 2008), for example by affecting arrival time, which tends to be positively related to productivity in seasonal environments (Morrison et al., 2019). Individuals of Pied avocet (*Recurvirostra avosetta*) that wintered closer to their breeding site arrived earlier and fledged more chicks than those that wintered further away (Hötker, 2003). Conversely, for the Icelandic black-tailed godwits (*Limosa limosa islandica*), those individuals wintering furthest arrived earlier at the breeding area (Alves et al., 2012a), probably leading to higher reproductive success (Alves et al., 2019). Taken together, these studies suggest that distance alone cannot explain the observed variation in arrival dates. Birds do not usually take the most direct and shortest route during migration. In fact, they often make detours to avoid major ecological barriers (e.g., deserts and seas), or to take advantage of favourable stopover sites (Alerstam, 2001; Alerstam et al., 2003).

Migration is a highly complex phenomenon, with habitat degradation (e.g. via pollution) and changes in climatic conditions (than may influence phenology) further affecting the underlying behavioural processes of migratory species (Chen et al., 2011; Piersma et al., 2016; Urban, 2015). For instance, due to a difference in phenology response to temperature between insects (ca. 6 ºC) and birds (ca. 2 ºC) (Root et al., 2003; Sparks and Menzel, 2002), a mismatch between date of egg-laying and peak of food abundance was created (Both et al., 2004), resulting in declines amongst populations of Pied flycatcher (*Ficedula hypoleuca*) (Both et al., 2006). Furthermore, migratory animals face the additional challenge of responding to changes on multiple fronts simultaneously, which may be changing at different rates or even in different ways (Gordo, 2007; Lees et al., 2022; Mustin et al., 2007; Robinson et al., 2009; Şekercioğlu et al., 2012). For example, coastal wetlands used by several wader species (e.g., *Charadri*) during the non-breeding period are currently affected to varying degrees of sea level rise and/or by coastal development (Austin and Rehfisch, 2003; Yang et al., 2011). At the same time, wader breeding sites may be further compressed towards the northern pole, as temperatures continue to rise in the Arctic (Lindström and Agrell, 1999; Rehfisch and Crick, 2003). Consequently, in order to assess the capacity of migratory bird populations to respond to environmental change, it is essential to better understand the links between changing environments and migratory behaviour (Sedinger et al., 2006). Furthermore, it is also important to establish a direct link between migratory behaviour, survival, and reproductive success, specifically between long distance migrants and short distance migrants or residents (Sedinger et al., 2006).

3. The importance of protected areas for highly mobile species and the role of wetlands managed for economic or recreational activities

Protected areas are the most widely used strategy in attempt to slow and ultimately reverse biodiversity declines (Soriano-Redondo et al., 2023). These areas can influence species demographic rates by successfully maintaining (Gray et al., 2016) or even boosting population abundances (e.g., by spillover effects, where populations in surrounding areas are supplemented by individuals dispersing from protected areas; Di Lorenzo et al., 2020; Kough et al., 2019). Furthermore, in the case of migratory species, protected areas can be beneficial at multiple spatial scales, as they are important not only at local scale, such as in large wetlands areas, where some sections are protected while others are not, both in breeding and non-breeding regions (Nightingale et al., 2023), but also during migration, through the preservation of critical stopover sites (Soriano-Redondo et al., 2023). Therefore, the designation, management, and restoration of protected habitats and sites are essential for the sustainability of mobile species in an increasingly degraded, patchy and complex landscape (Braun et al., 1978; Dobkin et al., 1998; Geldmann et al., 2019, 2013; Leberger et al., 2020; Manning et al., 2011; Murray and Hamilton, 2010; Weller, 1999). In the case of waterbirds, and despite the ongoing degradation of wetland habitats (Wetlands International, 2016), these species have benefited from the legal protection of numerous wetlands, for example under the Ramsar Convention (global; Bridgewater and Kim, 2021) and the Natura 2000 Network (European Union; Kallimanis et al., 2015). In addition, some wetlands have been improving in quality, particularly in Europe due to EU´s Water Framework directive (2000s) (e.g., see Alves et al., 2012b). Hence, several waterbird populations in Western Europe have been increasing and recolonizing their historical distribution range in recent decades (Amano et al., 2018).

Additionally, some waterbird species are likely to further benefit from other events that would typically be considered deleterious to biodiversity. For instance, the existence of anthropogenic wetlands managed for economic or recreational purposes (e.g., agriculture and hunting) can enhanced food availability for some waterbird species (Alonso et al., 2008; Hamza et al., 2015; Johst et al., 2001; Li et al., 2015). These anthropogenic areas (i.e. man-made) can also serve as valuable complements to natural (or naturalized) areas, providing suitable resting and foraging conditions that support waterbirds (Alves et al., 2010; Fasola et al., 2022; Rocha et al., 2016; Vallecillo et al., 2019; Vansteelant, 2023). However, reliance on intensively managed areas for economic or recreational purposes can have deleterious consequences for species that are highly dependent on them (Belo et al., 2023; Central Valley Joint Venture, 2006; Champagnon et al., 2023; Fasola et al., 2022; Pernollet et al., 2015). Not only can changing land management practices unexpectedly convert suitable foraging resources into areas of low resource quality (e.g., loss of agricultural habitats for urban development; Central Valley Joint Venture, 2006), or even unusable areas (e.g., abandonment of fish production; Mikuska et al., 2023), but continued use and increased reliance upon such artificial areas risks compromising the resilience of these species (Champagnon et al., 2023). This is the case of the Greater Doñana ecosystem, a major and crucial wetland during winter and migration of several migrating waterbirds, including both (mostly) natural protected areas and artificial wetland habitats. Despite being considered as a wetland of international importance (i.e., Ramsar site, National Park, Biosphere Reserve, and UNESCO World Heritage Site) and once the crown jewel in the European network of protected areas, its capacity to sustain migratory bird populations is increasingly threatened (Camacho et al., 2022; Green et al., 2017; Navedo et al., 2022). In fact, 60% of Doñana's lagoons have been lost since 1985 (de Felipe et al., 2023). Although the deterioration of Doñana is due to multidimensional factors such as climate warming (Bustamante et al., 2016; de Felipe et al., 2023; Díaz-Paniagua and Aragonés, 2015), the over-exploitation of groundwater for intensive agriculture (e.g., rice fields and berry production) has significantly contributed to the depletion of water in the natural wetlands and its capacity to host waterbirds (Acreman and Salathe, 2022; de Felipe et al., 2023; Díaz-Paniagua and Aragonés, 2015). At the same time, unprotected wetland habitats in the surrounding area of Doñana's protected area, have increasingly been converted (>40 000 ha) into rice fields and fish farms (Vansteelant, 2023). These economically managed wetlands have complemented the natural wetland habitats of the Doñana protected area by providing a permanent and reliable food source (e.g., invertebrates and rice seeds) for waterbirds each year (Vansteelant, 2023). However, as water becomes a scarcer and more expensive resource, the same rice fields (i.e., highly water dependent) upon which waterbirds currently rely, could rapidly disappear and give place to more profitable uses (e.g., strawberry production) (Green et al., 2024; Ruiz, 2024; Vansteelant et al., 2023). It is therefore important to gain a deeper understanding of the impact of different land management and conservation actions on highly mobile species (Allen and Singh, 2016; DeFries et al., 2007; He et al., 2019; Kämpfer et al., 2023; McDuie et al., 2021). This knowledge is essential to inform and implement management actions that will not only enhance the effectiveness of conservation efforts, but also improve wetland connectivity and species resilience (Champagnon et al., 2023; DeFries et al., 2007; Papeş and Gaubert, 2007).

An overview of the thesis topics can be seen in Fig. 1:

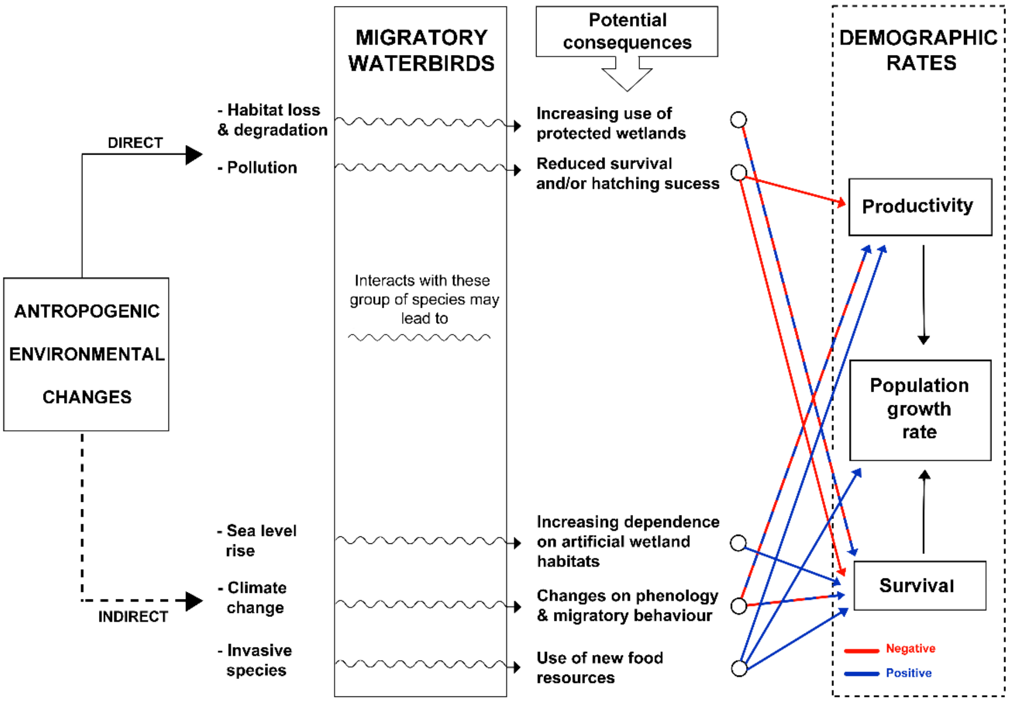


Fig. 1 – Schematic description of how waterbird species may interact with direct and indirect anthropogenic environmental changes, potential consequences and subsequent effects on the demographic rates of these species. This thesis addresses many of the relationships presented here.

4. The importance of tracking: low tech and large sample vs high tech and small sample

Understanding how site use at multiple scales influences demographic processes, requires the capacity to monitor movement within and between sites (Sakamoto et al., 2009; Wilson et al., 2008). However, this is not an easy task for highly mobile species, as they often rely on different habitats to meet their vital needs (e.g., breed, feed, and shelter), which often change over the annual and life cycles of the focal animal (Johst et al., 2001; Ouin et al., 2004; Pope et al., 2000). Two classic examples of this challenge are the studies of several marine species (e.g., cetaceans, fish, and sharks), which spend most of their time underwater, and migratory birds, which can have vast geographical ranges spanning several continents (Alexander, 1998; Brown et al., 2013; Yoda et al., 1999). Thus, until recently, studies have been limited by uneven observational efforts in space and time (Brown et al., 2013; Graf et al., 2015). Therefore, the development of new technologies and particularly the miniaturization of multiple sensors (e.g., GPS, pressure sensors, depth gauge, and accelerometer), is fundamental to: (1) collect information that more accurately reflects the movements undertaken by animals; (2) gain a better understanding of the costs-benefits of a particular animal movement (e.g., movement from one site to another, flying, and foraging); and (3) unravel the functional role of different habitats (e.g., foraging or roosting) (Ewing et al., 2018; Laich et al., 2008; Rodrigues et al., 2023a; Wakefield et al., 2009; Yoda et al., 1999).

Innovation in bird tracking studies has closely followed the development of new technologies. What started with the use of simple metal rings to identify recoveries and then colour rings for visual identification at a distance (e.g., Clark et al., 2009; Reichlin et al., 2009; Wood, 1945), has developed into the use of advanced tracking technologies such as GPS trackers (Cagnacci et al., 2010; Wilmers et al., 2015) and accelerometers (Shamoun-Baranes et al., 2012; Shepard et al., 2008). Nevertheless, both methods have their advantages and limitations. The use of traditional marking rings allows the tracking of a considerable number of individuals at a relatively low cost. Colour marks are easily detected and facilitate the involvement and engagement of the general public in the resighting efforts. The resighting information collected in conjunction with analytical methods (Choquet et al., 2009; Lebreton et al., 1992; Pradel et al., 1997) has significantly improved our understanding of how survival rates relate to individual condition (Cam et al., 2002), climate (Sillett et al., 2000) and other environmental variables such as the demographic effects of the inter-annual El Niño Southern Oscillation (ENSO) and inter-decadal oscillations (Champagnon et al., 2018). However, data collection relies on resighting of marked birds, which can be logistically demanding, infrequent and geographically limited (Brown et al., 2013; Graf et al., 2015). It also provides limited insight into the daily or migratory movements of birds, due to the low temporal resolution of data as no information is available between two resightings. Finally, due to its reliance on human observers, which are limited to certain sites and daylight conditions, it is susceptible to bias and error (Brown et al., 2013; Graf et al., 2015). Conversely, the development of electronic tracking technology (e.g., satellite telemetry or GPS), has provided higher resolution data on bird movements, allowing detailed tracking information such as migratory routes and habitat use (Berthold et al., 2004; Bridge et al., 2011; Cagnacci et al., 2010; Freeman et al., 2010; García-Ripollés et al., 2010; Wilmers et al., 2015). Additionally, accelerometers record the acceleration of inertial motion in three-dimensional space, which can be linked to the behaviour and are therefore becoming increasingly important for understanding how and why animals use specific habitats (Brown et al., 2013; Ladds et al., 2017; Ravi et al., 2005). However, in addition to much higher financial costs, which limits the number of individuals that can be monitored, welfare considerations, the tracking capacity is limited by battery and data acquisition frequency trade-offs, and the relatively short life span of the tags (Bridge et al., 2011). Concisely, ring tracking is ideal for large-scale, long-term studies with limited budgets and where detailed movement data is not required as is the case for estimating survival, and natal dispersal. On the other hand, GPS technology is recommended for short-medium term studies that require more precise or high-resolution movement data, such as quantifying habitat use. But the holy grail is to use both methods together (e.g., see Gregory et al., 2023), which allows to complement information regarding movement, survival and behavioural data. For example, combining long-term demographic trends from capture recapture data with tracking data, provides insights into what happens between observations.

5. The model species: Eurasian spoonbill

In order to address how anthropogenic environmental changes affect migratory waterbirds and the potential consequences of such interactions in demographic rates (Fig. 1), this thesis focuses on the Eurasian spoonbill (*Platalea leucorodia leucorodia*, hereafter spoonbill) as a study model.

The Spoonbill is a colonial-breeding species that exhibits wide geographical variation in both breeding and non-breeding ranges. Individuals, both between and within populations, display a wide variety of migratory routes and distances, including residency. This variation in behaviour, allows testing how different non-breeding sites (or regions), and consequently experiencing different wintering conditions (e.g., climatic conditions and food availability) and migration patterns (e.g., distance and flyway), might affect productivity and survival rates. Furthermore, the breeding season of this species tends to be long, and several of its colonies are easily accessible, making it possible to assess how phenology and demographic parameters vary over the course of the season and are affected by different environmental conditions. Finally, this species has been the subject of substantial conservation efforts and long-term monitoring programmes, providing several longitudinal datasets of demographic, resighting and tracking data.

5.1. Distribution and status

The spoonbill is a charismatic waterbird species of the family Threskiornithidae. It is easily recognised by its long spatula-shaped bill (Triplet et al., 2008), and has been named accordingly (Fig. 2).

Fig. 2 – Adult Eurasian spoonbill. © Hugo Ferreira

At the beginning of the 20th century, the European spoonbill breeding population declined dramatically. This was likely caused by the fast economic development in Europe following the Second World War, which led to an increase in anthropogenic pressure on natural wetland habitats (e.g., land reclamation, drainage, house building, intensive farming, and the use of chemicals/pesticides in agriculture) (Overdijk, 2013). By 1950, in Northwestern Europe, only four active breeding sites remained (one in Spain – Doñana; and the other three in the Netherlands – Naardermee, Texel, and Zwanenwater) (Overdijk, 2013), while Austria and Hungary contained most of the remaining breeding pairs of the Central European breeding population (Triplet et al., 2008). However, thanks to intensive recovery programmes, including increased or improved nature conservation legislation, the prohibition of pesticide use (i.e., organochlorine), and habitat restoration, the European breeding population of spoonbills has experienced a remarkable recovery and growth, leading to the recolonization of several former breeding sites in Europe (Champagnon et al., 2019b; Lok et al., 2009; Marion, 2013; Oudman et al., 2017; Overdijk, 2004, 2013; Ramo et al., 2013; Triplet et al., 2008; Tucakov, 2004). The species is currently distributed from the East-Atlantic Coast to Southeast Asia (Fig. 3; Triplet et al., 2008) and is listed as Least Concern (LC) on the European Red List (BirdLife International, 2019).

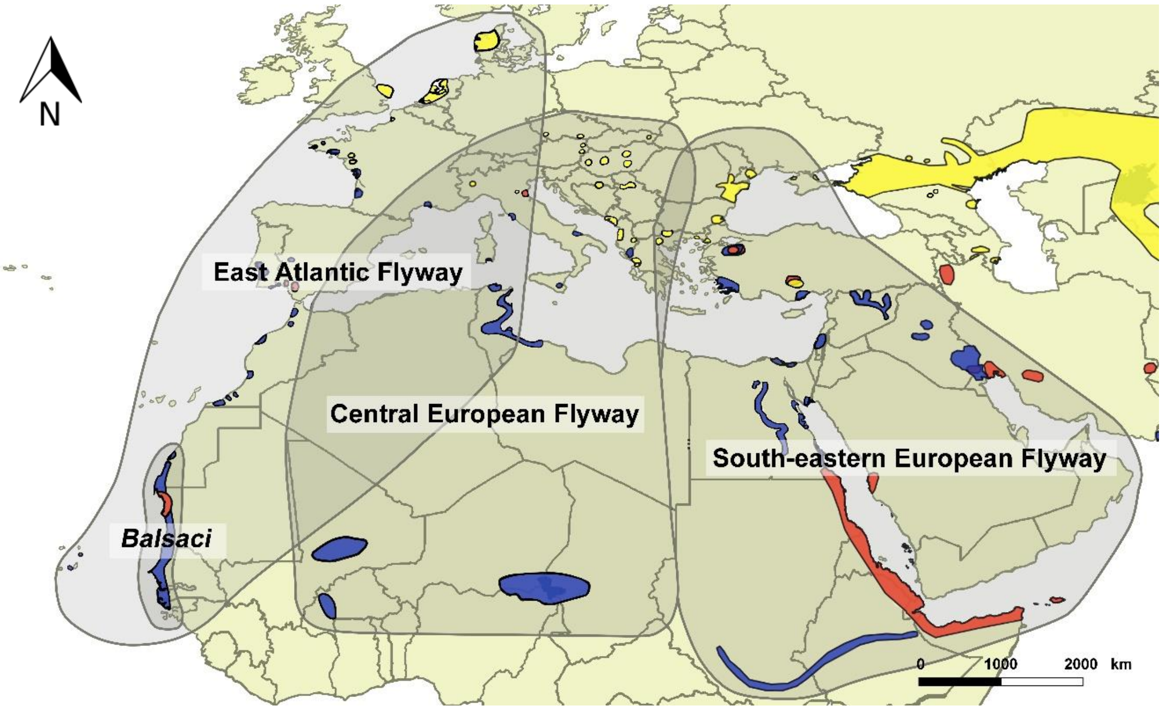


Fig. 3 – Eurasian spoonbill distribution highlighting breeding areas (yellow), wintering area (blue), and resident area (present all year; red) (Champagnon et al., 2019c). The three subspecies are shown: *archeri*, found on the coasts of the Red Sea and Somalia; *balsaci* found on the islands of the Banc d'Arguin, Mauritania; and *leucorodia*, (all range). Polygons represent different migratory flyways with *balsaci* being considered resident (hence its polygon shows this subspecies´ distribution range).

Due to the implementation of recovery programmes, this species has been extensively monitored (e.g., breeding numbers, number of colonies, identification of breeding, stop-over, and wintering sites). This, combined with the species' potential to engage professional and amateur ornithologists and its ease of detection (Triplet et al., 2008), has led to the establishment of several long-term colour-ringing programmes (details of all current and past ringing programmes are available at www.cr-birding.org). As a result, unique longitudinal resighting datasets are available (i.e., some spanning over 40 years, as in the case for the Dutch programme), comprising data collected across the main breeding regions in Europe and throughout the main non-breeding range of spoonbill.

5.2. Diet and foraging ecology

Fig. 4 – Eurasian spoonbill feeding.
© Hugo Ferreira

Spoonbills feed in shallow water (10-30 cm; Fig. 4) where they forage using a sweeping technique, moving their bill from side to side in the water column to catch small fish (e.g., Three-spined stickleback – *Gasterosteus aculeatus*; El-Hacen et al., 2014; Kemper, 1995) and invertebrates (Aguilera et al., 1996; Enners et al., 2020; Hancock et al., 2010; Veen et al., 2012). As was the case for several *Ardeidae* species (e.g., Grey heron – *Ardea cinerea*, Little egret – *Egretta garzetta*, Night heron – *Nycticorax nycticorax*, and the Purple heron – *Ardea purpurea*), spoonbills probably benefited from the introduction of additional food sources such as the Red-swamp crayfish (*Procambarus clarkii*) in Europe (Correia, 2001), which was found to be part of their diet in several breeding sites (Champagnon, Kralj, et al., 2019; Poulin et al., 2007; Rodrigues, et al., 2023b). Spoonbills are highly mobile birds, capable of travelling up to 50 km between feeding and roosting sites during their regular daily movements (Pigniczki and Végvári, 2015). Due to its high mobility and specialist foraging ecology, this species has the potential to illustrate how a moderately specialized species can select suitable habitats in fragmented landscapes.

5.3.Breeding biology

Spoonbills typically nest in or close to wetlands, either on the ground, on islands or dykes, in reed beds or in trees (Hancock et al., 2010; Svensson et al., 2023). Their breeding season tends to be long, with reports of egg-laying occurring between late March and early July (Lok et al., 2017, 2014; Triplet et al., 2008). Nevertheless, in South European breeding sites (e.g., South of Spain) laying can begin as early as February (Aguilera et al., 1996). Spoonbills are colonial birds that build their nests from branches and stems, and line them with grass and leaves (Fig. – 5a and 5b; Isenmann et al., 2010; Matheu et al., 2020). This species' breeding success and chick body condition tend to decrease over the season (Lok et al., 2017), although this has only been tested for the Dutch population thus far (but see Chapter 2 and 3). Such a long breeding season allows to assess how different demographic parameters (e.g., egg volume, hatching success, and chick body condition) vary seasonally and how they are affected by different environmental parameters (e.g., temperature and precipitation).

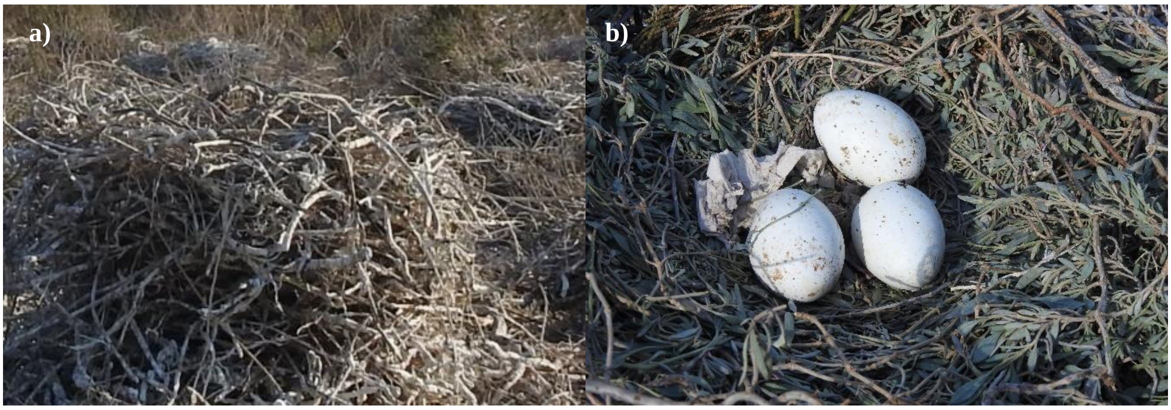


Fig. 5 – Eurasian spoonbill ground nest (a) structure and (b) lining in the Camargue, Southern France. © Hugo Ferreira

Spoonbills have delayed maturity that start breeding at ca. 3-4 calendar years of age and lay clutches of 3-4 eggs (on average), with 1-3 chicks hatching per nest (Cramp and Simmons, 1977; Lok et al., 2011; Triplet et al., 2008). Typically, spoonbills lay an egg every other day and begin incubation one to two days after the first egg is laid, resulting in asynchronous hatching (Cramp and Simmons, 1977; Lok et al., 2014; Triplet et al., 2008). Incubation typically lasts between 24-28 days, after which the parents begin parental care of the chicks until they are fully fledged (ca. 35 days old) (Cramp and Simmons, 1977; Triplet et al., 2008). It has been observed that spoonbills may lay a second clutch (Triplet et al., 2008), often if the first is unsuccessful.

Fig. 6 – Juvenile spoonbill, distinguished by their light-coloured bills and black tips on their remiges (flight feathers). © Hugo Ferreira

During the post-fledging period, juveniles (Fig. 6) are highly exploratory, moving considerable distances in the surrounding wetlands and even reaching distances of 100 km from their natal colony (de le Court and Aguilera, 1997; Hancock et al., 2010; Kralj et al., 2012; Volponi et al., 2008). Occasionally, individuals hatched in Southern Europe may remain in close proximity to the colony, adopting a resident behaviour, as it has been shown for the population in the Camargue (Southern France; Blanchon et al., 2019). Once at the witnering sites, spoonbills generally remain there until they reach maturity, especially in African sites (de le Court and Aguilera, 1997; Pigniczki and Végvári, 2015; Triplet et al., 2008). Nevertheless, some immature birds can still be present in breeding colonies, probably taking social cues (learning) or even attempting to breed (Lok et al., 2011). Studying multiple populations with large individual variations in breeding and migratory behaviour provides a unique opportunity to understand how those individual behaviours can affect population survival and productivity.

5.4.Spoonbill migration

Spoonbills are currently recognized to have three distinct flyway populations in Europe (Champagnon et al., 2019c): i) the East Atlantic Flyway population (hereafter EAF population), which includes the largest European breeding population of spoonbills (in the Netherlands; Lok et al. 2009), as well as colonies in Iberia and Northern France; ii) the Central European Flyway meta-population (hereafter CEF population), where various colonies such as those in Italy and the Carpathians have been monitored (Kralj et al., 2012; Pigniczki and Karcza, 2013; Pigniczki and Végvári, 2015; Tenan et al., 2017). The largest population of CEF breeds in Hungary, but relevant colonies (> 100 breeding pairs) are also found in Austria, Croatia and Servia (Pigniczki and Végvári, 2015); and iii) the South-eastern European Flyway (hereafter SEF population), that was recently separated from the CEF (Champagnon et al., 2019c) and for which knowledge regarding migration, non-breeding distribution and genetic differentiation are currently lacking (Kralj et al., 2023).

Autumn migration generally occurs in August/September, while spring migration occurs in February/March (Lok et al., 2013; Triplet et al., 2008). The EAF population (in general) follow a route along the Atlantic coast of Europe and West-Africa (Bauchau et al., 1998; Navedo et al., 2010), while the Central European flyway migrates south-west over the Adriatic Sea, through Italy to North Africa, with most individuals staying in countries such as Italy, Tunisia and Algeria during the non-breeding period (Fig. 3) (Kralj et al., 2012; Pigniczki and Karcza, 2013; Pigniczki and Végvári, 2015). As for the SEF, spoonbills from this population migrate through the Balkans to Anatolia or the Middle East as far as the upper Nile River (Triplet et al. 2008).

Spoonbills often show high fidelity to breeding and non-breeding sites (De Voogd, 2005; Lok et al., 2013, 2011; Pigniczki and Karcza, 2013). Additionally, previous studies on population in Western Europe and the Carpathians Basin have suggested that spoonbills arrive earlier at breeding sites with increasing age (de le Court and Aguilera, 1997; Kralj et al., 2012). In the case of the Dutch population, long-distance migrants were reported to breed later than short-distance migrants, and this difference in breeding timing was even more pronounced when accounting for the tendency of migrants to breed earlier with age (with the exception of long-distance migrating males) (Lok et al., 2017). Furthermore, it has been observed that spoonbills from different European breeding locations mix in the non-breeding sites (Lok, 2013; Smart et al., 2007), though flyway populations are largely separated (Lok et al., 2019; Overdijk and Zwart, 2003; Pigniczki, 2022).

6. Spoonbill population in the Camargue

6.1. Main study site

Camargue is a semi-natural region of 180,000 ha, situated along the Mediterranean Sea in Southern France, making it the largest wetland in the country (Blondel et al., 2013; Galewski and Devictor, 2016; Roche et al., 2009). This extensive wetland is formed by the Rhone Delta and consists of a diverse mosaic of habitats (Fig. 7), including natural and semi-natural wetlands, two important salt pans, rice fields and several other agricultural cultivations (Blondel et al., 2013).

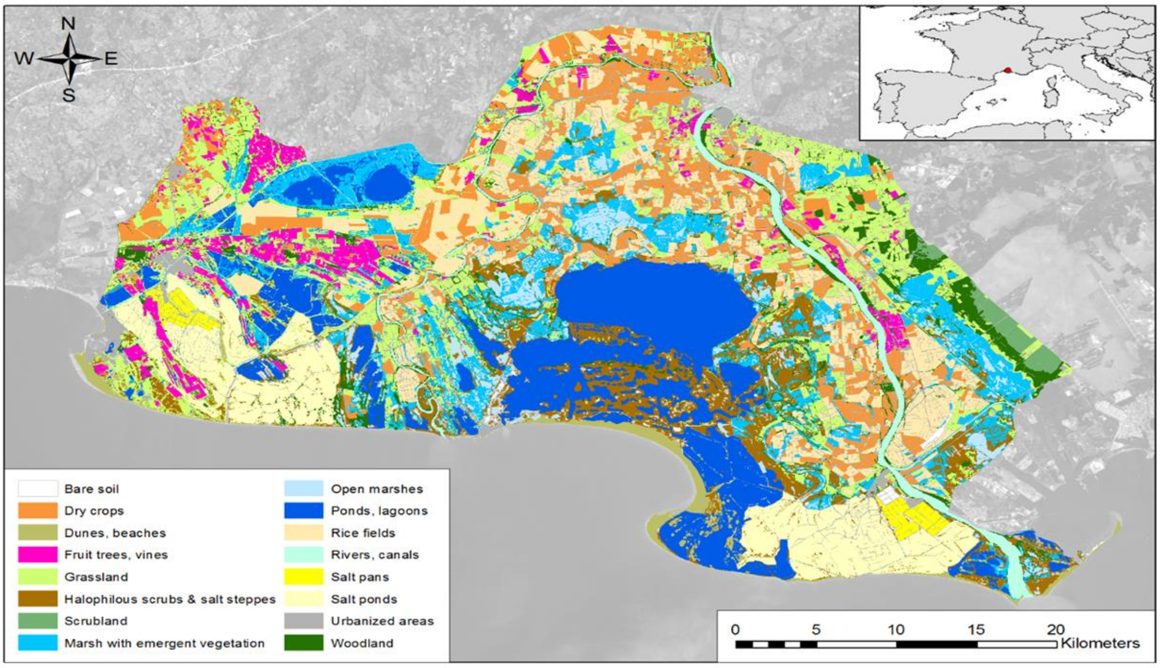


Fig. 7 – Map of Camargue region in the Mediterranean coast of France (red dot in the inset), highlighting the heterogeneity of land uses. Type of soils and land use are described in the figure legend and distinguished by colour. Camargue land use was based on: Parc Naturel Régional de Camargue Land Use 2016 (Bouches du Rhône department) and the SCoT Sud Gard & Syndicat Mixte de la Camargue Gardoise Land Use 2012 (Gard department). ©Wilm/Tour du Valat (2019)

This region has a high conservation value, providing important habitats for nesting (c.a. 132 species breeding in Camargue), staging and wintering site for several waterbird species, totalling 356 species ("Camargue | Ramsar Sites Information Service," 2024; Fraixedas et al., 2019; Heath and Evans, 2000). The Camargue involves a complex diversity of management regimens and multiple stakeholders in the management of natural (e.g., national, private, and regional reserves) and private areas (e.g., agriculture, salt pans, and waterfowl hunting areas) (Galewski and Devictor, 2016). The entire geographical area of Camargue is designated as a *Wetland of International Importance* by the Ramsar Convention benefiting from protection measures with overlapping international and national protection laws and conventions (Vallecillo et al., 2023; see Fig. 8 and Chapter 5 Table 1, for further details and breakdown of types of protection). Such heterogeneous wetland landscape makes this region a suitable model to investigate the usage of and dependence upon multiple habitats by waterbirds, such as the spoonbill, and thus to provide a better understanding on how habitat changes or loss may affect this and other wetland species.

6.2. Spoonbill setlement in the Camargue

During the first half of the 20th century, there were only two documented instances of brief sightings of spoonbills and it was not until the 1970s that the species was regularly reported in Camargue (Blanchon et al., 2019). The first record of a wintering bird was made in 1976, while the first breeding case was not reported until 1998 (Blanchon et al., 2019). Since then, the breeding population of spoonbills has grown exponentially from one breeding pair in 1998 to over 400 in 2023 (Fig. 9a) (Blanchon et al., 2019; Champagnon and Kralj, 2023; Marion, 2019). Resightings of individually marked spoonbills conducted at the colony between 2007 to 2010 indicated a mixed origin for this population, with 22 birds originating from the Netherlands, nine from Italy, and one from Serbia (Blanchon et al., 2019). This may explain why individuals from the breeding population in Camargue are using both migratory flyways (EAF and CEF) (Blanchon et al., 2019). Additionally, some individuals also display a resident behaviour, remaining in Camargue throughout the year (Fig. 9b); Blanchon et al. 2019). Thus, this population presents a unique opportunity to not only further investigate the relationship between survival rates and wintering sites, but also to directly compare survival rates within and between different flyways.

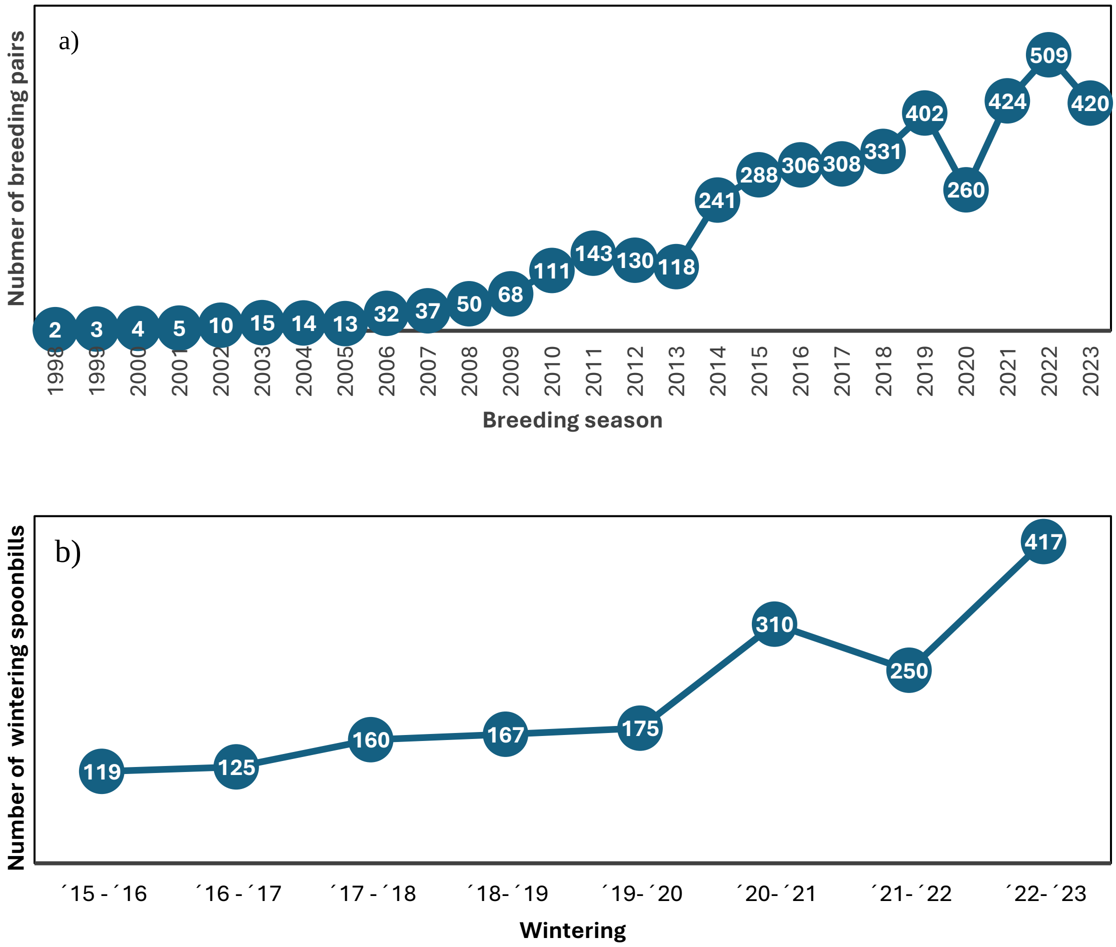


Fig. 9 – Number of spoonbills in the Camargue over the years, quantified as (a) pairs during the breeding season (data collected by Tour du Valat) and (b) wintering individuals (data collected by Tour du Valat/SMCG/OFB).

As in many sites, the spoonbills in the Camargue nest on the ground on small islets with abundant shrub and herbaceous vegetation (Fig. 10; Kayser et al., 2008). This population occupied two breeding sites up to 2017 (Blanchon et al., 2019), but has expanded to at least six by 2023 (Blanchon, *unpublished data*). These sites are located within or in the vicinity of vast saltmarsh area, which collectively cover 100 km^2 within the Camargue (Blondel et al., 2013; Marnotte and Carrara, 2006; Médail, 2018). Ground nesting allows easy access to nests by researchers (as opposed to tree-nesting colonies) and the quantification of multiple breeding and nest parameters. This information can be used, for example, to determine productivity and the potential consequences of the presence of artificial materials in nests.

Fig. 10 – Spoonbills nesting on the ground in a flat saltmarsh islet in the Camargue. © Hugo Ferreira

6.3. Monitoring of spoonbills in the Camargue

The monitoring of spoonbills in Camargue has been conducted by the Tour du Valat team and its partners. It involves census of the breeding and wintering numbers as well as a long-term colour-ring programme initiated in 2008 by Michel Gauthier-Clerc and Yves Kayser (Blanchon et al., 2010). Each year spoonbills are marked with a uniquely coded PVC ring allowing to individually identify marked birds visually without recapturing them (resightings). Resightings in the Camargue were initially conducted by experienced observers on breeding islets using telescopes, often from a hiding place, and typically lasted for bouts ranging from 45 minutes to two hours (Fig. 11).

Fig. 11 – Spoonbills resighting effort during the winter and breeding season in Camargue, carried out using camouflage, telescopes, and a hide. © Hugo Ferreira

Since 2016, the Tour du Valat team has been using automated camera traps (Fig. 12) as a complement to direct observation methods (Fig. 13). The aim was to increase the total number of individuals identified (i.e., breeders and residents – that remain in the colony area all year) and to minimise disturbance. From 2016 to 2020, only a small number of cameras (two or three) were deployed and left on site for several weeks (ca. three or four weeks) set to cover most of the colony. However, the efficiency of the camera traps was enhanced by rotating its position frequently and focusing on a smaller part of the colony at a time. This method allowed additional opportunistic data to be collected, including nest and egg destruction by Eurasian wild boar (*Sus scrofa*), the presence of other bird species in the colony like the African sacred ibis (*Threskiornis aethiopicus*), and nest abandonment.

Fig. 12 – Use of automated camera traps to monitor Spoonbills in Camargue. © Hugo Ferreira

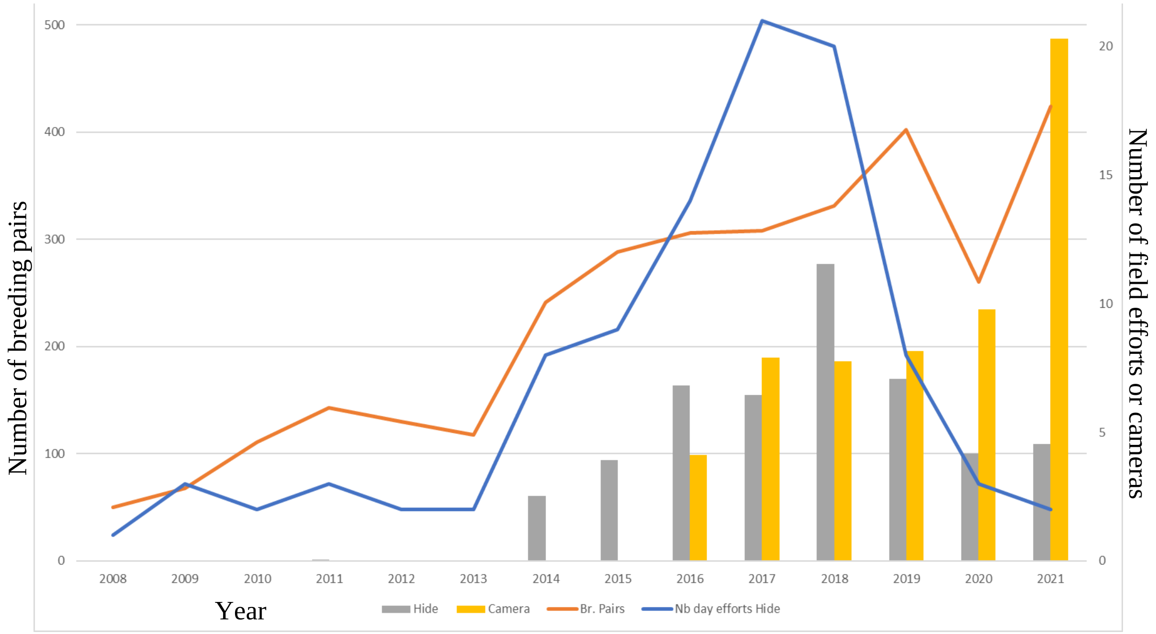
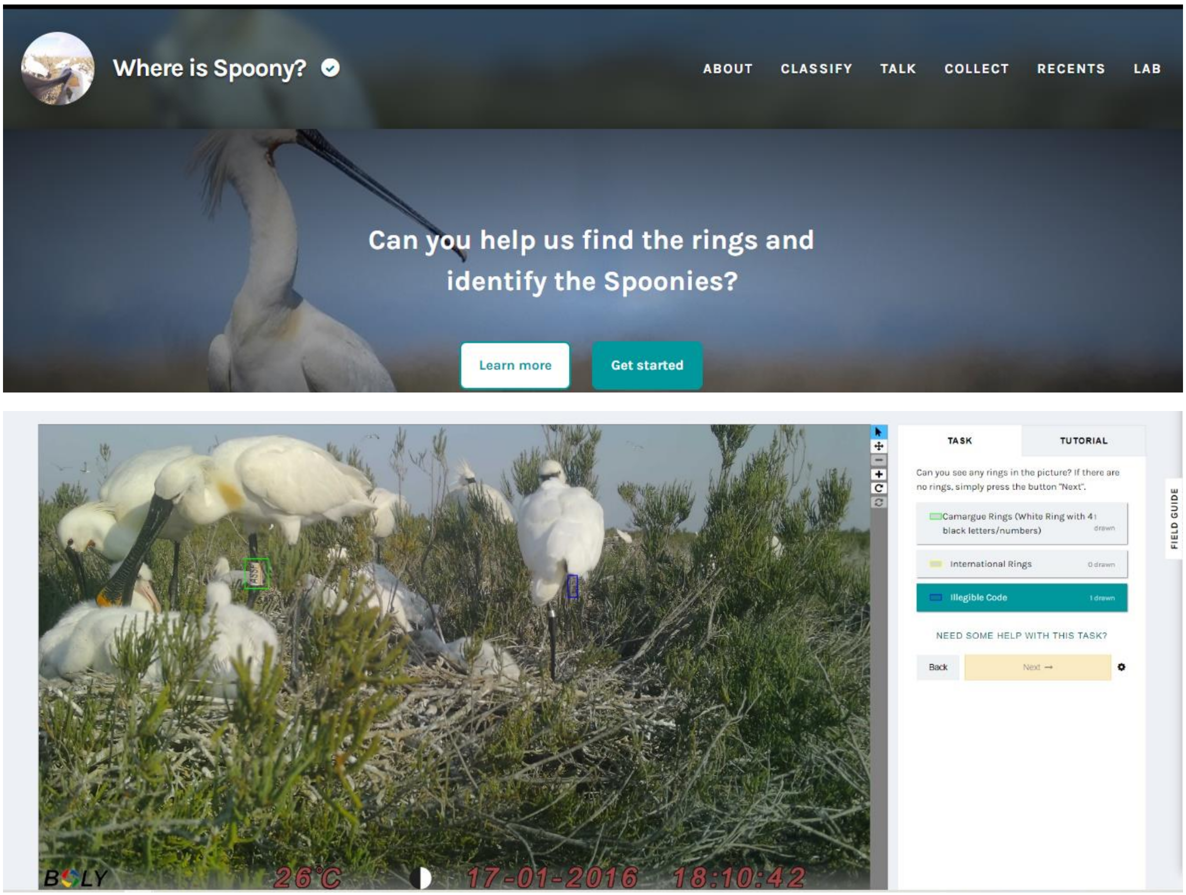


Fig. 13 – Number of spoonbills breeding pairs through the years (orange line) and number of field effort using a hide (blue line). Total number of different spoonbills resighted from the hide (grey bar) and by the camera traps (yellow bar). This graph shows rough data, only one observation per individual was considered and information from juveniles was not included.

Since 2016, the use of camera traps led to the accumulation of 30,000 to 80,000 images annually, which are then processed manually by experts, a time-consuming task. To facilitate this task, machine learning techniques and autonomous trained classifiers are being developed by the Georgia Tech College of Computing in collaboration with Tour du Valat (Bourbon, 2024). Therefore, within the framework of this PhD thesis a citizen science project (*Where is Spoony*; Fig 14), has been developed and launched on the citizen science platform Zooniverse (www.zooniverse.org). During a test year in 2021, 23,000 photos taken at breeding sites in the Camargue were viewed by two experts and 3,350 members of the general public. Each photo was seen by 10 different participants. The two experts were able to identify a total of 318 individuals with unique rings (including eight individuals not seen by the participants) over a period of ca. two months, while the participants identified more than 2,000 different individuals, including several misclassifications but at least 13 valid identifications not made by the experts.



Can you help us find the rings and identify the Spoonies?

Can you see any rings in the picture? If there are no rings, simply press the button "Next".

Fig. 14 –*Where is Spoony* citizen science project, where participants can identify marked spoonbills in Camargue breeding sites, pilot launched in 2021 on the Zooniverse platform.

The annual monitoring effort, together with reports from amateur and professional ornithologists in Camargue and other relevant sites (i.e., reports from other breeding, but also stopover and wintering sites), has provided the necessary resighting data to apply mark-capture-recapture models. Mark-capture-recapture models were developed to study species that are difficult to observe or count directly due to factors such as high mobility, wide geographical ranges, or cryptic behaviour, while minimizing disturbance (Lebreton et al., 1992). By capturing and marking individuals with unique codes that are visible from a distance (i.e., recapture or resighting), it is possible to assemble individual encounter histories. These encounter histories combined, allow for the modelling of population and estimate parameters such as detection, survival or dispersal rates (Choquet et al., 2009; Cormack, 1964; Jolly, 1965; Lindberg et al., 2001; Pradel et al., 1997). Individuals encounter histories can be further combined and modelled according to groups such as age classes, sex, and periods or site (Lindberg, 2012). Furthermore, when marking individuals, field operations enable the collection of valuable demographic information on the Camargue population, including chick biometrics and laying dates. This information was fundamental throughout this thesis, as it enabled comparing the Camargue population to other breeding populations and test the impact of global changes on breeding phenology and chick body condition.

7. Thesis outline and objectives

This thesis is comprised of six empirical chapters (Chapters 2-7), preceded by a general introduction (Part I: Chapter 1) and ends with a general discussion (Part V: Chapter 8). To assess how anthropogenic environmental changes affect spoonbills and the potential consequences of such interactions in their demographic rates, I have divided this thesis into three main sections:

7.1. Part II: Breeding phenology, productivity, and juvenile migratory behaviour

Due to their wide distribution range, spoonbills can serve as a model species for studying how waterbirds in a highly anthropogenic region of the world (Europe) cope with ongoing environmental change, both in terms of climate and habitat.

Chapter 2 is a collaborative (joint first co-authorship manuscript) chapter in which Manuela Rodrigues and I compile data collected from different breeding colonies in Europe to explore spatial variation in breeding parameters (e.g., chick body condition, egg volume, hatching success, and laying dates) and how these may be influenced by geographical and climatic factors. Here, we also consider the impact of different environmental variables (i.e., temperature and rainfall) on the demographic parameters previously analysed.

In **Chapter 3**, I focus on the breeding phenology of the Camargue population and investigate how breeder age may influence the timing of breeding and, in turn, how this may affect chick body condition and their subsequent migratory behaviour. Chick body condition has never been assessed for the expanding Camargue spoonbill population, and its variation can be useful when contrasted with that of other European populations, which may be stable or even declining (**Chapter 2**), and also contribute to explain the mechanisms underlying spoonbill migratory behaviour (**Chapters 6** and **7**).

7.2. Part III: Increasing anthropogenic influence in the heterogeneous Camargue wetlands and its impacts on breeding success and habitat use

Anthropogenic influence in the Camargue is widespread, with several human activities such as agriculture and tourism dominating the area. However, this wetland is also an important nesting and non-breeding region for several waterbirds.

During the collection of breeding parameters for **Chapters 2** and **3**, the presence of artificial materials in spoonbill nests was observed. In **Chapter 4,** I assess the prevalence of such artificial materials, their potential function within spoonbill nest and their potential impact in breeding success.

I then scale up from anthropogenic impacts apparent at the breeding colonies, to explore spoonbill habitat use across a heterogeneous and fragmented wetland such as the Camargue. Specifically, I explore how the use of strongly protected areas and privately managed areas (including areas disturbed by hunting) varies across the annual cycle and according to different spoonbill age classes (**Chapter 5**).

This information can be used to further understand how animals may respond to anthropogenic perturbations or fail to adapt to their changing landscapes. Such knowledge is essential to inform and implement specific management actions that will not only enhance the effectiveness of conservation efforts, but also improve wetland quality and species resilience.

7.3.Part IV: Linking migratory behaviour, challenges and dynamics to survival rates

While the previous two sections addressed mostly breeding ecology, despite also exploring links with migratory behaviour (**Chapter 3**) and non-breeding habitat use (**Chapter 5**), the final section of this thesis investigates annual survival rates. Although considerable within- and between-species variation in wintering site use has been shown to affect demographic parameters, few longitudinal studies have been able to compare the survival rates of a population using different flyways and migratory ranges (specifically, contrasting residency vs short-distance vs long-distance).

First, I investigate the relationship between wintering site and apparent survival rates of the Camargue breeding population for individuals that vary in both migratory flyway (East Atlantic vs. Central European) and migration distance (long-distance vs. short-distance vs. resident), comprising five main non-breeding regions (**Chapter 6**). To do this, I used data collected from camera traps in Camargue breeding sites and from a network of dedicated observers along the migratory range, including the wintering sites of this species.

In **Chapter 7**, I further investigate the mechanisms linking migratory behaviour and survival rates, expanding from **Chapter 6**. Here, I combine capture-recapture data from several interconnected spoonbill populations across Europe and assess the impact of breeding and non-breeding sites in spoonbill apparent survival. By combining different datasets, I was able to overcome several limitations of capture-recapture analyses (e.g., limited to comparisons of single populations and few sites) and obtained survival estimates closer to true survival.

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CHAPTER 2

Continental wide variation in breeding phenology, investment and productivity in a colonial waterbird, the Eurasian spoonbill (Platalea leucorodia)

Collaborative work with Manuela Rodrigues

Observation of spoonbills, Ria Formosa, 2021.

According to the latest report of the Eurasian Spoonbill International Expert Group, the estimated number of breeding pairs in the East Atlantic flyway is around 8300 breeding pairs, while the Central European flyway is likely to have between 1607 to 2370 breeding pairs. Finally, the South-European flyway is estimated to have around 1500 breeding pairs, however, recent estimates from Turkey and Ukraine are lacking.

Continental wide variation in breeding phenology, investment and productivity in a colonial waterbird, the Eurasian spoonbill (Platalea leucorodia)

Abstract

Global changes in climate and land use are occurring at an alarming rate as a result of continued human expansion and growth. Although all ecosystems have been affected and transformed to some extent, the consequences to wetlands, and therefore waterbirds, have been particularly severe. Nevertheless, some species appear to be recovering from earlier declines, likely due to increased environmental legislation and their capacity to use some anthropogenic habitats. Here, we compiled information from 2021 to 2023 on Eurasian spoonbill (*Platalea leucorodia leucorodia*) breeding colonies in several European countries from Portugal to the United Kingdom (latitudinal extremes) and from Portugal to Greece (longitudinal extremes), to gain a better understanding of the spatial variation in breeding parameters and how these may be influenced by geographical and climatic factors. There was no evidence of overall breeding patterns and phenology gradients along geographical or climatic axis, although a latitudinal trend in timing of breeding, with spoonbills at lower latitudes generally starting to lay earlier than those at higher latitudes was apparent. Nevertheless, local conditions such as food availability, predation or local quality of breeders, can disrupt this pattern. Our study highlights the need for high quality standardised data collection methods to better identify patterns and exceptions driven by local conditions. In addition, understanding variation in biological parameter across different sets of environmental conditions is essential to improve predictions of how species may respond (positively or negatively) to changes in habitats and/or climatic as patterns, which may become more similar to others, owing to increasingly prevalent global environmental changes across wide geographical ranges. Ultimately, the information presented here can contribute to the effective conservation of waterbird such species.

Keywords/phrases: Body condition; Egg volume; Environmental changes; Fledging success; Long-term monitoring.

Introduction

The world and its habitat composition are rapidly changing. Concomitant with human expansion and growth, global changes in climate and land use are occurring at a very fast pace (Foley et al., 2013). In the last decade, global temperature has continued to rise, reaching 1.1ºC above the 1850–1900 value (IPCC, 2023). Extreme climatic events have become more frequent and intense in recent decades (NAS, 2016; Wernberg et al., 2013), with heat extremes and heatwaves now more prevalent globally, heavy precipitation occurring in Northen and Central Europe, and ecological droughts being more frequent in Central Europe and the Mediterranean (IPCC, 2023). These events are known to affect not only species distributions, but also the structure and functioning of ecosystems worldwide (Hawkins et al., 2009).

Owing to the growing human need for natural resources (e.g., food, freshwater and fuel), the rate of habitat loss is equally alarming to climate change (Cushman, 2006; Flockhart et al., 2015; Reif et al., 2010), with evidence showing that human development gains over the past 50 years have largely been achieved at the increasing cost of habitat loss and degradation (IPBES, 2019). For example, increased demand for cropland over the last century has led to an increase in land conversion, and in water reservoirs becoming more common and larger, with water retention quadrupling since 1960 (IPBES, 2019; MEA, 2005). Although all ecosystems have been affected and transformed to some extent, the cost to wetlands has been particularly severe, with estimates of global area loss ranging from 21% to 85%, depending on the methods and baselines used (Fluet-Chouinard et al., 2023; Hu et al., 2017; IPBES, 2019). However, it is clear that some regions have suffered highest wetland losses, with Europe, United States and China being the most severely impacted (Fluet-Chouinard et al., 2023)(Fluet-Chouinard et al 2023). As a result, these changes have a profound impact on wetland ecosystems and species (Wetlands International, 2024), being highlighted as one of the major causes of biodiversity loss and species extinction (MEA, 2005; Murphy and Romanuk, 2013).

Waterbirds are a diverse group of birds so intrinsically dependent on wetlands that they have been described as bioindicators of the wellbeing of these habitats (Green and Elmberg, 2014; MEA, 2005). As such, waterbirds have suffered from both severe wetland habitat degradation and climate change, and many species experience rapid decline worldwide (Belo et al., 2023; Kirby et al., 2008; Studds et al., 2017). However, this is not the case for all waterbirds, and some seem to be recovering from earlier declines, at least locally, as is the case for several species in Europe (Amano et al., 2018, 2020; Wetlands International, 2024). For instance, those that can take advantage of artificially managed wetlands which can directly or indirectly increase food availability, such as those managed for economic or recreational interests (e.g., agriculture and hunting) or for conservation purposes are currently increasing (Alonso et al., 2008; Hamza et al., 2015; Johst et al., 2001; Li et al., 2015; Rodrigues, 2018; Rodrigues et al., 2023a).

In 2013, Overdijk described the remarkable recovery of the North Atlantic breeding population of Eurasian spoonbill (*Platalea leucorodia leucorodia*, hereafter spoonbill), which has increased exponentially after years of severe decline (Overdijk et al 2013). Spoonbills were once an abundant breeding species in Western Europe but declined dramatically at the start of the 20th century, when they were confined to only four breeding colonies: three in The Netherlands (Naardermeer, Texel, and Zwanenwater) and one in Spain (Doñana). But, in recent decades, spoonbills have been increasing in Europe and (re)colonising traditional breeding areas within their former range (Rodrigues, 2024). The main factors promoting the initial recovery of the colonies in The Netherlands were the implementation of legislation to protect birds, eggs and habitats, the banning of some water pollutants and the creation of protected areas (Overdijk, 2013). Breeding spoonbills then spread to other countries in Northern Europe such as Belgium, Germany, and the United Kingdom (Overdijk, 2013). In Southern Spain, rescue of eggs from nest flooding, subsequent hand raising of chicks, and reintroduction in the wild (Doñana National Park) have helped to increase productivity of this population (Cuadrado et al., 2017). Several other reasons have contributed to the general expansion of spoonbills in Europe, such as its increasing use of anthropogenic habitats (Chapter, 5; Rodrigues et al., 2023b; Tucakov, 2004), the appearance of invasive species in their diet, such as Red-swamp crayfish (*Procambarus clarkii)*, which provide a stable and abundant food resource (Rodrigues et al., 2023a), and various wetland habitat conservation measures, particularly the European Birds Directive (1979) and the Water Framework Directive (2000) in the European Union (Alves et al., 2012; Galewski et al., 2011; Garaita and Arizaga, 2015; Pigniczki and Karcza, 2013; Ramo et al., 2013).

The spoonbill is currently listed as Least Concern on the IUCN Red List and its breeding distribution in Europe spans across almost the entire continent, ranging from Denmark and the British Isles in the north, to the Iberian Peninsula in the south, and spreading east to the Balkans and the Black Sea (BirdLife International, 2024). Such a wide distribution range in Europe means that spoonbills can serve as a study model to explore how waterbirds may be able to cope with ongoing environmental changes, in both climate and habitat, in heavily modified habitats over a vast area. Spoonbills in Europe are divided into three distinct flyway populations (Champagnon et al., 2019): (i) the East Atlantic Flyway population (EAF), characterised by spoonbills breeding along the Atlantic coastal area of Europe, and the most studied (Lok, 2013; Rodrigues, 2018); (ii) the Central European Flyway population (CEF), of which some colonies have been monitored, in the Carpathians and Italy, (Kralj et al., 2012; Pigniczki, 2022; Tenan et al., 2017); and (iii) the South-eastern European Flyway population (SEF), recently separated from the CEF (Champagnon et al., 2019), and for which knowledge is scarce despite some exceptions, such as in Greece (Kazantzidis et al., 2023). Currently, the East Atlantic Flyway population is steadily increasing in several breeding sites (e.g., Belgium and United Kingdom), in contrast to the CEF and SEF populations, which are experiencing stable and declining trends, respectively (Champagnon and Kralj, 2023). Nevertheless, different trends are also observed within the CEF, with the registered decline of the Hungarian population contrasting with the high survival and expansion of the Italian population (Tenan et al., 2017).

Species that span wide geographic ranges offer the possibility to explore how variation in demographic and other biological parameters relates to the disparate environmental conditions experienced locally, in different breeding colonies. Furthermore, establishing baseline information on those relationships can help predict how some species may respond (positively or negatively) to changes in habitats and/or climatic patterns in some parts of their range, which will resemble conditions currently present in other parts of the range. This is particularly relevant for the conservation of species associated with habitats currently undergoing high levels of change, such as wetlands, which are predicted to be under increasing pressure given current climatic scenarios (IPCC, 2023), especially in regions with high human population densities, such as Europe.

In this study, we compiled data from spoonbill breeding colonies across seven European countries, ranging from Portugal to the United Kingdom (latitudinal extremes), and from Portugal to Greece (longitudinal extremes). Our aim was to investigate the spatial variation in breeding parameters and to understand how these differences may be influenced by geographical and climatic factors. Specifically, (1) we assessed how breeding phenology was affected by latitude and longitude. We hypothesized that spoonbills breeding at lower latitudes would initiate the breeding season earlier, as favourable climatic conditions are expected to occur earlier in the year in those colonies. However, with increasing longitude, colonies are increasingly influenced by warmer continental temperatures (in Europe), which may also advance the onset of the breeding season. Conversely, due to more favourable climate conditions, we expect larger egg volume, higher hatching success and chick body condition at lower latitudes and higher longitudes. (2) We then explored how climatic factors, specifically precipitation and temperature, can influence spoonbill breeding performance. We expected that breeding success and chick body condition would be lower in colonies with periods of intense precipitation, but also in colonies with low precipitation, particularly in those colonies more heavily reliant on freshwater. We further expected that both higher and lower temperatures would negatively impact spoonbill breeding success, as both may force higher levels of nest attendance (to provide shadow or to brood the chicks) potentially reducing provisioning rates; Finally, (3) we investigated seasonal trends in breeding performance, considering that earlier breeders may be more experienced adults and likely responsible for the higher body condition of early chicks (as reported in the Camargue, Chapter 3), and therefore we expected that breeding parameters such as egg volume, hatching success and chick body condition would decrease seasonally in all breeding colonies.

Material and Methods

Study area

Data presented in this study were collected between 2021 and 2023 in seven European countries (Fig. 1) during monitoring visits to spoonbill breeding colonies performed as part of long-term monitoring programmes (apart from Portugal and France, where targeted data collection was performed). Only one colony per country was sampled, and for simplicity, the name of the country (*Country*) is used to identify each colony in the following sections.

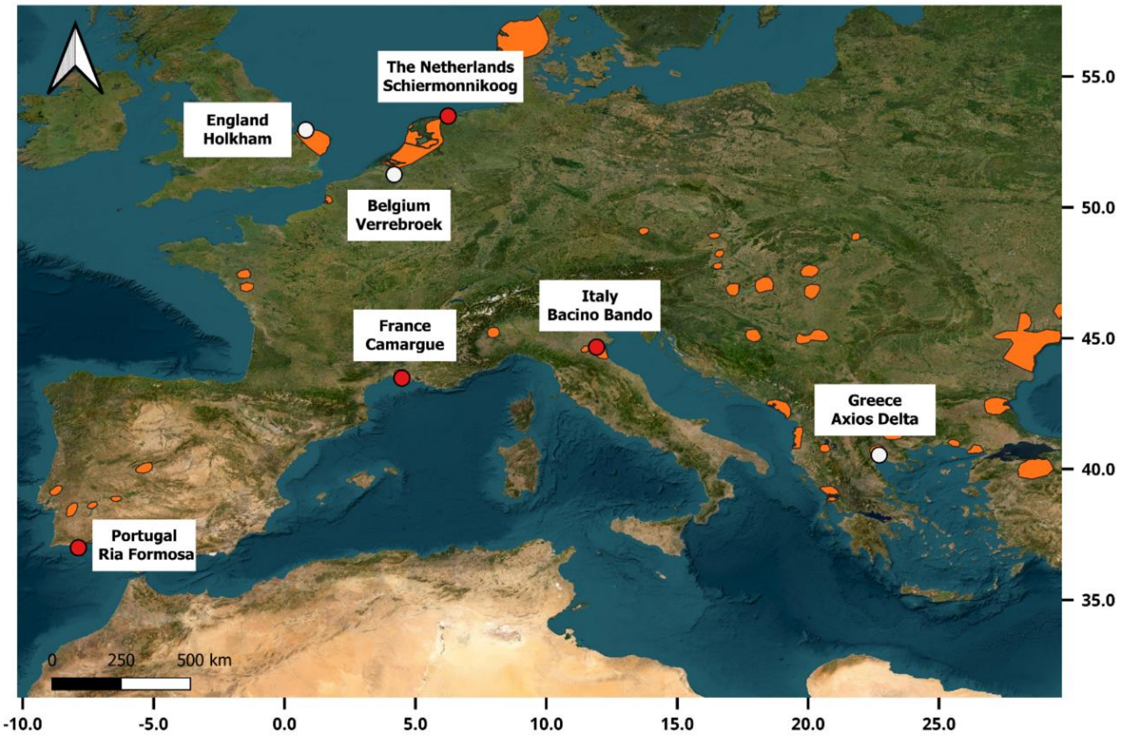

Fig. 1 – Spoonbill breeding range in Europe (orange; adapted from BirdLife International, 2023). Circles show colonies that contributed data to this study and red circles dots show colonies from countries with suitable data for statistical analysis. In any case data from all countries (including colonies marked with white circles) are presented descriptively and considered when discussing the statistical results.

In The Netherlands, sampling was carried out in the colonies on Schiermonnikoog (coordinates: 53°29’24’’N 6°15’0’’E). Spoonbills started breeding on Schiermonnikoog in 1992, and numbers rapidly increased to *ca.* 200 breeding pairs in the early 2000s, after which numbers stabilized and fluctuated between *ca.* 200 and 300 breeding pairs. The majority of spoonbills on Schiermonnikoog breed on the east side of the island (Oosterkwelder), mostly in saltmarsh, often in mixed colonies with herring and Lesser black-backed gulls (*Larus argentatus* and *Larus fuscus*), and increasingly in Seaberry (*Hippophae rhamnoides*) bushes. In 2011, a second colony established in a freshwater lake on the west side of the island (Westerplas), where they breed in reed and willow trees, adjacent to Great cormorants (*Phalacrocorax carbo*). Spoonbills from these colonies are mainly foraging on the intertidal flats of the Wadden Sea, while particularly adult males also regularly forage in the shallow freshwater lake Lauwersmeer, at *ca.* 10 km distance from the colony (Lok et al., 2024).

In England, sampling was carried out at Holkham (52°57’20.8’’N 0°48’27.9’’E). Spoonbills began prospecting this site in 2004, with 1-2 pairs attempting to breed there each year. However, successful nesting did not occur until 2010, when six pairs were recorded breeding in at this site. Since then, the number of breeding pairs has increased each year, slowing down and stabilising in 2023 2024. The main habitats in the area are freshwater marshes surrounding a wet woodland of mostly willow trees (or hawthorn *Salix sp.*) where spoonbills nest. Successful spoonbill colonisation followed the site adoption by Grey heron (*Ardea cinerea*) in 1993, Great cormorant in 1999 and Little egret (*Egretta garzetta*) in 2004, as well as the management of marshes (through grazing) for wading birds, and the protection of the area from human disturbance. Due to high spoonbill productivity over the years, other subsequent sites with successful breeding have now been reported in the UK (Bloomfield, 2018).

In Belgium the sampled colony is located in Verrebroek (51°15'21.6"N 4°11'16.8"E). Spoonbills started breeding here in 2003 and the number of breeding pairs has been increasing. The area consists of tidal wetlands, shallow freshwater bodies and reeds. In this colony most spoonbills breed in an artificial island (made of branches), but some pairs also breed in reeds and meadows. Most spoonbills breed inside an electric fenced area, constructed to prevent attacks from terrestrial predators. In the same area are also present breeding pairs of Black-headed gull (*Chroicocephalus ridibundus*) and Grebes (*Podiceps sp.*).

The colony sampled in Italy is located in Bacino di Bando (44°39'37.6"N 11°55'21.5"E), a freshwater basin where spoonbills nest in reedbeds. First breeding attempts in this colony were recorded in 1992, but it was not until 2012 that the area became regularly used, and the number of breeding pairs increased, peaking in 2014, at 104 breeding pairs. Since then, numbers have fluctuated, with 55 breeding pairs recorded in 2023. These changes are likely due to the deterioration and reduction of the reedbed area (Volponi, personal observation). In the surroundings of the colony, spoonbills have access to freshwater bodies, extensive agricultural fields and agricultural channels. The reedbed traditionally housed a mixed heronry composed by Grey heron, Purple heron (*Ardea purpurea*), Night heron (*Nycticorax*

nycticorax), Little egret, Great white heron (*Ardea alba*), and Squacco heron (*Ardeola ralloides*), but the reed has deteriorated to such an extent that only spoonbills and Greylag goose (*Anser anser*) currently breed at this site.

In France, sampling occurred in the Camargue Regional Natural Park (43° 28' 36.012" N 4° 29' 3.0012" E). Spoonbills breed in this area since 1998 and are experiencing exponential growth, reaching around 510 nests in 2023 (Blanchon et al., *unpublished data*). Here, spoonbills breed in small bushes and on the ground of six small islets separated by distances ranging from two to about 20 km. Camargue is a semi-natural region of 180,000 ha, along the Mediterranean Sea in South France, where several shallow waters, and salt marshes are available to the species (Blondel et al 2013, Galewski & Devictor 2016, Roche et al 2009). In the same islets, nests of Yellow legged gull (*Larus michahellis*) are regularly recorded with occasionally Great cormorant, Shelduck (*Tadorna tadorna*), and Little egret.

In Greece, the colony sampled is located in the Axios Delta National Park (40° 32' 23.16" N 23º8'44.71"E). Spoonbills breed here since the 80’s making it one of the oldest colonies in the country. It is a growing colony with an average of 67.5 breeding pairs per year (2020-2023), reaching 109 nests in 2023 (Kazantzidis et al., 2023). This is a coastal wetland where spoonbills build their nest in the top of trees, and is surrounded by salt marshes, marine coastal areas, rice fields, freshwater marshes and riverbeds. Spoonbills breed together with Little egret, Black-crowned Night heron, Grey heron, Pygmy cormorant (*Microcarbo pygmaeus*), Great cormorant, Squacco heron, Glossy ibis (*Plegadis falcinellus*), and occasionally, Cattle egret (*Bubulcus ibis*).

Lastly, in Portugal, a colony located in the Ria Formosa National Park (36º59'45.6"N 7º52'30"W) was sampled. This is one of the oldest colonies in the country, where spoonbill breed since 1993. This colony is currently growing and in 2022 a total of 121 nests were recorded. Ria Formosa is a coastal wetland, and spoonbills breed on a small islet, with nests built on the ground or in the top of small bushes. The islet is part of a system of small barrier islands that form a coastal tidal lagoon. The colony is surrounded by extensive mudflats, salt marshes, and salt pans. This is a mixed colony where Little egret and Cattle egret also breed. Apart from Italy, all spoonbill breeding colonies studied are protected as part of the Natura Network 2000 and the Ramsar Convention.

Data collection and breeding parameters

Due to the *a posteriori* compilation of data and fieldwork constraints, several data collection methods were used (see Appendix, Table A2.1 and A2.3 for further details in data collection and methodology in each country).

From the monitoring of nests we calculated the following breeding parameters: Colony size, the total number of occupied nests; 1st laying date and 1st hatching date, defined as the day in which the first egg was laid or hatched in each country and year; laying and hatching periods, that were calculated as the interval in days between the first and last laid/hatched egg; Egg volume calculated using Hoyt's formula (Hoyt, 1979); Clutch size, the number of eggs laid in each nests (in the same nesting attempt); Hatching success per nest, calculated as the percentage of hatched eggs of the total number of eggs in the nest; Nest success (per country and year), calculated as the percentage of nests that have at least one hatched egg of the total number of nests sampled in the colony; Dead chicks and fledged chicks per nest, calculated as the percentage of chicks that fledged or died from the total hatched eggs from the nest.

Besides the monitoring of nests, in some colonies chick body measurements were also collected (tarsus size, the combined size of head and bill, the eight primary feather length, and mass) to allow the estimation of chick body condition. Body condition was calculated using the Scaled Mass Index (hereafter SMI) proposed by Peig and Green (2009), which is considered to reflect the energy capital accumulated in the animal's body due to food ingestion, and as such, an indicator of an animal´s general health and quality. This method can be used for chicks of different sizes, sexes, and ages, as it standardises body mass along a standard body measurement based on the scaling relationship between length and mass (Peig and Green, 2009). A preliminary analysis identified tarsus size as the body measurement most correlated with body mass in a log-log scale (Peig and Green, 2009) (R^2= 0.83, $p<0.001$, see other correlation results in Appendix, Table A2.1), and thus this was the metric chosen as body length in the next formula. SMI was thus calculated by applying the formula:

$$SMI = W_i \left(\frac{L_0}{L_i}\right)^{b_{SMA}}$$

where Wi is the weight of the bird, L_i is length, in our case is tarsus length, L_0 is the arithmetic mean of the tarsus length of all chicks analysed, and b_{SMA} is the scaling exponent estimated by the standardized major axis (SMA) regression of ln(mass) on ln(tarsus) (Peig and Green, 2009). We acknowledge the existence of a species-specific method for assessing chick body condition proposed by Lok and collaborators (2014), that also accounts for differences in sexes. However, this index is only suitable for chicks older than 25 days, which reduced our sample size by 72.56% (from 492 chicks to 135). Furthermore, data from Italy would be excluded when using this method, as the measurement of the eight primary feather, which is essential for age estimation in this approach, was not performed. Nevertheless, we compared the results obtained using both methods (calculated for the chicks that had all required biometrics) and the values obtained from each method were significantly correlated (r=0.66, $p < 0.001$, Appendix, Fig. A2.1).

Climatic data

To investigate potential climatic drivers of variation in the phenological and breeding patterns of spoonbills, we used daily climatic data, specifically precipitation and temperature (mean, maximum and minimum) for the years 2020 to 2023.

Daily climatic data was obtained from the European Climate Assessment & Dataset (ECA&D) (Klein Tank et al., 2002). This dataset contains meteorological data from stations across Europe and presents blended and unblended data. We selected blended data, i.e. datasets that contain climatic information from a specific meteorological station, but also, in cases of missing data, use data from nearby stations (up to 12.5 km distance between stations and with less than 25 m of altitude difference). We collected data from the nearest meteorological station with more complete climatic information to each colony (Appendix, Table A2.2), but in a few cases (three days for Italy and eight days for France), we needed to complement it with data from other nearby stations, as even the stations with more complete information had some data gaps (for more details see Appendix, Table A2.2). For some countries (The Netherlands and Italy) we had to use different stations for precipitation and temperature data. The distances between the meteorological stations used and the colonies ranged between 2 and 87.42 km (Appendix, Table A2.2).

The package *Climwin* (Bailey and Pol, 2016) in *R* software was used to conduct an exploratory analysis of when the selected climatic factors influenced the phenology and breeding parameters of spoonbills. This was done because we had no *a priori* knowledge of which time window of each climatic factor would have an effect on phenology and breeding parameters. Specifically, we tested the effects of climatic factors on the variables for which we had more robust data: laying date, egg volume, hatching success, and chick body condition (due to fledging date being unknow for some chicks, fledging success was not considered in the *Climwin* exploratory analysis). To be able to analyse the effects of climate on laying dates we transformed this variable into a new one termed laying density (because 1st laying date is a singular event per year and colony and does not have with multiple data points that can be used like that in *Climwind*). We determined the density of laying (at colony level) on each day (i.e. the number of nests whose 1st egg was laid on that day). But as suitable climatic conditions for egg laying might continue even after laying has ended (due to lack of space or breeders), we considered only the days until the end of the 1st laying peak of each colony in each year. As there may have been isolated days with no laying within the duration of the 1st laying peak, we used a sliding window of five days of the mean 1st eggs laid per day, to determine the length of this peak period of laying. This allowed to clearly identify peaks that ended when the moving mean was zero for the first time.

The effects of each of the four climatic factors (cumulative precipitation and averaged maximum, minimum and mean temperatures) on breeding parameters were tested independently, with univariate models. For temperature, we selected in each case the factor with highest (and statistically significant) effect on the studied variable. A complete and detailed explanation of this analysis, as well as its results, can be found in the Appendix.

Climatic factors (during the identified time windows) that had an effect on the phenology and breeding parameters were retained for subsequent analysis, combining climatic factors with other exploratory variables.

Statistical analysis

In order to explore variation in phenology and breeding parameters along geographical, climatic and seasonal gradients, we used a linear regression framework. The response variables were laying date, egg volume, hatching and fledging success, and chick body condition. The explanatory variables considered were Latitude and Longitude (geographical gradient), day of the year as Julian day (seasonal gradient: excluded for laying date models; calculated as number of days since the 1st laying date on each combination of colony/year), previously selected climatic factors (climatic gradient) and year (controlling for possible year effects). For all response variables considered (see below) we followed the same procedure: 1) build the *full model* with all possible explanatory variables checking for correlation and multicollinearity assumptions with package *performance* (Lüdecke et al., 2021); 2) built all possible *reduced models* with those same exploratory variables, including the null model; 3) use the second-order Akaike information criterion (*AICc*) to select the most supported model, i.e., the one with the lowest *AICc*; 4) when several top ranking models differed by less than two *AICc* points, we averaged the model coefficients. The following paragraphs describe the specifications of each set of models created for each response variable:

Laying dates were studied through two different response variables: a) 1st laying in each country and year (in order to assess how early spoonbills were able to lay eggs in each country); and b) average laying date of the first peak in each country and year (by considering the first peak, we ensure that 2nd clutch was not considered), with peaks defined through sliding window means of density of nests whose 1st egg was laid on that day (see above; which allowed to define the most suitable period of laying used in the subsequent analysis and calculate the average day of that period). For this analysis we excluded data from France during 2021. This was due to nests and eggs being destroyed or abandoned following predation by Wild boar (*Sus scrofa*) during the 1st peak of laying, before laying dates could be calculated.

For modelling egg volume and chick body condition, mixed-effect models were used with nest ID as random effect, as eggs and chicks from the same nest may be more similar than eggs and chicks from different nests.

Hatching and fledging success models were built using binomial error distribution, having as response variables the combinations of number of hatched and not hatched eggs per nest and of fledged and not fledged chicks per nest, respectively. All the other models had normal error distribution.

As indicated above, several nests predated in France 2021 prior to hatching were not considered in the analysis of hatching success as laying date was not available. However, as this excluded all nests with zero hatching success (due to nest destruction), a second modelling exercise without Julian day as an exploratory variable was performed including these nests, for which results are reported in Appendix, Table A2.7. Similarly, in Portugal it was not possible to link chick body condition to each nest, so despite being able to back estimate hatching date, the laying dates of the eggs of those chicks was unknown, and therefore Portugal was excluded from chick body condition models. Also here, we performed a second modelling exercise without Julian day as explanatory variable, including the Portuguese chick body condition data, for which results are reported in Appendix, Table A2.7.

The explanatory variables Julian day, cumulative precipitation, minimum and maximum temperatures (see Appendix, for how these are calculated) were standardised in every model. Country and method (used for accessing each variable) were not used as independent variables because of correlation and multicollinearity.

All models were fitted with *stats* (R Core Team, 2022) and *lme4* (Bates et al., 2023) packages and assumptions checked with the package *performance* (Lüdecke et al., 2021). All data analyses were conducted in R software version 4.2.2. (R Core Team, 2022).

Results

We amassed breeding parameters from seven colonies spanning the distribution range of the species in Western Europe (Fig. 1). However, as there is no standardised protocol for data collection between monitoring programmes, the number of parameters and sample sizes differed between countries (Appendix, Table A2.5). As a consequence, only data collected in 2021 and 2022, in The Netherlands, Italy, France, and Portugal using comparable was used for statistical analysis.

The smaller colonies (i.e. with fewer occupied nests) were Verrebroek (Belgium), Holkham (England) and Bacino bando (Italy), whereas the largest was Camargue (France) (Table 1). Nevertheless, it should be noted that in some cases, “colony” means several breeding clusters in separate islands while in other cases it is just one breeding cluster (see discussion).

Climatic data from the 1st of January to the 30th of September of the years 2021 and 2022 varied considerably between colonies, with daily precipitation being on average highest in The Netherlands (19.68 ± 1.69 mm) and lowest in Portugal (6.11 ± 1.17 mm). Conversely, temperature was highest in Portugal, both maximum (25.95 ± 2.87 ºC) and minimum (13.77 ± 2.32 ºC), and lowest in The Netherlands (maximum: 14.70 ± 2.95 ºC, minimum: 9.04 ± 2.50 ºC), suggesting that the latitudinal axis could account for some of the variation in breeding parameters across colonies. All climatic data can be seen in Appendix, Table A2.6 and Fig. A2.2.

Phenology

Spoonbills began laying as early as January 26th in Italy, but in some countries, such as The Netherlands and Greece, they do not start laying until late April. The duration of the laying period also varied greatly, ranging from 35 days (Greece) to almost four months (France) (Fig. 2). The duration of the 1st peak of laying was also variable (average days ± SE: The Netherland: 22.5 d ± 4.6; Italy: 41.5 d ± 7.42; France: 15 d ± 2.83; Portugal: 35.3 d ± 6.72), with France having the shortest peak and Italy the longest (Table 1). Hatching followed similar patterns, with the exception of Portugal in 2022, where hatching period was shorter than the laying period (due to extensive loss of first laying), and of Italy in 2022, where the opposite pattern was apparent (Table 1).

Table 1. Phenology and number of nests of Eurasian Spoonbill in seven European breeding colonies. Methods used in each country are indicated with superscript letters. For more details about methods see Appendix. Some spaces were intentionally left empty as the parameters were not calculated in given country/year. Dates are expressed in Julian days.

	Year	**Colony size**	**1st laying date**	**Average 1st laying date**	**Duration laying period (days)**	**Duration of first peak of lay (days)**	**1st hatching date**	**Average 1st hatching date**	**Duration hatching period (days)**
The Netherlands (e, i)	2021	266	114	109.5 ± 3.2	50	29	139	134.5 ± 3.2	50
	2022	214	105		34	16	130		35
England	2022	43	67				105	107 ± 1.4	
	2023	46	82				109		
Belgium	2021	37	81	83.7 ± 3.5			102	110.7 ± 8.3	
	2022	38	78				99		
	2023	51	92				131		
Italy **(d, e, f, g, i)**	2021	55	41	33.5 ± 5.3	68	52	67	59.5 ± 5.3	61
	2022	53	26		84	31	52		99
France **(b, c, g, h, i)**	2021	424	79	62.3 ± 6.9	88		104	90.5 ± 9.5	88
	2022	631	52		112	19	77		113
	2023	510	56			11			
Greece **(b, i)**	2023	109	114		35		142		34
Portugal **(a, e, g, h, i)**	2021	120	86	86.0 ± 0.0	53	26	114	122.0± 5.7	53
	2022	121	86		65	45	130		43

Notes: Methods for estimating number of nests: a) One count by foot; b) Several counts by foot; c) One count with drone; d) Several counts with drone; e) Count and mark nests; Methods for estimating laying and hatching dates: f) Observation on the day the egg was laid/hatched; g) Latest possible date of laying/hatching given the date and nest state on the visit; h) Estimated by egg flotation; i) Estimated by measurement of chick(s) size.

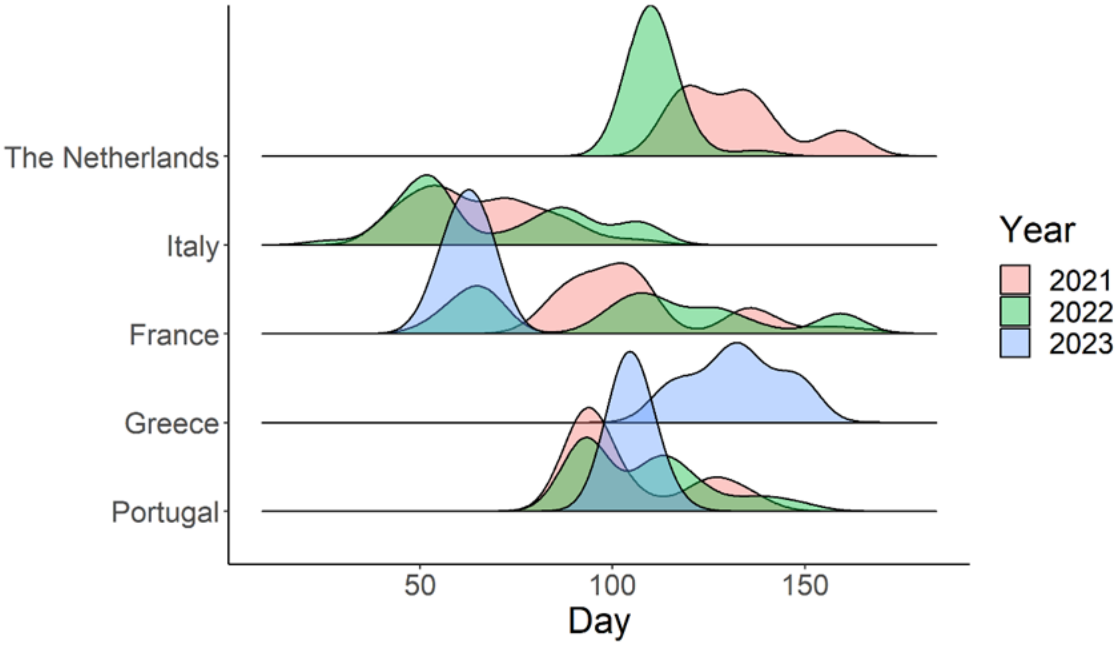

Fig. 2 – Density histogram of spoonbills laying dates per day (Julian day) in each country and year. Only countries with data on number of laid nests per day are included.

The day when the first spoonbill egg was laid was influenced by both latitude and longitude, but not by temperature or precipitation (Table 2; see Appendix for the relevant time windows).

Table 2. Results of top ranking linear and generalized linear mixed models for each response variable. Top ranking models were selected based on Akaike Information Criterion *(AICc)* (see methods for more details and Appendix, for model selection). For response variables marked with * we present the full averaged results and adjusted standard errors (SE). Nest was used as random factor on models predicting Egg volume and Chick body condition. The reference Year is 2021 and p values < 0.05 are highlighted in bold. Results of the top-ranking model sets for each response variable are presented in Appendix, Table A2.8.

Response	***N***	**Fixe effects**	**Estimate**	***SE***	***t or z value***	***p***
1st laying	7	Intercept	-1.6	27.1	*-6.0*	***0.004***
		Latitude	5.7	0.63	*9.0*	***p< 0.001***
		Longitude	-4.9	0.51	-9.6	***p< 0.001***
Average laying date	7	Intercept	87.6	11.0	*8.0*	***p< 0.001***
Egg volume*	582	Intercept	69733.1	2068.4	33.7	***p< 0.001***
		Precipitation	-2900.0	502.2	5.8	***p< 0.001***
		Longitude	314.1	69.9	4.5	***p< 0.001***
		Year 2022	1186.0	2022.7	0.6	*0.558*
		Year 2023	1687.0	2621.6	0.6	*0.520*
		Day	-60.1	234.6	0.3	*0.798*
Hatching success	428	Intercept	4.4	0.8	5.7	***p< 0.001***
		Longitude	0.1	0.02	8.5	***p< 0.001***
		Year 2022	0.6	0.1	4.1	***p< 0.001***
		Day	-0.3	0.1	-3.6	***p< 0.001***
		Latitude	-0.1	0.01	-4.9	***p< 0.001***
Fledging success*	313	Intercept	8.4	1.0	8.2	***p< 0.001***
		Latitude	-0.1	0.02	6.5	***p< 0.001***
		Longitude	-0.2	0.02	6.7	***p< 0.001***
		Year 2022	-1.0	0.2	6.2	***p< 0.001***
		Day	0.02	0.1	0.4	*0.71*
Chick body condition*	418	Intercept	789.4	101.0	7.8	***p< 0.001***
		Precipitation	33.8	7.0	4.8	***p< 0.001***
		Day	0.5	0.4	1.2	*0.23*
		Latitude	7.7	1.8	4.3	***p< 0.001***
		Longitude	12.2	2.5	4.9	***p< 0.001***
		Year 2022	-3.8	9.5	0.4	*0.69*

Egg laying started earlier at lower latitudes (Fig. 3A), but also at higher longitudes (Fig. 3B). Although average maximum temperature (11 to 1 day before) had an effect on average laying date (Appendix, Table A2.4), this variable was not included in the top-ranking model of 1st lay date or average lay date (Table 2).

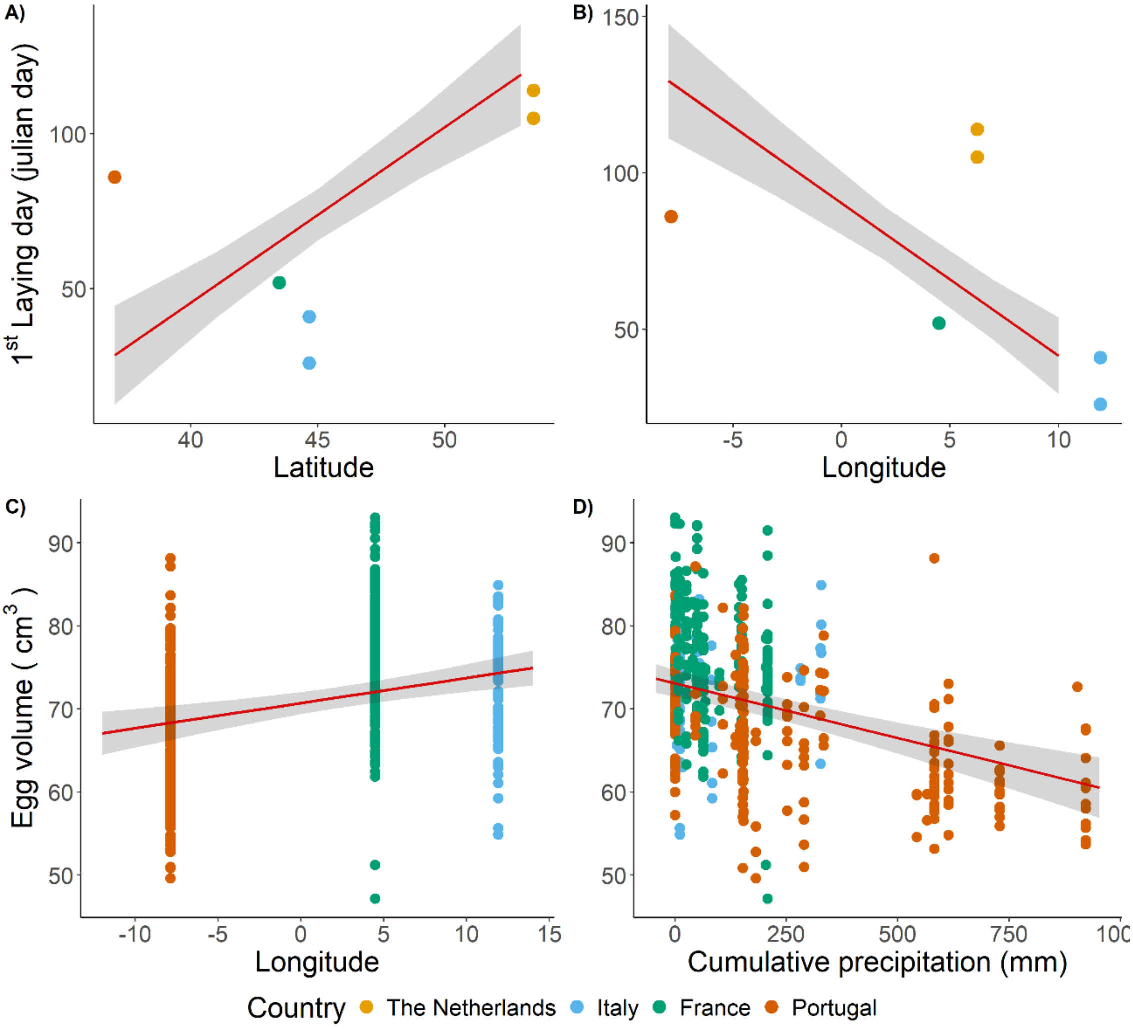

Fig. 3 – Variation on date of 1st laying with (A) latitude and (B) longitude. And variation on spoonbill egg volume (C) with longitude and cumulative precipitation (D) in the 20 to 6 days before laying (precipitation values are standardized). The red lines represent the effects resulting from the top-ranking linear models. The grey shaded areas represent the 95% confidence interval of the predictions, and coloured circles represent the raw values for each country.

Conversely, for the average laying date of the first peak, the top-ranking model was the null model, meaning that neither latitude, longitude, nor year, explained any substantial variation on this variable (Table 2).

Clutch size and egg volume

Spoonbills had an average (±SE) clutch egg size of 3.2 ± 0.03, ranging from one to seven eggs. This number is very similar to the average clutch size per colony and year (Table 3) indicating little variation in this parameter. For egg volume, data from three colonies were considered (Italy, France and Portugal, Table 1). The average (±SE) volume of spoonbill eggs was 71204.9 ± 337.4 mm^3, with eggs from France having the largest volume and those from Portugal the smallest. (Table 3).

Table 3. Breeding parameters of Eurasian Spoonbills in seven European colonies. Methods for estimating number of dead and fledged chicks are indicated with superscript letters. For more details about used methods see Appendix. Some spaces were intentionally left empty when the parameters were not calculated in a given country/year.

	Year	**Average clutch size**	**Clutch size range**	**Average egg volume (*mm^3*)**	**Average hatching success per nest (% ±*SE*)**	**Nest success (%)**	**Average dead chicks per nest (%±*SE*)**	**Average fledged chicks per nest (%±*SE*)**
The Netherlands (b,2)	2021	3.4 ± 0.1	1 - 5		66.5 ± 3.5	73.6	24.9 ± 3.7	75.1 ± 3.7
	2022	3.6 ± 0.1	2 – 5		82.3 ± 2.5	85.5	59.5 ± 3.6	40.5 ± 3.6
Italy (a,b,2,3)	2021	3.1 ± 0.1	2 - 5	73188.3 ± 1061.3	90.0 ± 3.3	81.3	24.3 ± 4.4	75.7 ± 4.4
	2022	3.1 ± 0.1	2 - 5	71606.3 ± 760.4	86.9 ± 3.6	90.0	32.9 ± 5.3	31.0 ± 4.9
France (a,b,2,3)	2021	2.9 ± 0.1	1 - 5		70.5 ± 4.7	78.9	17.1 ± 3.8	82.7 ± 3.7
	2022	3.1 ± 0.1	1 - 5	76375.6 ± 510.3	60.6 ± 5.6	67.7	8.3 ± 2.7	88.1 ± 3.2
	2023	3.5 ± 0.1	3 - 4	75305.8 ± 814.4				
Greece (a,2)	2023	3.1 ± 0.1	2 - 4		69.4 ± 9.0	100.0	0.0	79.6 ± 8.7
Portugal (a)	2021	3.4 ± 0.1	1 - 7		50.7 ± 3.7	72.1	12.8 ± 3.2	
	2022	2.8 ± 0.1	1 - 5	65297.9 ± 483.9	39.2 ± 4.9	48.1	20.2 ± 4.9	
	2023	3.2 ± 0.2	2 - 4	69283.7 ± 876.7				

Notes: Methods for estimating number of dead chicks: a) Count of dead chicks in the nest cup; b) Count of individually marked dead chicks in the nest cup or in the colony area; Methods for estimating number of fledged chicks: 1) Chicks alive until they leave the nest; 2) Counts of marked "almost fledglings" (chicks of 15 days of age or older) at ringing session; 3) Counts of marked "almost fledglings" (chick of 15 days of age or older) at the end of the season.

Egg volume was influenced by longitude and cumulative precipitation (between 20 to 6 days before laying) (Table 2). Egg volume increased with increasing longitude (Fig. 3C) and decreased in periods of more rain (Fig. 3D). We found no statistically significant effect for day of the season or year. Latitude and minimum temperature (60 to 18 days before laying) were removed from these models due to multicollinearity effects, but in exploratory climatic analysis egg volume decreased with increasing minimum temperatures (Appendix, Table A2.4).

Breeding success (hatching and fledging)

Spoonbill nests generally had a high nest success rate (i.e. proportion of nests with at least one egg hatched), particularly in Greece (2023, 100%) and Italy (2022, 90%), but it was particularly low in Portugal in 2022 (48.1%; Table 3). Hatching success, quantified as the percentage of eggs hatched from the total number of eggs per nest, was higher in Italy (2021: 90.04 ± 3.31 %; 2022: 86.94 ± 3.56 %) and lower in Portugal (2021: 50.68 ± 3.74 %; 2022: 39.18 ± 4.88 %). Furthermore, hatching success seems to vary with year in each colony, with The Netherlands having the largest variation across the studied years.

Both latitude and longitude influenced hatching success, with the estimated effect being higher for longitude (latitude: -0.09 *vs* longitude: 0.14; Table 2). In fact, in the model of hatching success that includes data from France 2021 (Appendix, Table A2.7), latitude was not statistically significant. Hatching success seemed to increase with longitude and decrease with latitude (Fig. 4 A and B). In the year 2022, spoonbills had a higher hatching success than in 2021 and hatching success decreased with day of the season (Table 2, Fig. 4 C).

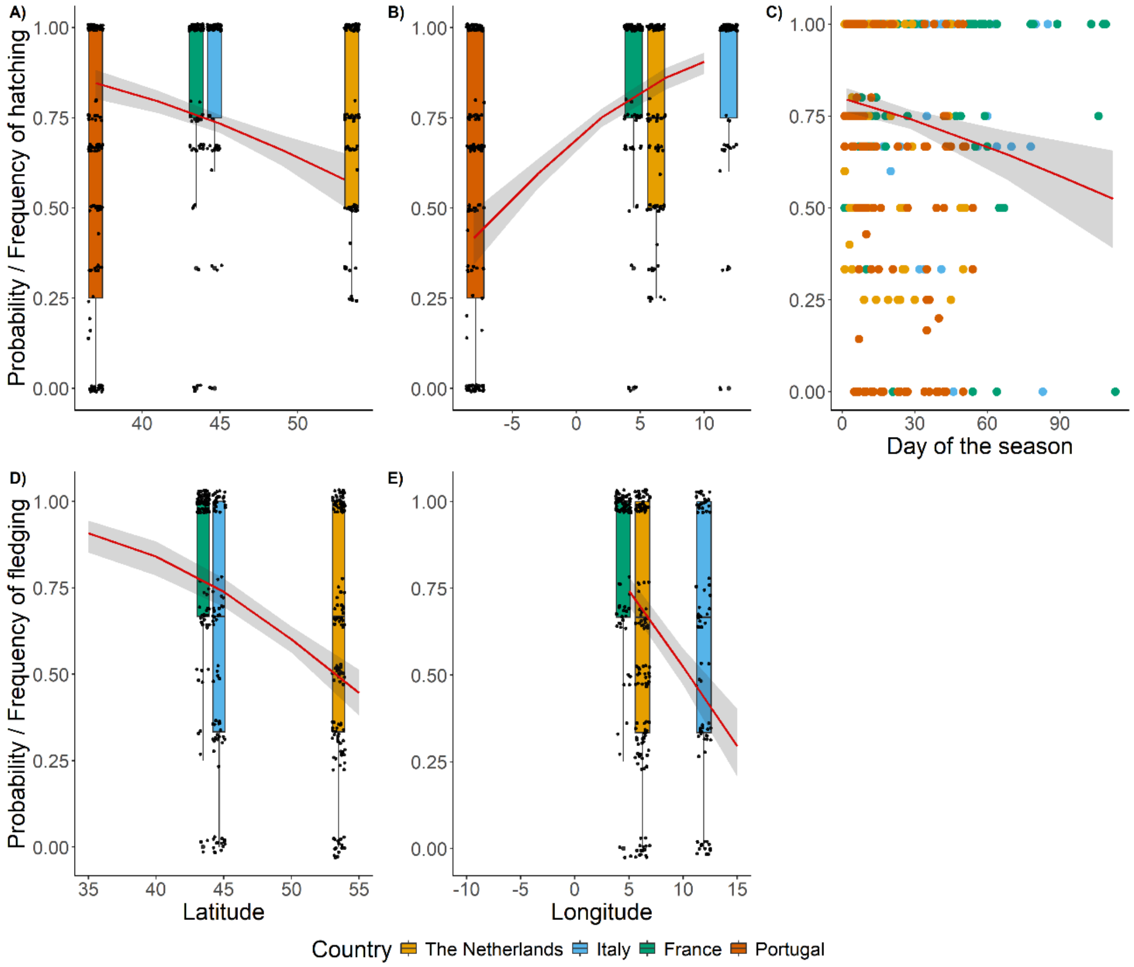

Fig. 4 – Variation on the probability of: spoonbill eggs to hatch (A-C; top row); and of spoonbill chicks to fledge (D-E; bottom row) along latitudinal (left column), longitudinal (middle column), and seasonal gradients (only for hatching). The red lines represent the effects resulting from the top-ranking linear models, the grey shaded areas the 95% confidence interval of the predictions and black circles show the values for each country. Coloured boxplots represent the distribution of raw values for each country (frequency of hatched eggs/fledged chicks per nest).

The percentage of dead chicks per nest was generally low, ranging on average (±SE) from zero (Greece) to 32.87 ± 5.26 % (Italy) (Table 3). It should however be noted that this metric is biased to chicks that are found dead and therefore it represents only the minimum value. Conversely, the percentage of fledged spoonbills per nest was overall high (Table 3), being highest in France (2021: 82.74 ± 3.73 %; 2022: 88.1 ± 3.19 %) and Greece (2023: 79.63 ± 8.69 %), and lowest in Italy (31.02 ± 4.9 %). Longitude and latitude had an effect on fledging success (Table 2), which was lower at higher latitudes and longitudes (Fig. 4 D and E). Year also had an effect, being the opposite of the effect on hatching success; while 2021 was the year with the lowest hatching success, it had the highest fledging success. We found no effect of day on fledging success (Table 2).

Body condition

Body condition was on average (±SE) 1249.72 ± 6.28 (Table 4), being lowest for France in 2022 (1159.07 ± 15.14) and highest for Italy in 2022 (1314.01 ± 20.66).

Table 4. Biometrics and body condition of Eurasian Spoonbill chicks (near fledging). Body condition was calculated as Scaled mass index (SMI) (Peig & Green 2009). This method standardizes mass to a given size of chicks (in this case, size was based on tarsus measurement).

	Year	**Average tarsus size (*mm*)**	**Range tarsus (*mm*)**	**Average body condition (SMI)**	**Range body condition (SMI)**
The Netherlands	2021	118.0 ± 1.1	87.0 – 149.0	1299.9 ± 7.6	439.5
	2022	118.5 ± 1.0	104.0 – 139.0	1281.8 ± 11.8	535.6
Italy	2021	76.2 ± 2.1	25.2 – 129.8	1264.1 ± 21.6	1456.0
	2022	79.4 ± 3.0	42.7 – 121.3	1314.0 ± 20.7	580.4
France	2021	121.0 ± 2.4	69.0 – 154.0	1197.7 ± 12.0	696.9
	2022	130.6 ± 2.3	85.0 – 160.0	1159.1 ± 15.1	1014.1
Portugal	2021	138.8 ± 1.9	91.1 – 152.7	1220.4 ± 13.1	323.0
	2022	134.4 ± 1.4	110.4 – 151.8	1179.6 ± 15.5	476.6

Both latitude and longitude had a positive effect on chick body condition (Table 2; Fig. 5A and 5B). Maximum temperature (averaged over the period between 13 to 7 days before measurement date) was excluded from this analysis because of multicollinearity effects. We found no effect of day of the season on chick body condition (Table 2). Finally, cumulative precipitation (between 16 to 8 days before measurement date) was retained in the top-ranking models, supporting the idea that chick body condition increases with increasing precipitation (Fig. 5C). However, when we built models including Portugal, and thus excluding the variable Day, only cumulative precipitation had a statistically significant result (body condition of chicks increased with increased precipitation; Appendix, Table A2.7).

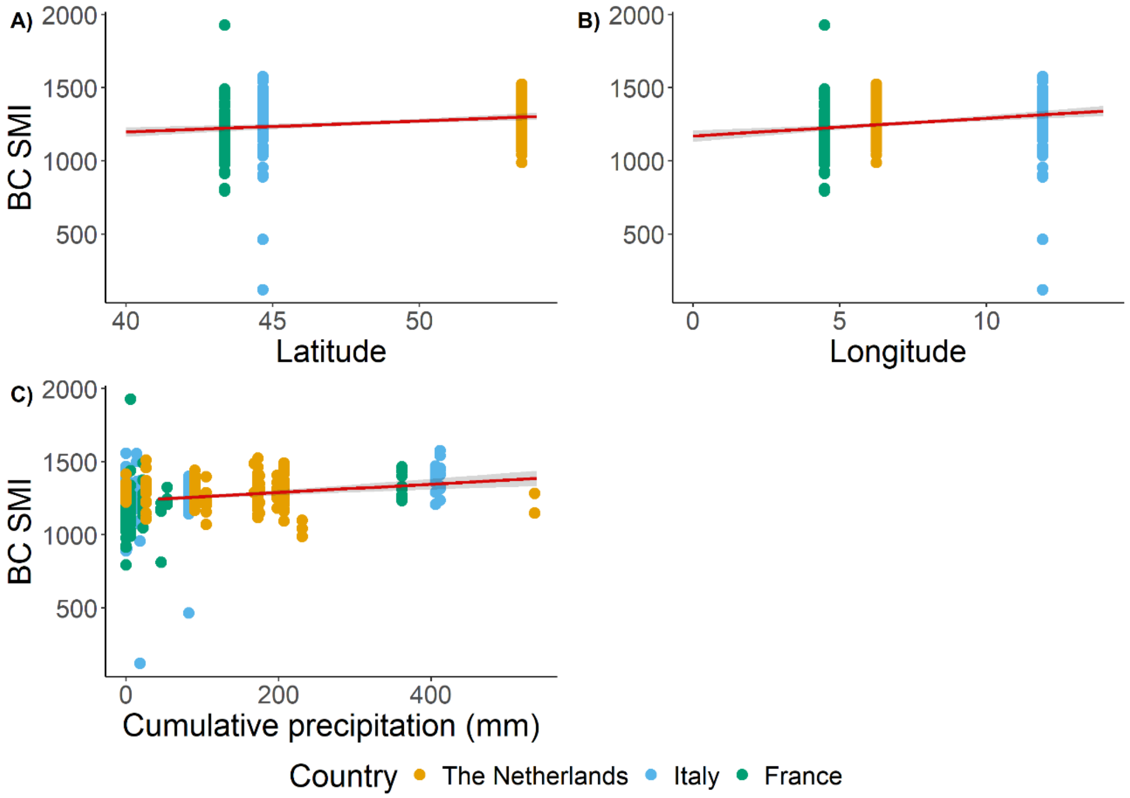

Fig. 5 –Variation on spoonbill chick body condition (BC) calculated as Scaled Mass Index (SMI) along (A) latitude gradient, (B) longitude gradient, and C) cumulative precipitation. The red lines represent the effects resulting from the top-ranking linear models. The grey polygons represent the 95% confidence interval of the predictions and coloured circles represent the fitted values for each country.

Discussion

In this study we have successfully compiled information on various breeding parameters and phenology of spoonbills throughout the European breeding range of the species. Generally, the data collected were in accordance with what is known for the species. Surprisingly, spoonbills at the lowest latitude and longitude (Portugal) start breeding as late as those at the highest latitude (England and United Kingdom) and longitude (Greece), which may be driven by local environmental factors. In fact, we found limited evidence supporting general large-scale patterns (geographically or climatic), suggesting that local conditions may be more important in influencing phenology and breeding parameters of spoonbills.

Phenology

Spoonbills are known to have a long breeding season, with previous reports of egg laying occurring between February and early July (Aguilera et al., 1996; Lok et al., 2014, 2017; Triplet et al., 2008), and the data presented in this study fits this pattern, despite laying in Italy could start earlier than described in the literature. The results are in alignment with our hypothesis that laying would be possible earlier at lower latitudes (i.e., favoured by higher temperatures) and at higher longitudes (i.e., due to warmer continental temperature), except for Greece, which started as late as the highest latitudes and lowest longitudes, but it is also the only colony for which one year of phenology data was possible to attain and could therefore be a spurious year. We did not find an influence of temperature on the overall model, but this may be explained by the fact that the analysis of *Climwind* were relative to laying density (due to methodological constraints, as 1st laying date is a singular event per and colony and not a distribution) and not to the actual date of first egg laying. Moreover, the fact that the average egg laying date of the first peak was not significantly correlated with any studied parameter, including climatic variables and thus, temperature, suggests that even if a temperature threshold may potentially influence the onset of laying, it is unlikely to determine average laying dates over all study sites. Furthermore, laying density throughout the season and average laying date may be affected by other local conditions, such as food availability or migration distance (Lok et al., 2017). Species and individuals breeding at higher latitudes tend to have shorter breeding windows due to the limited period of favourable climatic conditions, than those breeding at lower latitudes (Gauthier, 1993). Surprisingly, despite being at the lowest latitude of the study, laying in Portugal started as late as in some of the northern European colonies (i.e., The Netherlands and United Kingdom). Possibly, in addition to a shorter window of favourable environmental conditions (Gauthier, 1993), the later laying date of northern European colonies such as The Netherlands, could be due to the longer migration these spoonbills have to deal with (Lok et al., 2017). Nevertheless, this does not explain the later laying observed in Portugal where residents are present through the year. It may the case that as both these colonies are influenced Atlantic waters, vs the Mediterranean waters in Italy and France, food abundance may only increase later in the season (Sandvik et al., 2012). For instance, the fledging success of Atlantic puffins (*Fratercula arctica*) is influenced by the availability of first-year Herring (*Clupea harengus*), which in turn is mediated by sea temperatures (Durant et al., 2003). In Portugal (Ria Formosa), spoonbills feed their chicks with crustaceans but also with fish (Rodrigues et al., 2023a), so it is possible that spoonbills synchronise their laying period with the peak of prey availability in the Ria Formosa lagoons, a known nursery for fish species (Erzini et al., 2022; Ribeiro et al., 2012; Vasconcelos et al., 2010; Whitfield, 2017). Finally, these results can also be explained by flooding risk early in the season. In Portugal and in the Netherlands, extreme spring tides may prevent nest construction, and in The Netherlands, the timing of breeding is known to be influenced by the risk of early season flooding (Van De Pol et al., 2010). Yet, both Portugal and The Netherlands had a laying period within the time window reported for the species (Cramp and Simmons, 1977; Triplet et al., 2008), and in accordance with other monitored sites, such as Greece, which is influenced by the Mediterranean Sea and at a low latitude and thus an exception to our overall trend. Furthermore, in the United Kingdom, spoonbills are known to nest in trees (Bloomfield, 2023) and despite not facing a flooding risk, breeding starts as late as Portugal and The Netherlands. The early laying in France and Italy may be driven by a combination of factors, namely favourable environmental conditions (linked with lower latitudes), higher food availability (during laying period, e.g., high crayfish availability in Camargue, Meineri et al., 2014) and a higher prevalence of resident individuals compared to the other surveyed colonies (e.g., increasing resident population in Camargue, Moussy et al., 2023), with the exception of Portugal (which also contains resident individuals). It should also be noted that colonies in France and Italy have recently experienced high population growth (Champagnon and Kralj, 2023; Tenan et al., 2017) and this is likely to attract new recruits and even promote immigration, which may contribute to the longer laying if indeed incoming individuals each year breed later than those that have attracted them. However, the considerably longer laying period in the French colony may be further influenced by the individuals breeding in multiple breeding islets, while in the remaining locations only a single breeding site was considered, which may result in a smaller laying period. As for the multiple laying peaks observed in all surveyed colonies (usually two to three), these are unlikely to be related to environmental conditions such as temperature and precipitation, but instead to the breeding phenology of the species. In bird species, older and more experienced individuals tend to arrive at breeding sites earlier and in better condition than inexperienced breeders, which likely allows them to lay earlier than latter individuals in poorer condition (Balbontín et al., 2007; Bêty et al., 2003; Brown, 1969; Drent et al., 2003; Drent and Daan, 1980; Lack, 1966; Lok, 2013; Neate-Clegg and Tingley, 2023). This is partly the case for the Black kite (*Milvus migrans*), where the oldest individuals not only migrate more efficiently, but also depart from their wintering sites earlier to arrive earlier at breeding sites (Sergio et al., 2014). Previous studies on spoonbill populations in Western Europe and the Pannonian Basin have suggested that older, more experienced, spoonbills also arrive earlier at the breeding sites (de le Court and Aguilera, 1997; Kralj et al., 2012). Furthermore, in the case of the Dutch breeding population, older breeders undertaking short-distance migration were found to advance their breeding timing, whereas those undertaking long-distance migration did not (Lok et al., 2017). This resulted in a further widening of the gap in breeding timing between short-distance and long-distance migrants (Lok et al., 2017). In Chapter 3, older spoonbills were also found to arrive earlier and to be associated with the earliest nests in Camargue. Thus, the multiple peaks in laying are also likely to be related to age demographics and migratory behaviour in each site, with older individuals laying first, which is further accentuated by the differences in arrival time of migrants travelling different distances. Finally, multiple laying peaks may also be caused by renesting of breeders that lost their first clutch. For example, in France, following mass predation of chicks or eggs by wild boars, breeders generally abandon predated nests (Champagnon et al., 2021) and attempt to re-nest in nearby islets, thereby generating a new breeding peak.

Clutch size and egg volume

Although clutch size varied from one to seven eggs depending on the colony, the mean clutch size was consistent across colonies and years (3.18 ± 0.03 SE), and consistent with previous reports for this species (three to four eggs on average) (Cramp and Simmons, 1977; Triplet et al., 2008). From the exploratory climatic analysis, it seems that egg volume was affected by climatic conditions, decreasing with temperature and precipitation. There is no clear consensus on the general pattern of intraspecific variation in egg size with temperature (Christians, 2002), with some studies finding support for an increase in size with increasing temperature (Jàrvinen, 1994; Lessells et al., 2002), (Jarvinen 1994, Lessells et al 2002) while others reporting the opposite pattern (Potti, 2008; Tryjanowski et al., 2004). However, it is likely that other factors that are correlated with temperature may affect egg size, leading to variable effects of temperature on egg size pattern (Potti, 2008; Tryjanowski et al., 2004). The fact that neither temperature nor Julian day were selected in the most-supported model seems to support a lack of a direct relationship between temperature and egg volume. If there was indeed such a relationship, we could expect a global seasonal (i.e., common to all colonies) increase or decrease in egg volume, which was not the case. Moreover, as the best time window identified for a temperature effect on egg volume was 60 to 18 days prior to egg laying, it is unlikely that migratory individuals were already present in the colony during this period, especially in the case of The Netherlands, where the population is fully migratory. Alternatively, some studies suggest that productivity and egg size are related to the quality of the breeder, namely the female, such that lower quality breeders are generally associated with lower productivity and possibly smaller eggs (Reynolds et al., 2003; Styrsky et al., 2002). Different factors could lead to smaller eggs in Portugal than those in other sites, for example due to a higher presence of lower quality breeders in this site (compared to the other sites), or a lower food availability. In Portugal, spoonbills breed and feed in a tidal habitat, thus food availability might be constrained by tides which is not the case in France and Italy. In the case of the Cassin´s auklet (*Ptychoramphus aleuticus*), individuals whose pre-breeding diet consisted of lower quality food sources laid smaller eggs than those that feed on higher quality food (Sorensen et al., 2009). Common terns (*Sterna hirundo*) were able to produce eggs of apparently higher quality (presumably, because respective chicks were heavier than other chicks, although these eggs were not larger than those of conspecifics), by delaying their laying and potentially benefiting from a longer period of resource gathering (Arnold et al., 2006). This is also the case of females of Great tit (*Parus major*) which do not start laying before they find enough food to produce an egg (Perrins, 1965). Thus, low food availability (or a smaller food availability peak) could explain the patterns found in Portugal, specifically later onset of laying, lower egg volume, and relatively higher mean chick body condition than France (which had the largest eggs – see below). Furthermore, this would be consistent with the idea that breeder condition, rather than age or experience, may drive the timing of breeding (Gonzalez-Solis et al., 1999; Wendeln and Becker, 1999), at least when food availability is low. Alternatively, in Schiermonnikoog, a possible size-driven habitat preference was found, with females and smaller-billed (likely also smaller-sized) males being more likely to forage in marine habitats compared to freshwater habitats (Lepelaar, 2024). As birds from the Portuguese colony forage in marine/brackish habitats, this site might be more suited to smaller individuals who may lay smaller eggs.

While no clear relationship was found between egg volume and temperature, egg volume decreased with increased cumulative precipitation, suggesting that this breeding parameter is indeed affected by climatic factors as predicted. However, after plotting the raw data along with the model prediction (Fig. 3D) it seems that this result could be driven by the Portuguese data and as such may be related to local constrains (e.g., food availability), rather than being a true pattern. Finally, there was also no seasonal trend in egg volume. Nevertheless, the decreasing trend in egg volume with increasing minimum temperatures found in the exploratory climatic analysis, could indicate a seasonal effect too small to be detected in our analysis, driven by the smaller size of the eggs in the second or by the lower quality (younger and likely less experienced; Chapter 3) of breeders at the end of the season. Second clutches, and breeder inexperience might also explain the decreasing seasonal trend found for hatching success.

Breeding success (hatching and fledging)

Contrary to our predictions that climatic conditions would influence spoonbill breeding performance, hatching, and fledging success were highly variable among countries and years, with no consistent climatic (climate was only tested for hatching, see methods) or seasonal effect found (except for hatching success). Latitude and longitude seemed to affect hatching success, although this may be due to a higher probability of failure in extreme countries of the breeding range (Portugal and The Netherlands). Additionally, when including data from wild boar predation in France (2021), no significant latitude effect was found, further reinforcing a lack of an overall geographical pattern. Furthermore, when considering egg volume, Portugal which had the smallest eggs, also had one of the lowest hatching successes, reinforcing the hypothesis that these eggs and/or breeders were of lower quality. Thus, the fluctuating hatching success found in this study appears to be associated with stochastic events such as high levels of predation (e.g., wild boar predation in France Champagnon et al., 2021), flooding of nests due to rising water levels combined with spring tides and extreme wind and precipitation events in coastal colonies (e.g., Portugal and Netherlands) (de le Court 2013, van De Pol et al 2010), or other sources of disturbance that may lead to nest abandonment and hatching failure. This is consistent with what has been reported for this species, which generally has high hatching and fledgling rates (Cramp and Simmons, 1977; Triplet et al., 2008). However, this result should be taken with care as hatching estimates may be inflated due to variation on field protocols. Fledging success was also found to be significantly correlated with latitude and longitude, but this should also be considered with care as it seems to be caused by France having higher fledging success. If there was indeed a geographical pattern associated with environmental conditions, we would expect to see an increase in fledging success towards lower latitudes (associated with better conditions) and a decrease towards lower longitudes (associated with worse conditions), but the opposite occurred (Fig. 4 C and D). The higher fledgling success observed in France may be explained by a possibly higher food availability in the Camargue, particularly of crayfish (i.e., peaking between April to June; Meineri et al., 2014). Nevertheless, it can also be related to a higher success rate in identifying chicks from monitored nests in this site. This task can be particularly challenging in other sites with difficult access and is further complicated by the high rate of temporary mark loss of spoonbill chicks.

Chick body condition

Body condition appears to be mainly positively correlated with cumulative precipitation in the weeks preceding the measurement. We expected that a higher frequency or more intense local precipitation, would negatively impact the body condition of spoonbill chicks due to a lack of accumulated energy. When food availability is low, animals may reduce their overall growth or prioritise different organs and structures that are more advantageous for their current situation (e.g., fat accumulation for thermoregulation) (Schew and Ricklefs, 1998). Thus, body condition being higher with higher precipitation, could be due to a shift in the balance of chick investment, favouring fat accumulation over skeletal development (Starck and Ricklefs, 1998). Using the SMI method to estimate body condition, a higher weight associated with a small tarsus would translate into high body condition, so if chicks are fat, then they will have high body condition when precipitation is high. This is supported by the fact that the two countries with the lowest daily temperatures (Italy and The Netherlands) and the country with more precipitation (The Netherlands) (Appendix, Fig. A2.2), had the smallest tarsus but also the highest body condition, suggesting a large fat accumulation for a small tarsus. In Pied flycatchers (*Ficedula hypoleyca*), small tarsus length in chicks has been linked to lower food availability, likely due to competition between breeding pairs (Alatalo and Lundberg, 1986). Another possibility is that extensive periods of precipitation may have caused mortality of chicks with lower body condition (Kosicki and Indykiewicz, 2011), and therefore only surviving chicks with higher body condition were measured. This is the case for chicks of Rock ptarmigan (*Lagopus muta*), which, like spoonbills, are unable to self-thermoregulate properly during the first weeks of life, and therefore die during unfavourable weather from starvation while being brooded or from cold when the adult leaves to forage (Marti and Bossert, 1985; Wilson and Martin, 2008). Furthermore, in The Netherlands, the total amount of precipitation was negatively correlate with breeding success of spoonbill of the Schiermonnikoog colony (Lok et al., 2017). Finally, low precipitation could in fact also negatively affect the availability of food on freshwater habitats, but only if water levels are not artificially controlled, which happens commonly in irrigated fields and with damming of rivers. However, as spoonbills can feed both in freshwater and intertidal areas (El-Hacen et al., 2014; Oudman et al., 2017), this explanation seems unlikely, and it will be only relevant for freshwater dependent colonies, which is not the case here. Finally, as the time window defined for the effect of precipitation on chick body condition was 16 to 8 days before the measurements were taken, it seems unlikely that low precipitation in this short period would affect water levels to the extent necessary to reduce food availability.

Importance of monitoring programs, collaboration, and standardised field protocols

We hope that this work can serve as a baseline for better understanding spoonbill breeding ecology at large spatial scales. Furthermore, we consider that this study highlights the importance, not only of long-term monitoring programmes, that can detect temporal changes (and spatial if implemented in more locations, ideally covering the entire species range), but also of common standardised field protocols that can be used elsewhere and help to detect patterns, and exceptions to those patterns, that may indicate local mismatches with environmental changes or responses. In fact, the main constraint of this study was the low sample size for statistical analysis and the variation in data collection protocols, which sometimes limited our capacity to detect and interpret geographical patterns and their possible explanation due to association with other environmental or local factors. For example, fledging success was estimated by identifying temporary marked chicks, and as marks were different among countries detectability may vary. The same applies to chick mortality, as some dead chicks may be removed (e.g. by gulls) before detection. However, such removal rates should not vary considerably between the two years of the study and as the protocols are similar between years, most variation in this parameter should originate from other factors. Finally, while some colonies are fully monitored (i.e. all nests), others are sampled, but as long as, this is done randomly, as was the case here, any potential biases should be kept to a minimum .We found that local factors, such as food availability, predation or local quality of breeders, may be more important in driving breeding parameters and phenology of spoonbills than global patterns such as latitude/longitude and climatic factors. However, we found an overall latitudinal trend in timing of breeding where in general spoonbills at lower latitudes start laying earlier that those at higher latitudes. Moreover, we discuss how local conditions could potentially affect this trend and disrupt this pattern, as is the case with Portugal and Greece. Good quality data from the entire range is essential to identify patterns and exceptions driven by local conditions, and to better understand how different populations of the same species will respond to increasingly prevalent global environmental changes.

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Ethics approval

All ringing sessions were conducted in accordance with national legislation, animal welfare, and by experienced ringers.

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Appendices 2

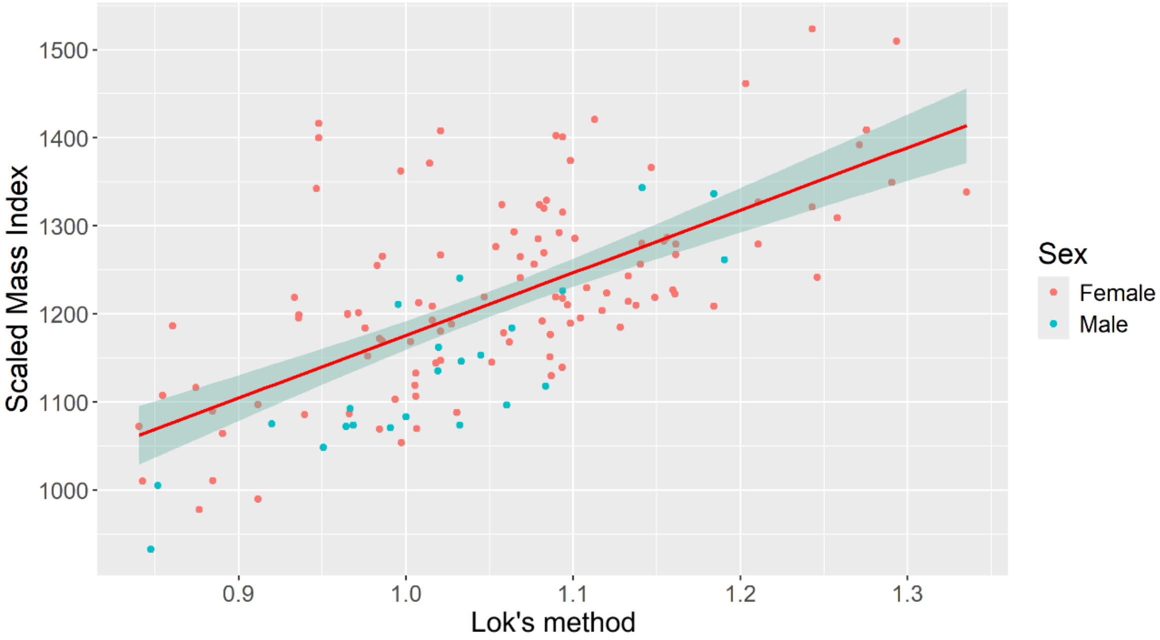

Fig. A2.1 – Correlation between body condition index results applied to Eurasian spoonbill chicks (r=*0.66, $p < 0.001$*). Scaled Mass Index was calculated based on Peig and Green (2009) using tarsus size and mass. Lok's method was calculated based on Lok et al (2014) using tarsus size, P8 feather length and mass.

Table A2.1. Results of correlations (in log-log scale) between body measurements of Eurasian Spoonbill and their body mass.

Body measurement	**N**	**Correlation R^2**	***p***
Tarsus	492	0.83	$p < 0.001$
P8 feather	368	0.43	$p < 0.001$
Head + bill	158	0.76	$p < 0.001$

Field data collection methods

Due to the a posteriori compilation of data and fieldwork constraints, several data collection methods were used. The methods used to estimate the number of nests were: a) Counting by foot, walking in the colony, and this could be done in one or several visits to the colony; b) Count done by observing drone acquired images, which could also be done once or several times; c) Counting the new nests each visit to the colony and marking each nest with unique label so they are identifiable. For estimating laying and hatching dates the methods used were a) Direct observation on the day the egg was either laid or hatched; b) Calculating latest possible date of laying given the date and nest state on the visit; c) Egg flotation (Liebezeit et al 2007); d) Measurement of chick(s) size and back calculation for obtaining lay and hatch dates. For calculating the egg volume only one method was implemented that was measuring the maximum length and width of the egg and following the formula of Hoyt (1979). The estimation of number of dead chicks was made either by counting only chicks found dead inside the nest cup or by counting unique labelled chicks in the nest cups or colony area. For inferring the number of fledged chicks, two methods were used: a) Count of chicks alive until they are able to leave the nest (around 15 days of age); b) Count of unique labelled fledglings (chick of 15 days old or older) at the end of the season or at ringing sessions.

Table A2.2. Details of the meteorological stations used to retrieve climatic data associated with each breeding colony in each country. Data from European Climate Assessment & Dataset project (Klein Tank et al 2002). The nearest station with more days of information of each country was selected. Climatic data from the years 2020 to 2023.

Country	**Precipitation**			**Temperature**		
	Station	**Distance (*km*)**	**Height (*m*)**	**Station**	**Distance (*km*)**	**Height (*m*)**
The Netherlands	Schiermonnikoog	4.42	1	Lauwersoog	9.45	2
Italy	Mezazno Nord-ovest	2.00	-4	Bando *	5.49	3
France	Montpellier-Aeroport **	51.49	2	Montpellier-Airport	51.49	2
Portugal	Huelva	87.42	17	Huelva	87.42	17

*Complemented with temperature data (maximum and minimum temperatures) from station Saiarino (distance: 9.67km, height: 8m) for three missing days (11/01/2021, 25/05/2021 and 31/05/2021). The minimum temperature for the year 2020 was attained from station Gaibanella (distance: 23.74km, height: 3m)

** complemented with precipitation data from station "Marignane" (distance: 53.42km, height: 9m) for a few missing days (07/09/2022, 24/10/2022, 17/01/2023, 09/03/2023, 30/03/2023, 04/04/2023, 16/06/2023, 10/07/2023)

Climatic windows analysis – methods and results

Climwin is a useful tool for evaluating the effect of climatic conditions on the ecology of species, as it does not require *a priori* delineation of the time windows in which the climatic factor would have largest effect on the focal parameter (van de Pol et al 2016). *Climwin* tested all the possible time windows with user defined restrictions, specifically how far or close in time those can be (see below), by comparing the result of a linear model containing the climatic factor in the specific time window, with a model of the same time window but without having the climatic factor. Then it uses information-theoretic model selection criteria, specifically Akaike Information Criterion (*AICc*) selecting the one with lowest *ΔAICc*. To avoid Type-I errors in this procedure, we followed the suggestion of run 100 randomizations of the dataset (Bailey & Van De Pol 2016, van de Pol et al 2016). This was done by creating random datasets with our data associated with different dates, and consequently different climate values, thus testing the likelihood of obtaining the same result at random. Because of the uncertainty of knowing the exact best model only by *ΔAICc*, we grouped the models whose Akaike model weights summed equalled to 95%. Then we used multi-model inferencing on those models to report the estimated time windows and effects on the studied variables. However, when this 95% confidence group was constituted by more than 10% of the tested models we did not use that climatic information as it may be associated with weak signals or with several windows of influence of the climatic factor and averaging it would not make a reliable response (Bailey & Van De Pol 2016). We used relative time windows, which consider the time windows relative to the date of the event, for example a time window of 20 to 12 days before each egg laying.

For laying density and egg volume, the range defined was 60 to 0 days prior to the egg laying. For hatching success, the range was only 26 to 0 days before the egg was hatched (average incubation time). Finally, for body condition, the range was 35 to 0 days before the chick was measured, in an attempt to encompass the entire growth period of the chick.

For analysing the effects of climate on egg volume and body condition we used linear mixed model with nest as random effect because eggs and chicks of the same nest are probably more similar in size and body condition than eggs and chicks of different nests. The models created to analyse density of laying dates and percentage of hatched eggs per nest were linear models.

The functions used to aggregate climatic data within time windows were *sum* for precipitation (that is, cumulative precipitation during time window) and *mean* for temperature (that is, average temperatures during time window. All four climatic factors (precipitation and maximum, minimum and mean temperature) were tested independently. For temperature, we selected in each case, the factor in models with lower $\Delta AICc$ compared to the null model (if it was also a true positive).

Maximum temperature was the temperature factor that had the greatest effect on laying density (Table SM3). The best identified window coincided with the median of the 95% confidence group (11-1 days) (Table A2.4). As the maximum temperature increased, the likelihood of having more eggs laid per day also increased (Model averaged $\beta=0.005$, Table A2.4). Both precipitation and maximum temperature results were not considered *False Positives* (both randomisation $p< 0.001$, Table A2.4), however, for precipitation, the 95% confidence group included 14% of tested models so we did not consider the results in the subsequent analysis. Nonetheless, the effect of the 95% confidence group was negative (Model averaged $\beta= -0.001$, Table A2.4), i.e. laying density per day decreased after more precipitation.

Minimum temperature was the temperature variable with the strongest effect on egg volume (Table A2.3). The best time window identified was 60 to 26 days prior to the egg being laid, but considering the 95% confidence group, we increased this window to 60 to 18 days before. Thus, when the average of minimum temperatures in this time interval was lower the egg volume increased (model averaged $\beta = -94.49$, Table A2.4). Precipitation also influenced egg volume (Table A2.4), but with the time window being shorter and closer to egg laying (95% confidence group: 20 to 6 days before). When cumulative precipitation increased in this time interval eggs were larger, even if this effect was smaller (model averaged $\beta = -19.81$, Table A2.4). Both the results of minimum temperature and precipitation were considered *True Positives* (randomisation $p < 0.001$).

The *climwin* analysis did not reveal any clear signal of the effect of climatic factors in hatching success (Table A2.4). Cumulative precipitation results were considered a *False Positive* (randomization $p = 0.21$).The best temperature predictor seemed to be minimum temperature (based on $\Delta AICc$ results; Table A2.3), and even thought this result was considered a *True Positive* (randomization $p = <0.01$), the 95% confidence group included

56% of the tested models (Table A2.4), indicating several possible peaks of effect of temperature in hatching success or a very small effect (Bailey & Van De Pol 2016).

The temperature factor with the greatest effect on body condition was maximum temperature (Table A2.3). When the maximum temperature in the 13 to 7 days before capture increased, the body condition of the chick decreased (model averaged $\beta = -0.817$, Table A2.4). However, cumulative precipitation in the 16 to 8 days before the ringing, had an opposite and positive effect on chick body condition (model averaged $\beta = 0.367$, Table A2.4). The results of these models were considered *True Positives* (both randomization $p < 0.001$).

Table A2.3. Comparison of results of top-rankingferred using Akaike information criterion (AICc)) fitted with temperature factors resulting from *Climwin* analyses. All models were considered True Positives after the randomization process. In bold is the variable selected for further analyses (the one with lower Δ AICc).

	Top models *ΔAICc*		
Variable response	**Maximum temperature**	**Minimum temperature**	**Mean temperature**
Laying density	**-93.83**	-44.35	-59.14
Egg volume	-53.03	**-64.38**	-46.890
Hatching success	-23.37	**-34.85**	-28.51
Body condition	**-51.30**	-18.55	-35.79

Table A2.4. Results of climatic analysis inspecting possible effects of climatic factors in several breeding parameters using *Climwin* (see methods for details). With this procedure we have information on the best window (the period when the climatic factor had more influence over a given response variable). We present the median start and end days of time windows and the model averaged estimate (*ϐ*). When more than 10% of the created models were part of the 95% confidence group, or if randomization *p* was higher than *0.05*, models were discarded. In bold are results of models that were used in subsequent analysis.

Variable response	**Climatic factor**	**ΔAICc**	**Best window (Open – Close)**	**Top ranking model ϐ**	**Randomization *p*-value**	**% of models within the 95% confidence group**	**Model averaged ϐ**	**Median of 95% confidence group (Start – End)**
Lay dates density	**Maximum temperature**	**-93.83**	**11 - 1**	**0.001**	***<0.001***	**2%**	**0.01**	**11 - 1**
	Precipitation	-26.27	46 - 0	-0.001	*<0.001*	14%	-0.001	43 - 3
Egg volume	**Minimum temperature**	**-64.38**	**60 - 26**	**-100.15**	***<0.001***	**4%**	**-94.49**	**60 - 18**
	Precipitation	**-73.63**	**19 - 7**	**-21.52**	***<0.001***	**3%**	**-19.81**	**20 - 6**
Hatching success	Minimum temperature	-34.85	25 - 23	-0.01	*<0.001*	56%	-0.01	21 - 6
	Precipitation	-4.81	10 - 9	0.01	*0.21*	84%	0.002	18 - 9
Body condition	**Maximum temperature**	**-51.30**	**31 - 30**	**-0.91**	***<0.001***	**6%**	**-0.82**	**13 - 7**
	Precipitation	**-48.78**	**16 - 7**	**0.39**	***<0.001***	**4%**	**0.37**	**16 - 8**

Table A2.5. Number of nests or individuals sampled for each breeding parameter in the several countries and years.

Country	Year	Number of nests sampled							Number of individuals sampled		
		Laying date	Hatching date	Number of eggs per nest	% of hatched eggs per nest	% of dead chicks per nest	% of fledged chicks per nest	Egg volume	Egg volume	Tarsus size*	Standard Mass Index (SMI)
Portugal	2021	120	66	120	104	75				22	22
	2022	79	25	77	77	38		73	203	48	48
	2023			12				12	38		
France	2021	58	58	72	71	56	56			58	58
	2022	56	56	77	62	42	42	65	205	56	56
	2023	20		20				20	68		
The Netherlands	2021	74	74	55	53	55	55			119	119
	2022	62	62	53	53	53	53			69	69
Italy	2021	52	50	48	48	39	39	11	34	76	76
	2022	43	42	47	47	33	33	31	89	44	44
Greece	2023	8	8	15	12	9	9				
* Only individuals with information about tarsus size and mass were included											

Table A2.6. Daily climatic data summary retrieved from European Climate Assessment & Dataset (ECA&D) (Klein Tank et al 2002) from meteorological stations in the vicinity of the spoonbill colonies (see Table A2.2 for more details). Climatic data from 1st of January to 30 of September of years 2021 and 2022.Temperature data in 0.1ºC.

Country	**Daily Precipitation (*mm*)**		**Daily Minimum Temperature (*ºC*)**		**Daily Maximum temperature (*ºC*)**		**Daily Mean temperature (*ºC*)**	
	Mean (±*SE*)	**Range**	**Mean (±*SE*)**	**Range**	**Mean (±*SE*)**	**Range**	**Mean (±*SE*)**	**Range**
The Netherlands	19.68 ± 1.67	0 - 279	90.42 ± 2.50	-81 – 206	147.01 ± 2.95	-20 - 352	117.54 ± 2.64	-46 - 274
Italy	12.55 ± 2.36	0 - 585	94.72 ± 3.57	-80 – 233	224.87 ± 4.06	-11 - 389	157.82 ± 3.75	-34 - 301
France	11.35 ± 2.60	0 - 1020	122.04 ± 3.11	-58 – 250	225.07 ± 3.15	55 - 386	176.58 ± 2.78	13 - 295
Portugal	6.11 ± 1.17	0 - 384	137.77 ± 2.32	-7 – 269	259.48 ± 2.87	88 - 439	198.62 ± 2.5	56 - 354

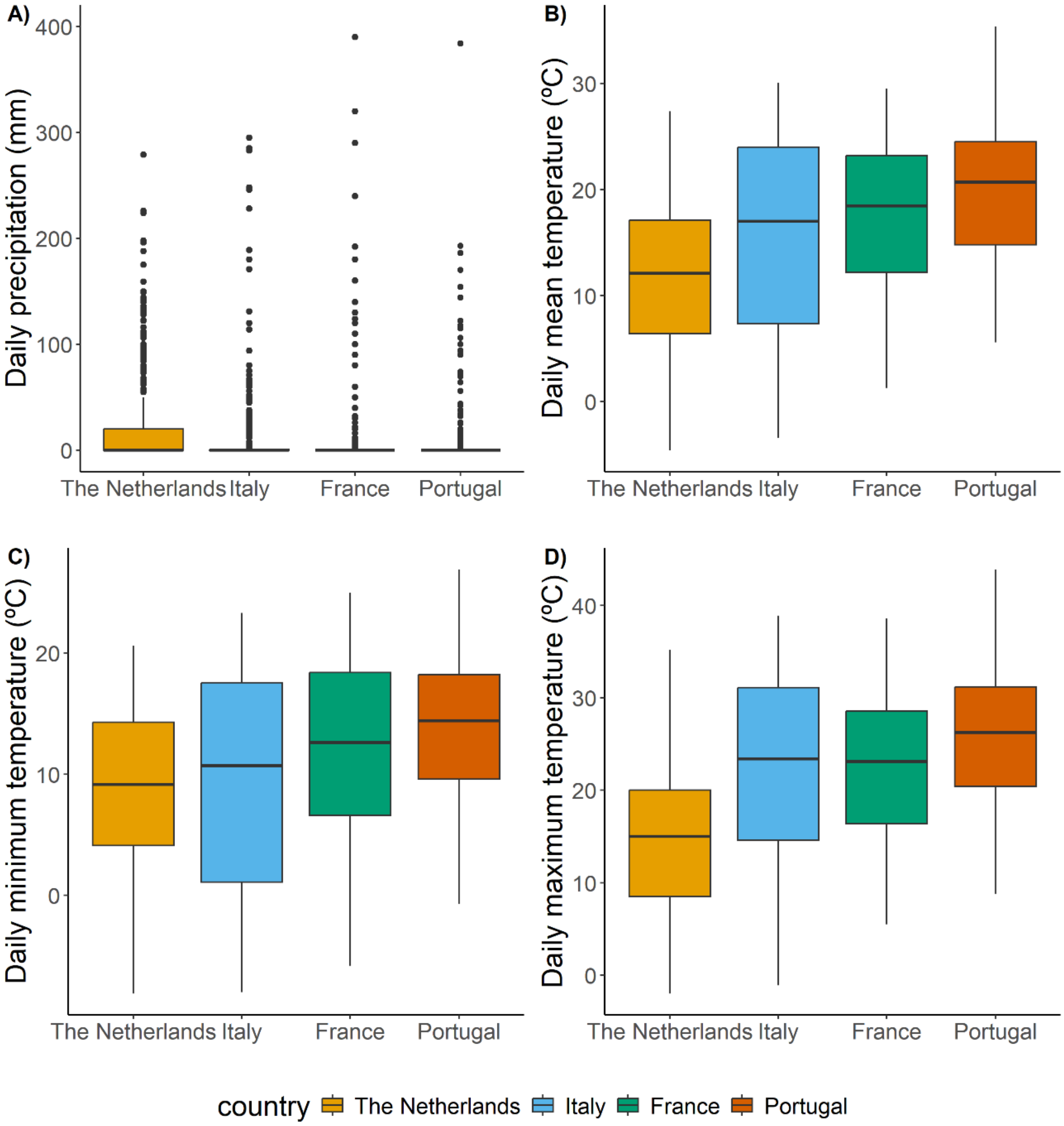

Fig. A2.2 – Daily climatic data registered in the closest meteorological station to the Eurasian Spoonbill colony in each country. Data retrieved from European Climate Assessment & Dataset (ECA&D) (Klein Tank et al 2002). Climatic data from 1st of January to 30 of September of years 2021 and 2022.

Table A2.7. Results of top linear and generalized linear (mixed) models for two response variables. Both set of models did not include the explanatory variable Day as do those presented in the main document (as it was not possible to use Day for predicting hatching success in France (in 2021) and for predictig chick body condition in Portugal). Top ranking models were selected based on Akaike Information Criterion (AICc) (see methods for more details and see Appendix for results of model selection). The full averaged results are presented. The reference Year is 2021. Nest was included as random factor on the models predicting Chick body condition. p values < 0.05 are highlighted in bold.

Response	***N***	**Fixe effects**	**Estimate**	**Adjusted *SE***	***z value***	***p***
Hatching success (including France 2021)	462	Intercept	1.41	0.76	1.84	*0.065*
		Year2022	0.37	0.12	3.01	***0.003***
		Latitude	-0.02	0.02	1.10	*0.271*
		Longitude	0.08	0.01	5.37	***p < 0.01***
Chick body condition (Including Portugal)	492	Intercept	1168.26	84.18	13.88	***p < 0.01***
		Year2022	-12.53	14.32	0.88	*0.382*
		Precipitation	33.62	7.62	4.41	***p < 0.01***
		Latitude	1.79	1.79	1.00	*0.318*
		Longitude	1.02	1.38	0.74	*0.46*
		Maximum temperature	-9.68	11.97	0.81	*0.419*

Table A2.8. Results of model selection for all linear and generalized linear (mixed) models presented in this study but filtered for top ranking models (within 2 ΔAICc). Null models are also present for comparison.

Variable in study	**Models**	***df***	***Log likeliwood***	***AICc***	***ΔAICc***	**Weight (W_i)**
1st laying	Null	6	-33.97	74.93	2.13	0.95
	Lat + Lon	4	-22.4	72.8	0	0.24
Average egg laying date	Null	6	-32.96	72.92	0	0.81
Egg volume	Null	579	-5868.29	11742.62	86.87	0
	Lon + Prec	577	-5822.82	11655.75	0	0.37
	Lon + Year + Prec	576	-5820.93	11656.05	0.3	0.32
	Lon + Prec + Day	576	-5822.59	11657.33	1.58	0.27
Hatching success (excluding France 2021)	Null	427	-594.43	1190.88	138.80	0
	Lon +Year +Lat +Day	423	-520.97	1052.07	0	0.99
Hatching success (including France 2021)	Null	461	-683.51	1369.02	87.89	0
	Lon + Year + Lat	458	-636.52	1281.13	0	0.68
	Lon + Year	459	-638.37	1282.8	1.66	0.29
Fledging success	Null	312	-385.86	773.74	112.91	0
	Lon + Year + Lat	309	-326.35	660.83	0	0.67
	Lon + Year + Lat + Day	308	-326.04	662.27	1.45	0.33
Chick body condition (excluding Portugal)	Null	415	-2659.03	5324.12	58.74	0
	Lon + Lat + Day + Prec	411	-2625.55	5265.38	0	029
	Lon +Year +Lat + Day + Prec	410	-2625.06	5266.47	1.09	0.17
	Lon + Lat + Prec	412	-2627.26	5266.73	1.35	0.15
Chick body condition (including Portugal)	Null	489	-3118.77	6243.6	58.85	0
	Lon + Year + Lat + Prec	485	-3085.26	6184.74	0	0.11
	Lon + Lat + Prec	486	-3086.33	6184.82	0.08	0.11
	Year + Prec + MaxT	486	-3086.35	6184.88	0.14	0.11
	Year + Lat + Prec	486	-3086.5	6185.16	0.42	0.09
	Year + Lat + Prec + MaxT	485	-3085.49	6185.22	0.47	0.09
	Lon + Year + Prec + Maxt	485	-3085.68	6185.6	0.85	0.07
	Lat + Prec + MaxT	486	-3086.89	6185.96	1.22	0.06
	Lat + Prec	487	-3087.96	6186.05	1.31	0.06
	Lon + Year + Lat + Prec + MaxT	484	-3084.94	6186.18	1.44	0.06
	Lon + Prec + MaxT	486	-3087.02	6186.21	1.47	0.05
	Prec + MaxtT	487	-3088.06	6186.24	1.5	0.05
	Lon + Lat + Prec + MaxT	485	-3086.06	6186.36	1.61	0.05
	Lon + Year + Prec	486	-3087.25	6186.67	1.93	0.04

Lon: Longitude, Lat: Latitude, Year (factor with 2 levels: 2021 and 2022 (for Egg volume also also 2023), Day: julian day, Prec: Cumulative precipitation (during resulting time windows), MaxT: Average maximum temperature (during resulting time windows)

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CHAPTER 3

Do older parents do better? The effect of parental age on chick’s body condition and migratory behaviour in a colonial-breeding waterbird

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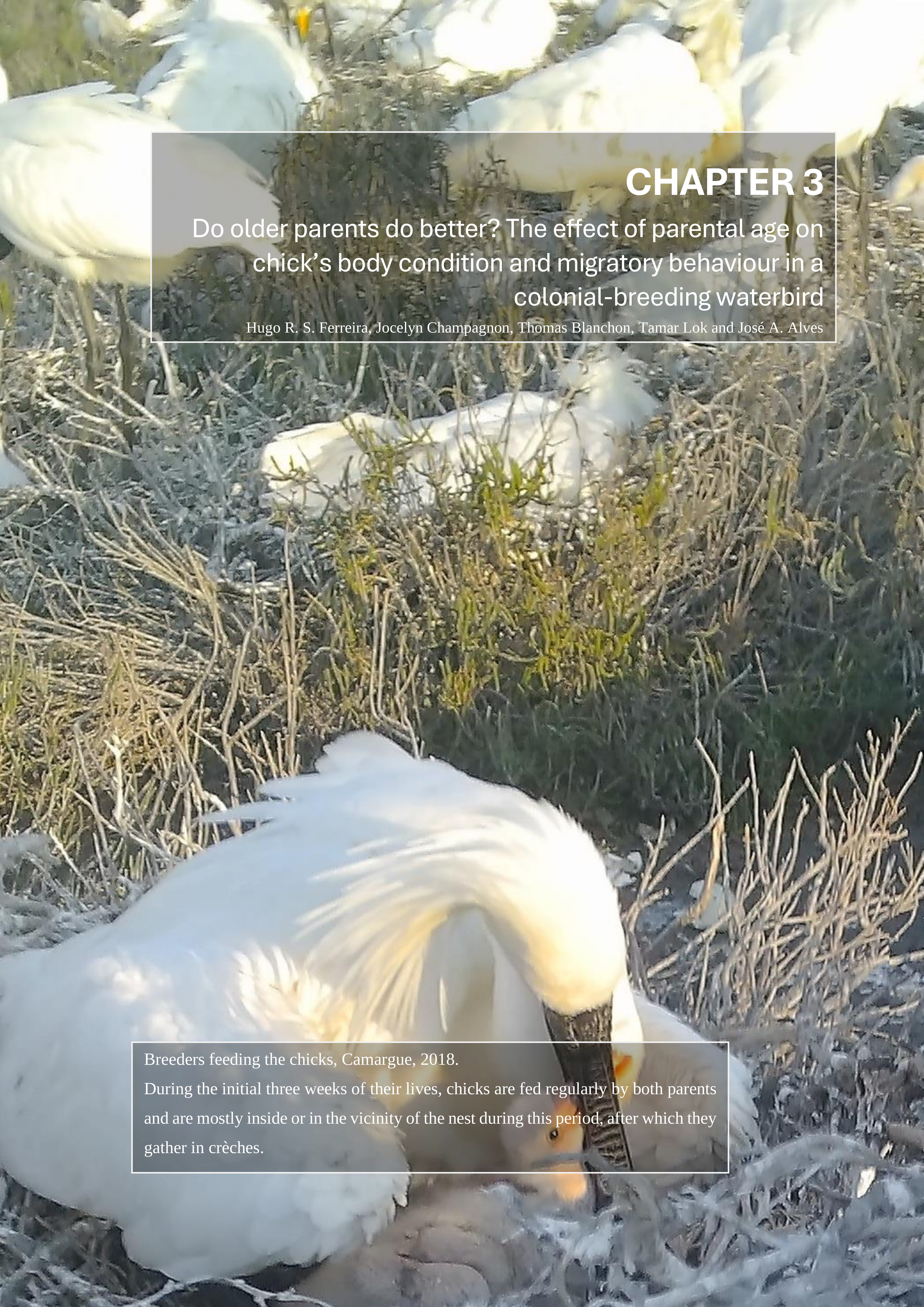

Breeders feeding the chicks, Camargue, 2018.

During the initial three weeks of their lives, chicks are fed regularly by both parents and are mostly inside or in the vicinity of the nest during this period, after which they gather in crèches.

Do older parents do better? The effect of parental age on chick's body condition and migratory behaviour in a colonial-breeding waterbird.

Abstract

Animals' performance of basic functional behaviours such as foraging and movement, may improve with age as a result of past experiences. In migratory bird species that breed seasonally, this may explain why older individuals outperform younger ones during migration and the breeding season. Due to earlier or more efficient migration, older and likely more experienced individuals tend to arrive at breeding sites earlier and enjoy better breeding conditions, resulting in a higher reproductive success than younger individuals. However, how a higher body condition at fledging or early hatching may influence chicks' future fitness prospects remains mostly unknown. In partial migration systems, low quality or socially subordinate individuals may be constrained to sub-optimal migratory behaviours with lower demographic rates. Therefore, producing high quality chicks may promote the survival of breeder´s offspring. Here, we sampled and monitored the breeding population of Eurasian spoonbills in Camargue (Southern France), which is growing exponentially and has been subject to a long-term colour ring programme since 2008. In this study, we show that older spoonbills tend to breed earlier in the season than younger individuals, and that early breeders are more likely to produce chicks with higher body condition than late breeders. Finally, migratory behaviour of juveniles appears to be influenced by the timing of breeding (but not by body condition), with later-born juveniles tending to undertake less demanding migration (without crossing major ecological barriers) than juveniles born earlier in the season. Our study therefore highlights the relevance of long-term studies to better understand the complex breeding phenology of a migratory species, which can lead to changes in population-level patterns and processes.

Keywords/phrases: Breeding performance; Ecological barriers; First migratory behaviour; *Platalea leucorodia*; Scale-Mass-Index; Social migration.

Introduction

As animals age, past experience can improve their performance of basic functional behaviours (e.g., foraging and movement; Rotics et al., 2016). This is often associated with the relatively higher mortality rates of juveniles in comparison to adults (Anders et al., 1997; Corbeau et al., 2020; Daunt et al., 2007; Harel et al., 2016; Sullivan, 1989). In species that breed seasonally, accumulated experience may also explain why older individuals often outperform younger ones during the breeding season (Clutton-Brock, 1988; Daunt et al., 1999). However, due to the difficulty of tracking individual animals throughout their annual cycle and lifetime (Brown et al., 2013; Graf et al., 2015; Lok et al., 2011; Riotte-Lambert and Weimerskirch, 2013), comparisons of performance of complex behaviours (e.g., migration and timing of breeding) are often simplified to dichotomous comparisons between juveniles or immatures, and adults of unknown age or experience (Berthold, 2001; Desprez et al., 2011; Dodge et al., 2014; Hake et al., 2003; Newton, 2008; Pradel et al., 2012; Rappole, 2013; Sergio et al., 2014). However, long-term colour ring programmes (e.g., Clark et al., 2009; Neate-Clegg and Tingley, 2023; Reichlin et al., 2009), has enabled to examine how certain behaviours (e.g., breeding and migration at the individual level) and performance (e.g., survival and productivity) change over an individual's lifetime (Alerstam et al., 2006; Brønnvik et al., 2022; Campioni et al., 2020; Corbeau et al., 2020; Grist et al., 2017; Reid et al., 2020; Robinson et al., 2010).

In seasonal environments, birds that breed earlier in the season tend to achieve higher reproductive success (including better quality chicks), than those that breed later (Alves et al., 2019; Benharzallah et al., 2015; Both et al., 2006; Costa et al., 2021; Daan et al., 1989; Drent et al., 2003; Kentie et al., 2015; Klomp, 1970; Lok et al., 2017; Perrins, 1966; Smith and Moore, 2005). Thus, it is not surprising that several bird species are known to advance their breeding timing with increasing age (Balbontín et al., 2007; Campioni et al., 2020; McCleery et al., 2008; Perdeck and Cavé, 1992; van de Pol and Verhulst, 2006; Zhang et al., 2015). For instance, as both males and females of the Eurasian coot (*Fulica atra*) grew older their laying date advanced. This was attributed to the increasing quality of older females (relative to younger ones) and the fact that older males were better able to compete for early-laying females (Perdeck and Cavé, 1992). In the case of migratory birds, arriving at the breeding sites first often means the priority of access to better quality sites, greater resource availability, higher quality partners, and higher productivity (Emmenegger et al., 2014; Gauthreaux, 1978; Ketterson and Nolan, 1976; Kokko, 1999; Morrison et al., 2019). Thus, to maximise their reproductive success, migratory birds face the additional challenge of timing their spring migration to coincide with favourable local environmental conditions at their breeding sites, while being hundreds of kilometres away (Costa et al., 2021). For these species, accumulated experience gained during previous migrations plays a significant role in improving performance at stopover sites (Alerstam et al., 2003; Rus et al., 2017; Sergio et al., 2014). Experienced individuals are likely to achieve a more efficient migration (Harel et al., 2016; Hedenström and Alerstam, 1997; Miller et al., 2016; Rotics et al., 2016; Sergio et al., 2014) with shorter stopover durations (Campioni et al., 2020; Crysler et al., 2016; McKinnon et al., 2014; Péron and Grémillet, 2013) and faster refuelling times compared to inexperienced migrants (Lindström, 2003; Newton, 2010; Sergio et al., 2014; Votier et al., 2017). This is the case of the Eurasian griffon vulture (*Gyps fulvus*), in which adults have been reported to outperform juveniles not only in their ability to adjust fine-scale movements under challenging conditions, but also to be more efficient along the migratory route in terms of both time and energy (Harel et al., 2016). Indeed, it is widely reported that older and more experienced individuals often arrive at the breeding sites earlier and enjoy higher reproductive success than younger ones (Balbontín et al., 2007; Brown, 1969; Crawford, 1977; Lack, 1966; Neate-Clegg and Tingley, 2023; Watson and Moss, 1970).

Although the effects of age have been relatively widely explored with regards to breeder performance (e.g., Charlesworth, 1994; Forslund and Pärt, 1995; Limmer and Becker, 2010; Newton, 1988; Ortega et al., 2017; Sæther, 1990), the benefits that chicks may derive from the performance of older and likely more experienced adults remains mostly unknown in terms of their effect on chick body condition and migratory behaviour. However, it is widely known that chicks can be affected by age or status of the breeder (Crawford, 1977; Newton, 2010; Richner, 1989; Ricklefs, 1983). For example, highly stressed females can transfer corticosterone (stress hormones) to the egg yolk, which can subsequently affect chick growth and behaviour (Hayward et al., 2006; Naguib et al., 2006; Naguib and Gil, 2005). In addition, younger adults may also be less efficient at feeding and brooding thermally dependent chicks, as observed in the European shag (*Phalacrocorax aristotelis*) (Snow, 1960). These links between adult age and associated breeding performance, can therefore produce variation in chick body condition, which may in turn influence chick survival and subsequent behaviour (e.g., migration).

Body condition is a major concept in ecology and widely regarded as an important determinant of an animal’s fitness (Gosler, 1996; Peig and Green, 2010; Schulte-Hostedde et al., 2001; Stevenson and Woods, 2006). Peig and Green (2009) define body condition as the energy capital accumulated in the animal body due to food, and as such, an indicator of an animal´s general health and quality. Individual-level processes such as migratory and dispersive behaviour are reported to be influenced by variation in body condition (Barbraud et al., 2003; Buchan et al., 2020; Chapman et al., 2011; Kaitala et al., 1993; Ketterson and Nolan, 1976). Indeed, both these movements are energetically expensive and involve a high risk of mortality, thus, the acquisition of a good body condition prior to departure influences the extent to which an animal can disperse or migrate (Barbraud et al., 2003; Sanz-Aguilar et al., 2012). Therefore, producing higher quality chicks likely contributes to migratory behaviour and survival outcome of the breeder´s offspring. Partial migration is an extreme case of within species variation in migratory behaviour, where some individuals are not migrating at all (residents) (Chapman et al., 2011; Lundberg, 1988; Newton, 2008). In partial migratory systems, low quality (*body-size hypothesis,* or *foraging-limitation hypothesis* Boyle, 2008) or socially subordinate individuals (*dominance hypothesis*) may be pushed to sub-optimal migration strategies to reduce the negative effects of competition and winter environmental conditions in survival (Cristol et al., 1999; Hegemann et al., 2015; Ketterson and Nolan, 1976, 1983). Thus, it is expected that larger individuals will adopt a resident behaviour due to their ability to withstand long periods of food deprivation, while younger individuals are presumed to be more likely to migrate as they are unable to compete with dominant individuals when food is scarce (Cristol et al., 1999; Hegemann et al., 2015; Ketterson and Nolan, 1976, 1983). Nevertheless, the hypothesis behind the mechanism of partial migration were mainly based on passerine systems, and exceptions to these hypotheses do exist. For example, juveniles of the Greater flamingo (*Phoenicopterus roseus*) that presented higher body condition were more likely to migrate than those in poorer condition, which became residents (Scridel et al., 2023).

Since 2008, the population of Eurasian spoonbill (*Platalea leucorodia,* hereafter spoonbill) in Camargue (Southern France) has been growing exponentially and the subject of a long-term colour-ring monitoring programme (Blanchon et al., 2019; Champagnon and Kralj, 2023; Marion, 2019). Spoonbills in Camargue have a relatively long breeding season (egg laying occurring between February to June) and a diverse migratory behaviour, with a wide range of migratory routes and distances (Blanchon et al., 2019; Chapter 6). Thus, this population presents not only a unique opportunity to assess chick body condition variation over time (i.e., breeding season and over the years), but also to evaluate its potential influence on migratory behaviour. Furthermore, monitoring data collected during the breeding season allowed the identification of breeding individuals, their age (i.e., as more than 5000 individuals were marked as chicks), and in some cases their nests.

Here we monitored spoonbill nests, collected chick biometrics, and recorded their subsequent migratory behaviour with three main objectives: i) explore how breeders' age varies throughout the season. As with other bird species (Balbontín et al., 2007; Brown, 1969; Crawford, 1977; Lack, 1966; Neate-Clegg and Tingley, 2023; Watson and Moss, 1970), we predict that older and likely more experienced spoonbills will breed earlier in the season than younger ones; (ii) assess seasonal and annual trends in chick body condition over the past 14 years (2009 to 2023). We predict that body condition declines seasonally due to increasing resource competition between breeders (Gauthreaux, 1978; Kokko, 1999; Lack, 1968) and decreasing breeder quality (potentially due to the arrival along the season of inexperienced younger birds). Furthermore, years when extreme weather events occurred (e.g., abnormal precipitation or dryness), are also expected to have a negative impact on body condition (Lok et al., 2017); (iii) test the impact of chick's body condition and timing of fledging on its migratory behaviour. Spoonbills are social birds (de Goeij et al., 2012; Lok et al., 2019; Navedo and Garaita, 2012) and as such, by the time later-born juveniles (previously termed chicks) are able to migrate, experienced individuals undertaking such migrations may have already left the breeding sites, thereby potentially limiting the ability to travel with adults to more distant sites (Cresswell, 2014; Gill et al., 2014, 2019; Gunnarsson, 2006; Meyburg et al., 2017; Nightingale, 2023). Furthermore, since spoonbills are known to adopt mainly a long-distance migratory behaviour with higher mortality rates than less challenging behaviours (Chapter 6; Lok et al., 2011a), we expect that chicks with higher body condition will undertake the most challenging migratory behaviour, or at least to be those that survive such journeys and are successfully recorded as performing this behaviour. Therefore, we predict that timing of breeding and body condition will influence the migratory behaviour of spoonbill juveniles.

Material and Methods

Study site and population

Camargue is a semi-natural region of 180,000 ha, along the Mediterranean Sea in Southern France, making it the largest wetland in France (Blondel et al., 2013; Galewski and Devictor, 2016; Roche et al., 2009). Since 1998, the breeding population of spoonbills has increased from two breeding pairs to more than 400 since 2019 (Blanchon et al., 2019; Champagnon and Kralj, 2023). This species nests on the ground on small islets laying clutches of usually three or four eggs per nest (Cramp and Simmons, 1977). During their first three weeks of life spoonbills chicks are mostly in their nest, where they are regularly fed by both parents (Cramp and Simmons, 1977).

During the breeding seasons of 2009 to 2023, spoonbill colonies in Camargue were monitored (N43°28, E4°28 and N43°22, E4°39, Fig. 1). Resightings of PVC rings over the years have shown that the same individual can be seen in multiple breeding areas of Camargue. Therefore, hereafter, we considered Camargue as a single site.

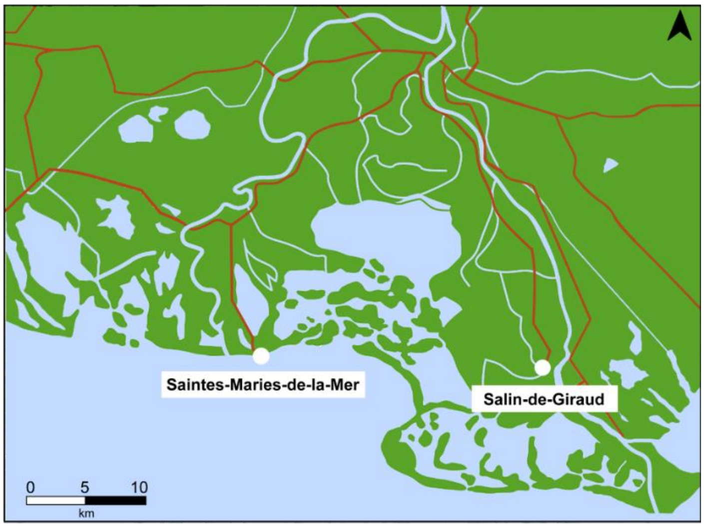

Fig. 1 – Map of Camargue (green) in the Mediterranean coast of France and approximate location of spoonbill colonies (black ellipse) where nests were monitored, and chicks were measured. Red lines represent the main roads and white dots the cities of Saintes-Maries-de-la-Mer and Salin-de-Giraud.

Data collection and selection

Determining breeders' age and timing of breeding

Since 2008, more than 5,000 spoonbills chicks have been ringed with a unique code engraved PVC ring allowing to individually identify marked birds and to discern their age. In addition to observations performed by experts at a distance using telescopes (from a hide), camera traps were deployed close to the nests since 2016, during the first weeks of incubation. These cameras were set to take pictures every ten minutes and were rotated regularly to identify the highest number of breeding adults possible, until all chicks have fledged. This allowed not only to determine the age (*Age*) of breeding individuals based on the code reading, but also to link it to the first time it was recorded breeding in a season (from 2014 to 2022; a single observation from 2011 was excluded and data from 2023 were not available at the time of this analysis). Here, we excluded birds which were not confirmed as breeders (i.e., those seen at the colony but not recorded building a nest, incubating, or with chicks), and birds younger than four calendar years due to a higher chance of being misclassified as breeder. In total we were able to identify 451 marked breeders (*Breeder*). For each individual, for each year, the first day of the year in which it was observed breeding was considered its observation date (*First_Obs*). Age of each breeding adult in any given year was obtained as the time difference between the year of ringing (all breeding adults were individual ringed as chicks) and the year of sighting, resulting in a dataset of 968 cases, corresponding to 451 different breeders across eight years (Appendix, Table A3.1).

During the breeding seasons of 2021 and 2022, using the same camera traps, it was possible to determine the age of 121 marked breeding adults on a subset of 101 individually marked nests (i.e., using small, marked flags; *Nest*) in which chick biometrics were also measured. From those, using species adapted Gompertz growth curves (head plus bill biometrics of chicks younger than two weeks, Lok et al., 2014) or the egg flotation method (Liebezeit et al., 2007), we were able to estimate the laying date of 49 nests (*Laying_day_Br*) corresponding to 54 different marked breeders (*Breeder*). This resulted in a new dataset of breeders with known age and laying date (hereafter referred as *Br_Lay* dataset). Some marked birds (n = 4) were associated with multiple nests in the same or different breeding seasons, and in ten nests both individuals of a breeding pair were marked. To account for these, when considering the initial models of this subset of breeders with known age and laying date, both *Breeder* and *Nest* were included as random variables.

Chick body condition

From 2009 to 2023 (*Year*), a total of 2,461 spoonbill chicks were captured prior to fledging, at an age of ca. 15-30 days, as part of a long-term ringing programme. Sampling occurred between April and July of each year during the early hours of the day and only under favourable weather conditions (i.e., no precipitation and/or strong wind), to minimise disturbance. Hereafter, ringing date will be referred to as *Session* when considered as a categorical variable and *Ring_day* when considered as a continuous variable (Julian day). During each *Session*, chicks' tarsus length (*mm*) and body mass (*g*) were recorded using metal rulers (±1 *mm*) and Pesola spring balances (±10 *g*), respectively. The body condition of each chick was then calculated using the Scale Mass Index (SMI) developed by Peig and Green (2009). SMI provides a reliable depiction of body condition as it standardises all individuals to their specific growth stage, thus accounting for the changing slope in the relationship between body mass and length measurements (Peig and Green, 2009, 2010). Individuals fitted with a GPS logger were excluded from this analysis (n = 79), as larger individuals were selected for GPS logger deployment and this likely biased the sampling of those individuals on those *Session*. A total of 2,382 individuals were thus considered for this analysis (hereafter referred as *BC_SMI* dataset; Appendix, Table A3.2).

From 2016 to 2023, the eighth primary feather of a total of 1,274 spoonbill chicks was also measured using metal rulers (±1 *mm*). With this additional biometric we were able to estimate chick age (days after hatching), using the estimated growth curves developed for this species (Lok et al., 2014). Then, by subtracting the estimated chick age from *Ring_day*, we calculated hatching date and the corresponding laying date (hereafter *Laying_day* estimated hatching date minus 25 days of incubation and 2 days between laying of first egg and start of incubation; Lok et al., 2014), thus obtaining the variable *Laying_day* for each individual. Furthermore, using the combination of the length of the eight primary feather and tarsus length, we were able to determine the sex of each chick (Lok et al., 2014; Oudman et al., 2017). Differences in growth between sexes become pronounced after 25 days of age, so to avoid misclassifications of sex, only individuals estimated to be older than 24 days were included in this analysis (hereafter referred as *BC_P8* dataset; $n_{BC\_P8} = 411$; Appendix, Table A3.2). Body condition of this subset of chicks, with estimated age and sex (*Sex*), was then calculated as the proportional deviation in body mass from the predicted sex- and age-specific body mass (Lok et al., 2014).

Migratory behaviour of juveniles

Due to a large network of dedicated amateur and professional ornithologists, we were able to determine the first wintering site on a subset of 105 spoonbill juveniles in which body condition was measured when they were chicks (hereafter referred as *Chick_W* dataset). We considered winter as the period between October and February and individuals were assigned a migratory behaviour according to the site where they were resighted during that period. To prevent the potential misclassification of individual migratory behaviour due to a late-autumn or early-spring stopover resighting, we only considered winter resightings during the months of November to January from the individuals seen in: France, Italy, Morocco, Portugal, and Spain (Lok et al., 2011; Navedo et al., 2010).

In the single case of an individual that was observed at different sites within the same flyway (East Atlantic flyway), we selected its southernmost site as its wintering site. We classified three migratory behaviours, considering the country of observation and the crossing of major ecological barriers (*Barrier*) as these are known to influence demography in this population (Chapter 6): None – migrants which do not cross any major ecological barrier (Portugal, Spain, and France, including Camargue, i.e. residents); Single – migrants which cross the Mediterranean Sea (Algeria, Italy, Morocco, and Tunisia); and, Multiple – migrants which cross the Mediterranean Sea and the Sahara Desert (Cape Verde, Gambia, Mauritania, and Senegal) (Appendix, Table A3.3).

Statistical analysis

An exploratory analysis (package *lattice*, Sarkar, 2008) was first undertaken to ensure that the body measurements data conformed with the requirements for the SMI calculation (Peig and Green, 2009) (for the relationship between body mass and tarsus per *Session*, see Appendix, Fig. A3.1). Multicollinearity was tested with the package *performance* (Lüdecke et al., 2021) and no relevant collinearity between the predictors *Ring_day* and *Year* was found (VIF < 2; Regarding, 2007; Zuur et al., 2009, 2010).

To test if younger adult breeders (*Age*) are recorded breeding later in the season, we considered the Julian day at which the individual was first recorded as a breeder in any given year (*First_Obs*, numerical and scaled) as the response and *Age* as a predictor (numerical).

To incorporate the dependency among observations of the same year or the same individual, we used *Year* and *Breeder* as the random intercepts. The linear mixed model, which included day of the season as a fixed effect (equation $_1$) was then compared to a null model through an analyse of variance (ANOVA) test.

$$First\_Obs_i = \ Age_i + Breeder_i + Year_i$$

$$Breeder_i \sim N(0, \sigma_{Breeder}{}^2)$$

$$Year_i \sim N(0, \sigma_{Year}{}^2)$$

(equation $_1$)

To more precisely examine the relationship between age of breeder and timing of breeding, we examined the subset *Br_lay*. We considered *Laying_day_Br* (numerical and scaled) as a fixed effect and both the variables *Nest* and *Breeder* as the random intercepts. This was done to incorporate the dependency among observations (i.e. chicks) from the same nest (i.e., nest laying date was set according to the estimated youngest chick using the head plus bill biometrics or the earliest laid egg using the egg flotation method) and breeder. However, this led to convergence issues and a singular fit, which indicates an overfitted model, likely due to the small number or lack of observations for the same breeders and nests. Thus, random variables were removed from the final model. The linear mixed model, which included laying date as a fixed effect (equation $_2$: *Laying_day_Br ~ Age*) was compared to a null model through an ANOVA test.

To investigate an annual trend in chick body condition and test for potential within year (i.e. seasonal) variation, generalized linear mixed models were performed in an information-theoretic model election framework (Burnham and Anderson, 2003). We manually developed the models for competition in the model selection, having body condition (*BC_SMI*) as response, day of the season (*Ring_day*, numerical and scaled), and year (*Year*, categorical of 14 levels) as predictors. To account for the fact that multiple observations originate from the same ringing session, we included *Session* as the random intercept. All combinations from equation $_3$ were considered by including or excluding predictor variables:

$$BC\_SMI_i = Ring\_day_i + Year_i + Session_i$$

$$Session_i \sim N(0, \sigma_{Session}{}^2)$$

(equation $_3$)

The different models developed were ranked and selected according to the Akaike´s Information Criterion adjusted for small sample size (*AICc*) (Anderson and Burnham, 2002). When there were multiple models within two AICc points of the top-ranking model, the model with the fewest number of parameters was selected (i.e., the most parsimonious model, Anderson and Burnham 2002).

For the subset of chicks with known sex and age and considering the body condition estimated by the growth curves (*BC_P8*), the models included a seasonal effect (*Laying_day*, numerical and scaled) and year (*Year*, categorical with eight levels). All combinations from the equation (equation $_4$: $BC\_P8 \sim Laying\_day + Year$) were considered. Subsequent pairwise Tukey HSD post-hoc test comparisons were conducted in the most parsimonious model to explore the differences among the marginal means of each group, using the emmeans package (Lenth et al., 2024). A Sidak correction was applied, which adjusts for the family-wise error rate across all tests and provides a more conservative control over Type I errors (Sidak, 1967).

Lastly, to explore if a chick’s body condition (*BC_SMI*) or timing of breeding (*Ring_day*) influences its subsequent migratory behaviour as a juvenile, number of barriers (*Barrier*) was considered as a variable response of three levels (None, Single, and Multiple) of a multinomial model (Venables and Ripley, 2002). A quadratic effect of body condition and timing of breeding were also considered. All combinations from equation $_5$ were considered by including or excluding predictor variables:

$$Barrier_i = Ring\_day_i + Ring\_day_i\hat{}2 + BCSMI_i + (BCSMI_i)\hat{}2$$

(equation $_5$)

Model coefficients were then tested for significance using multiple Wald tests (Hayashi et al., 2011). The scarcity of data (n = 29) also limited our capacity to test a linear model containing migratory behaviour as a fixed effect considering the *BC_P8* dataset, and thus, such analysis was not carried out for this dataset.

All analyses were carried out in the software R version 4.2.1 (R Core Team, 2022) and plots were created using the package *ggplot2* (Wickham, 2016) and *sjPlot* (Lüdecke et al., 2023). Our linear models were estimated using ordinary least squares (*OLS)* through the function *lm* and the linear mixed models using the function *lmer* in package "*lme4*" (Bates et al., 2015).

Results

Breeders' age and timing of breeding

A pairwise comparison between a null model and a model including *First_obs* (equation $_1$) indicated the existence of a significant relationship between breeder´s age and timing of breeding, [F (1, n = 968) = 21.68, $p < 0.001$]. Overall, younger individuals breed later than older individuals (*Beta* = *-0.08, 95%* CI [*-0.12, -0.05*], t(*963*) = *-4.72, p < 0.001*; Fig. 1 and Appendix, Table A3.4).

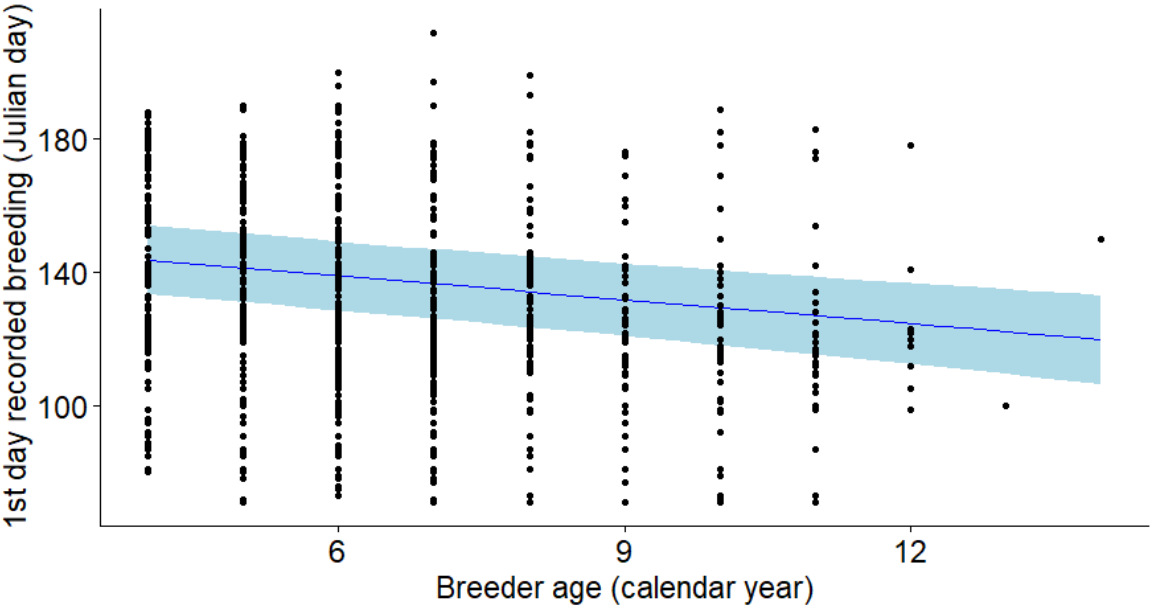

Fig. 1 – Variation in breeder age (calendar year; n = 968) throughout the season according to equation $_1$ model: *First_Obs ~ Age* (blue). *Year* and *Breeder* were considered as random variables. Black dots represent the actual age recorded and shade blue area a 95% confidence interval. In this plot, Julian day was not scaled for clarity of interpretation.

The existence of a significant negative relationship between breeder´s age and laying date was also confirmed by a pairwise comparison between a model containing *Age* (equation $_2$) and the null model, [F (1, n = 59) = 10.78, $p < 0.01$], indicating that older individuals lay eggs earlier in the season than younger ones (*Beta* = *-0.16, 95%* CI [*-0.26, -0.06*], t(*57*) = *-3.28*, $p = 0.002$; Appendix, Table A3.4).

Seasonal and annual variation in chick body condition

When considering the *BC_SMI* dataset (equation $_3$), the most parsimonious model included a seasonal (*Ring_day*) effect (Model 2, Table 1), implying a decreasing body condition as the season progresses (*Beta* = *-23.45, 95%* CI [*-34.43, -12.47*], t(*2378*) = *-4.19*, $p < 0.001$; Fig. 2; Appendix, Table A3.5). Despite *Year* being present in the most supported (though not most parsimonious) model (Model 4, Table 1), a comparison between the estimated marginal mean of each year confirmed the lack of significant differences among years (Appendix, Fig. A3.2).

Table 1. Generalized linear mixed models' selection for body condition estimated by the SMI (n_{BC_SMI} = 2382). *Session* was included as a random variable. Models were ranked according to the Akaike value, and the most parsimonious model is indicated in bold.

Number	Model	*K*	AIC$_c$	ΔAIC$_c$	Akaike weight
4	*Ring_day + Year*	18	30444.82	0.00	0.62
2	*Ring_day*	***4***	**30445.84**	**1.02**	**0.37**
1	*Constant*	*3*	30458.22	13.40	0.00
3	*Year*	17	30462.92	18.10	0.00

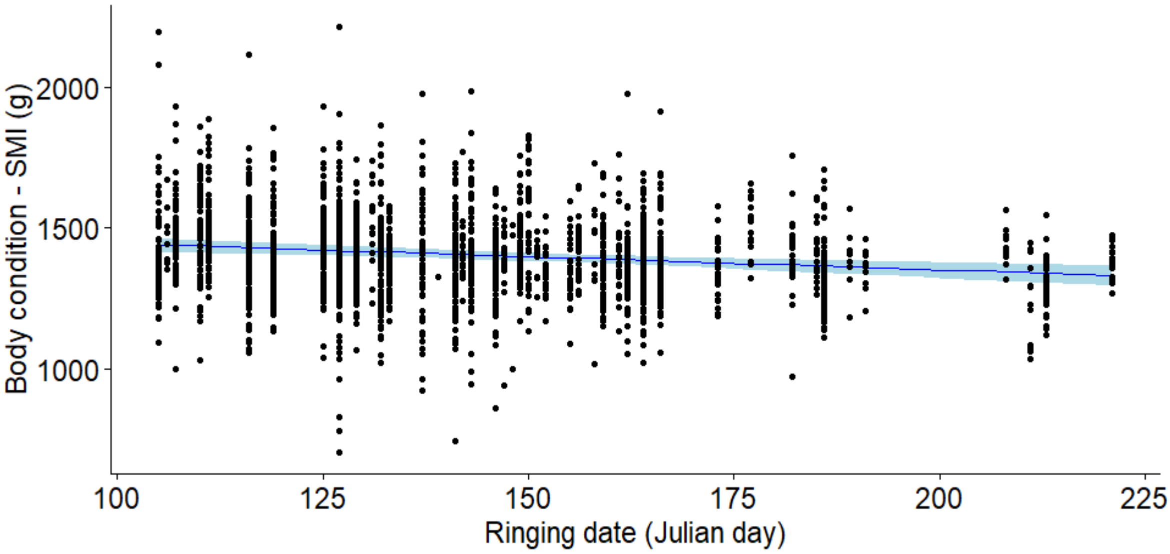

Fig. 2 –Variation in body condition (obtained using the SMI: n_{BC_SMI} = 2382) throughout the season predicted by the most parsimonious model (Model 2, Table 2). Black dots represent the actual body measurements obtained using the SMI and shade blue area a 95% confidence interval. In this plot, Julian day was not scaled for clarity of interpretation.

When considering the smaller subset (*BC_P8*) comprising chicks with known laying date and sex (n_{BC_P8}= 411; equation $_4$), the most parsimonious model (Model 4, Table 2) did not detect any differences in body condition depending on a chick's sex or laying date. However, laying date was present in one of the two most supported models (i.e. within 2 delta AICc; Model 4, Table 2).

Table 2. Generalized linear mixed models' selection for testing the effect of laying date and year on chick body condition considering chick age and sex (BC_P8 dataset; $n_{BC\_P8} = 411$). Models were ranked according to the Akaike value, and the most parsimonious model is indicated in bold.

Number	Model	*K*	AIC_c	ΔAIC_c	Akaike weight
3	***Year***	***9***	**-745.22**	**0.00**	**0.55**
4	*Laying_day + Year*	10	-743.50	1.73	0.23
1	*Constant*	2	-742.06	3.16	0.11
2	*Laying_day*	*3*	-741.99	3.24	0.11

Despite *Year* being present in the most parsimonious model, only 2020 was significantly different and lower than most other years (*Beta = -0.21, 95%* CI [-0.*35, -0.07*], t(*403*) = -*2.96, p = 0.003*) with the exception of the years 2016, 2018, and 2021 (Appendix, Table A3.6). This result was mainly driven by two individuals sampled in 2020.

Migratory behaviour of juveniles

When testing the drivers of juvenile migratory behaviour (equation $_5$), the most parsimonious model included a seasonal (*Ring_day*) effect (Model 3, Table 3), implying that the later in the season a chick fledges, the higher the probability of not crossing an ecological barrier (Fig. 3). Body condition was not present in the most parsimonious model, suggesting that there is no significant difference between the body condition of individuals adopting different migratory behaviours.

Table 3. Generalized linear mixed models' selection for explaining the recorded migratory behaviour of first calendar year spoonbills ($n_{Barrier}$ = 105). *Session* was included as a random variable. Models were ranked according to the Akaike value, and the most parsimonious model is indicated in bold.

Number	**Model**	***K***	**AIC$_c$**	**ΔAIC$_c$**	**Akaike weight**
5	$Ring\_day + Ring\_day^2$	*6*	222.96	0	0.26
3	***Ring_day***	***4***	**223.15**	**0.19**	**0.24**
6	$BC\_SMI + Ring\_day$	**6**	223.67	0.71	0.19
8	$BC\_SMI + Ring\_day + Ring\_day^2$	**8**	223.72	0.76	0.18
2	*BC_SMI*	**4**	226.15	3.19	0.05
1	*Constant*	**2**	227.06	4.1	0.03
7	$BC\_SMI + BC\_SMI^2 + Ring\_day$	**8**	228.29	5.33	0.02
9	$BC\_SMI + BC\_SMI^2 + Ring\_day + Ring\_day^2$	**10**	228.41	5.45	0.02
4	$BC\_SMI + BC\_SMI^2$	**6**	230.17	7.21	0.01

A subsequent Wald test confirmed that late juveniles were significantly less likely to cross ecological barriers compared to adopting migratory behaviours that cross a single barrier (*Beta* = 2.*58*, *p = 0.010)* or multiple barriers (*Beta* = 2.*20*, *p = 0.028*). No significant differences were found between single and multiple barriers (*Beta* = 0.*79*, *p = 0.430*).

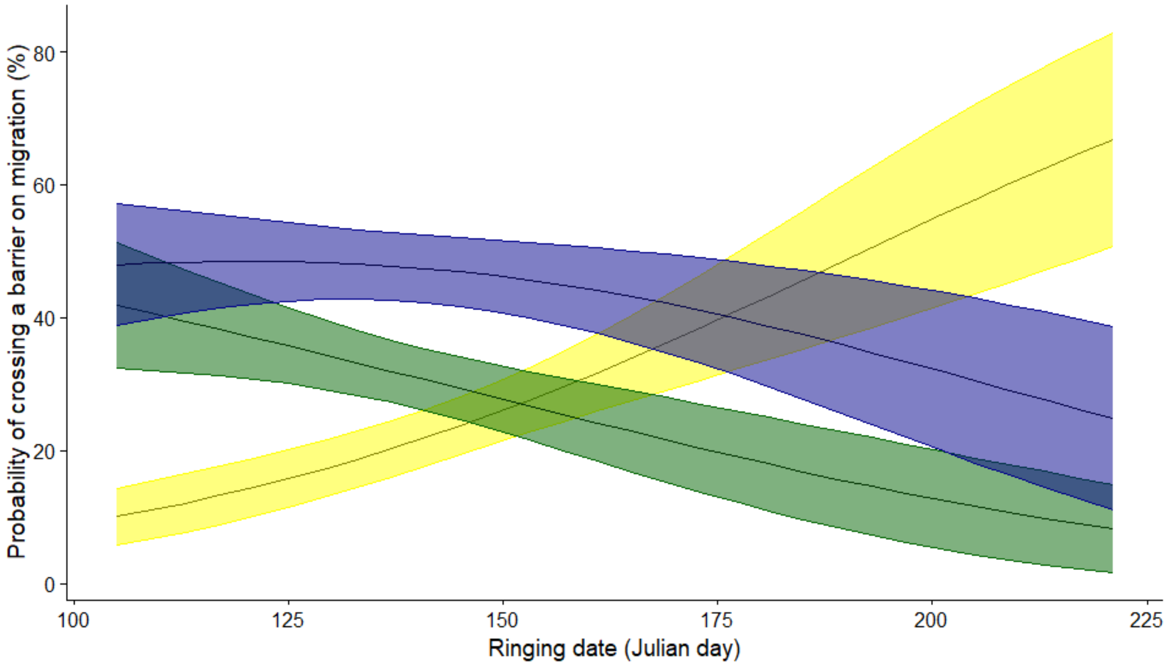

Fig. 4 –- Probability of adopting a migratory behaviour as modelled by Model 3, Table 3. Each line represents the predicted probability of crossing no barrier (yellow- “residents”), one barrier (dark green – “short distance migrants”) or multiple barriers (dark blue – “long distance migrants”) given the ringing day ($n_{Barrier}$ = 105). Shaded areas represent a 95% confidence interval.

Discussion

In this study we showed that older, likely more experienced, spoonbills tend to breed earlier in the season than younger individuals, and that early breeders are more likely to produce chicks with higher body condition than late breeders. There was limited annual variation in chick body condition and no variation between years (except for 2020). Finally, juvenile’s migratory behaviour seems to be influenced by timing of breeding, as later-born juveniles tend to undertake a less challenging migratory behaviour than early season juveniles. Interestingly, although not statistically significant, early juveniles that cross one or more barriers also tend to have higher body condition than later-born juveniles that do not cross any barriers.

Breeders' age and timing of breeding

In bird species, older and more experienced individuals tend to arrive at breeding sites earlier and have higher reproductive success than younger ones (Balbontín et al., 2007; Brown, 1969; Crawford, 1977; Lack, 1966; Neate-Clegg and Tingley, 2023; Watson and Moss, 1970). Furthermore, better migratory performance could also mean that more experienced individuals arrive in better condition than inexperienced ones, and thus may lay earlier than individuals in poorer condition (Bêty et al., 2003; Drent et al., 2003; Drent and Daan, 1980; Lok, 2013). For example, due to a shorter delay on the breeding grounds, Snow geese (*Chen caerulescens atlantica*) females with high premigration body condition had an earlier laying date and higher breeding success than those in low condition (Bêty et al., 2003). In accordance, our results show that older spoonbills tend to be seen breeding earlier in the season, and a subsample of nests with known laying date supported that the earliest nests tend to be associated with the oldest breeders. Spoonbills of the Dutch breeding population have previously been seen to advance their breeding timing, but this was mainly the case for the short-distance migrants (Lok et al., 2017). As with the Dutch population and other species (e.g., Black kite – *Milvus migrans*; Pied flycatcher – *Ficedula hypoleuca*), a likely mechanism behind our result is an earlier departure from the wintering sites or a faster and/or more efficient migration of the oldest individuals (Lok et al., 2017; McCleery et al., 2008; Potti and Montalvo, 1991; Sergio et al., 2014). Nevertheless, given the long breeding season in Camargue, with the last breeders laying eggs in June, while long-distance migrants are already observed in Camargue as early as February (*pers. obs.*), it is unlikely that migratory performance can fully explain our results. Therefore, besides arriving later, it is possible that younger birds are also more susceptible to social interference in the colony and during pair formation (Lok et al., 2017; McCleery et al., 2008). For example, preliminary information suggested that young Mute swans (*Cygnus olor*) are more likely than older birds to spend more time fighting in early season, and consequently, delaying their laying (McCleery et al., 2008).

As spoonbills age, they seem to cope better with migratory challenges and wintering conditions, as suggested by the lack of differences between the survival rates of experienced individuals with different wintering strategies Chapter 6. Thus, it is likely that spoonbills improve their migratory and breeding performance due to accumulated experience, which is in accordance with the constraint or experience hypothesis (Curio, 1983; Wood et al., 2016). This hypothesis assumes that reproductive success may improve with age due to increased parental efficiency in activities such as brooding, foraging, protection of chicks from adverse weather conditions (e.g., wind and precipitation) and feeding (Curio, 1983; Limmer and Becker, 2009; Pyle et al., 2001). This was the case in European shags where, when breeding in similar environmental conditions, old pairs performed consistently better than young pairs due to intrinsic differences in brood rearing capacity (Daunt et al., 1999). Detailed analysis of the reproductive success of Western gulls (*Larus occidentalis*) showed that increased clutch size was related to female experience and enhanced hatching success to experience of both sexes (Pyle et al., 1991). Furthermore, fledging success was likely influenced by age-related improvements in foraging skills (Pyle et al., 1991). The impact of experience has also been widely reported in other groups, where reduced foraging skills of inexperienced individuals have been suggested to lead to low productivity in aerial insectivores such as Tree swallow (*Tachycineta bicolor*; Steven, 1978) and Bee-eater (*Merops apiaste*r; Costa et al., 2021). For several Passeriformes, an increase in foraging skills with age has also been documented (Desrochers, 1992; Enoksson, 1988; Franks and Thorogood, 2018; Jansen, 1990). Furthermore, younger breeders may suffer from reduced access to resources due to competition with older individuals (Curio, 1983; Emlen, 1978, 1982).

Seasonal and annual variation in chick body condition

Spoonbills in the Camargue breed in protected islets that are relatively undisturbed, except for opportunistic predation events by Eurasian wild boar (*Sus scrofa*) and Red fox (*Vulpes vulpes*) (Champagnon et al., 2021). Furthermore, the abundance of food sources in the surrounding area (e.g. temporary and permanent marshes), including the high abundance of Red-swamp crayfish (*Procambarus clarkii*) (Martino et al., 2011; Meineri et al., 2014; Ottonello et al., 2005; Poulin et al., 2007; Roche et al., 2009; Rodriguez-Perez et al., 2014) are likely sufficient to meet the energetic needs of the Camargue spoonbill population and support its continued and ongoing growth (Champagnon and Kralj, 2023). Although we did not conduct any diet analysis in our study, in Camargue, crayfish species are important prey for several waterbird species, such as the Eurasian bittern (*Botaurus stellaris*; Poulin et al., 2007) and the Glossy ibis (*Plegadis falcinellus*; Champagnon et al., 2019). Furthermore, previous opportunistic sampling at the breeding sites by the Tour du Valat team in 2007, detected a dominance of crayfish remains in spoonbill regurgitates (*unpublished data*).

A relatively undisturbed breeding site and high food availability in the surrounding area may partly explain the lack of variation in body condition between years. Nevertheless, if the population continues to grow (Champagnon and Kralj, 2023), it may reach a capacity limit, resulting in increasing competition between spoonbills and likely decreasing body condition of chicks (Bechet and Johnson, 2008; Forero et al., 2002; Lack, 1954; Lok et al., 2013, 2017). This is the case for the spoonbill population in the Netherlands, where colony size is thought to be regulated by local food constraints (Lok et al., 2009; Oudman et al., 2017; Overdijk and Horn, 2005). There, the body condition of chicks measured in stable colonies was found to be lower than that of those measured in growing colonies (Lok et al., 2009; Oudman et al., 2017; Overdijk and Horn, 2005). When considering the body condition estimated by the growth curves adapted to the species (Lok et al., 2014), we did detect significantly lower body condition. However, this result was mainly driven by the small sample size (only two individuals measured in 2020) and if a larger pool of individuals were available, we would expect no significant differences in body condition between years.

Our analysis showed significant variation within years, indicating that early chicks have higher body condition than later-born chicks. This is commonly attributed to the fact that later-born chicks are likely to be more exposed to increased competition (i.e., adult individuals, plus the early chicks) and/or lower food availability (Drent and Daan, 1980; Evans et al., 2020; Lack, 1968; Verboven and Visser, 1998). Nevertheless, the fact that the population is still growing (Champagnon and Kralj, 2023) and that the crayfish abundance peaks between April and June (Meineri et al., 2014), suggests that other factors may also influence chick body condition. In the case of the Glossy ibis, no seasonal effect on chick body condition was detected, suggesting that food availability in Camargue, particularly crayfish, as also consumed by spoonbills, is sufficient to satisfy the colony energetic demands throughout the breeding season (data collected from 2005 to 2017; Ferreira et al., 2019). In addition to a decrease in food availability, the observed seasonal decline in body condition may be caused by the lower quality or experience of late-breeding parents. Less experienced breeders could lack the skills to feed the chicks as successfully, forage efficiently, and/or provide the needed thermal support (Marchetti and Price, 1989; Martin, 1995; McCleery et al., 2008; Sæther, 1990; Snow, 1960; Wunderle, 1991) for example by failing to properly lining the nest, which is a structure associated to temperature regulation in the nest (Hansell, 2000, 2005).

Migratory behaviour of juveniles

In social species, the timing of breeding can have consequences for juvenile migratory behaviour, as experienced individuals may have left the breeding sites by the time later-born juveniles are able to migrate (Cresswell, 2014; Gill et al., 2014, 2019; Gunnarsson, 2006; Meyburg et al., 2017; Nightingale, 2023). This may be the case for Camargue spoonbills, as our results suggest that later-born juveniles tend to undertake a less challenging migratory behaviour. Indeed, spoonbills are social birds (de Goeij et al., 2012; Lok et al., 2019; Navedo and Garaita, 2012), that often migrate in mixed-age flocks (Lok, 2013). Consequently, later-born juveniles are more likely to find themselves with fewer adults to follow, that cross major ecological barriers such as the Mediterranean Sea and the Sahara Desert. This could potentially explain the considerable number of juveniles that stay in France and Iberia for their first winter, but subsequently move to further locations in the following winter (*pers. obs.*; Lok et al., 2011). Socially mediated migratory behaviour is also found in other species. For example, young Oystercatchers (*Haematopus ostralegus*) are known to adopt the same migratory behaviour as their father, which waits for its offspring to be ready to migrate (Méndez et al., 2020, 2021). As for Lesser spotted eagles (*Clanga pomarina*), despite not following their parents, successful arrival at non-breeding sites was higher for individuals that migrated with adults, who are therefore likely to benefit from adult navigational cues (Meyburg et al., 2017). Finally, and potentially like the spoonbills, late-fledged juveniles of Black-tailed godwits (*Limosa limosa islandica)* are more likely to join flocks dominated by juveniles, as adults depart the breeding areas shortly after breeding and are thus more likely to winter at northern sites (Gill et al., 2019; Gunnarsson, 2006; Nightingale, 2023).

Despite a significantly lower probability at the end of the season, it is still possible that later-born juveniles can follow experienced individuals that have left the breeding site later and still cross major ecological barriers. This could happen because later-born juveniles may encounter such individuals, including those from other breeding populations Chapter 6 and 7, at the stop-over sites. This is the case for juvenile of Short-toed snake eagles (*Circaetus gallicus*) which can learn detours to complete trans-Mediterranean migration from older individuals encountered during migrating (Agostini et al., 2017). Likewise, the departure date of continental Black-tailed godwit (*Limosa limosa limosa*) juveniles from the Netherlands, was related to hatching date, and while monitored juveniles all left the breeding grounds later than adults, they joined adult flocks at stopover sites around the Mediterranean (Verhoeven et al., 2022). Furthermore, such social learning can significantly increase the resilience of individual birds to cope with environmental change and extreme events, while also mitigating the need for juveniles to migrate synchronously with adults (Agostini et al., 2017).

We hypothesised that chicks' body condition could influence their migratory behaviour in two different ways: i) like flamingos, higher quality juveniles would be more likely to move away from the natal area (Barbraud et al., 2003; Dufty and Belthoff, 2001) and thus be able to undertake more challenging migrations and cross major barriers (e.g., Mediterranean Sea); or ii) because Camargue is a high-quality site, birds in good condition could potentially remain over the winter (Boyle, 2008; Cristol et al., 1999; Gauthreaux, 1978; Ketterson and Nolan, 1976) and potentially outcompete lower quality birds to undertake a more challenging migration to distant non-breeding sites. Our results have shown that early-born juveniles have higher body condition and are more likely to cross barriers. Thus, although not statistically significant, the poorer body condition of later-born juveniles may also contribute to their less challenging migratory behaviour. Alternatively, first postnuptial migration is risky, and we cannot rule out the possibility that low quality juveniles also undertook long demanding migrations but died at higher rates than high quality juveniles and were therefore less observed at non-breeding sites.

While supporting previous studies suggesting that spoonbills improve their migratory performance with age Chapter 6, this study indicates that their breeding performance may also improve as they become more experienced. Additionally, our results suggest that early-born chicks (with a tendency to have higher body condition) are more likely to undertake more challenging migrations. Our study therefore highlights the relevance of long-term studies to better understand the complex breeding phenology of a migratory species, which can lead to changes in population-scale patterns and processes (Gil et al., 2018; Nightingale, 2023).

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Ethics approval

All fieldwork procedures were compliant with applicable animal welfare regulations by the Centre de Recherches sur la Biologie des Populations d'Oiseaux (Museum National d'Histoire Naturelle, [https://crbpo.mnhn.fr]), programme personnel 580.

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Appendices 3

Fig. A3.1 – Relationship between body mass and tarsus per ringing *Session* (n = 2382).

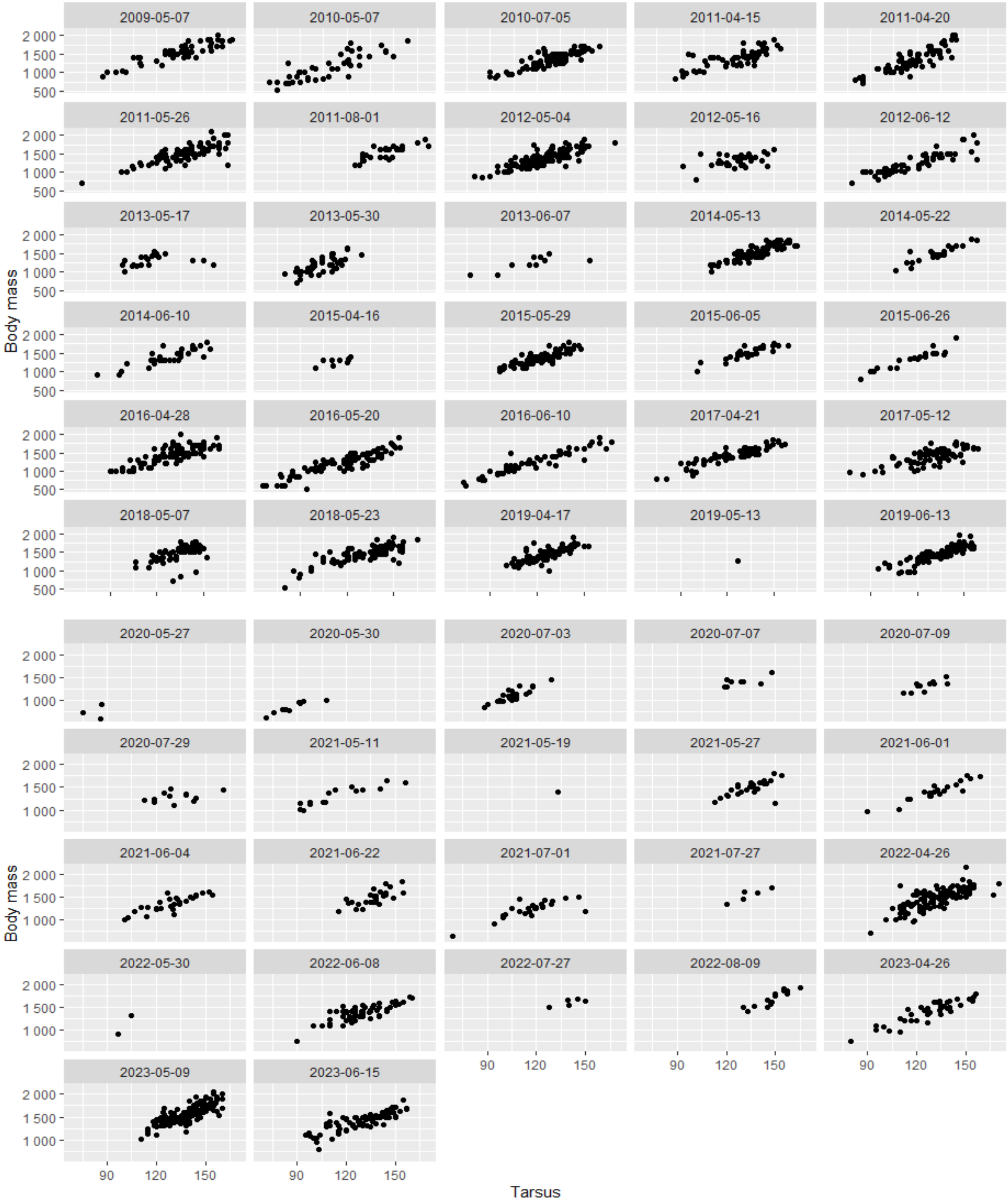

Table A3.1. Total number of adult breeding spoonbills resighted in the breeding season per age ($n_{Breeders} = 451$; $n_{Year} = 8$; $n = 968$).

Age (year of resighting – year of ringing)	Number of different spoonbills seen
4	147
5	177
6	203
7	175
8	101
9	73
10	49
11	32
12	9
13	1
14	1

Table A3.2. Total number of spoonbills chicks measured (including or not the eight primary feather – P8), per year ($n_{BC\_SMI} = 2382$; $n_{BC\_P8} = 411$).

Year	Total number of spoonbills sampled	Subset with measurement of P8
2009	55	0
2010	138	0
2011	239	0
2012	206	0
2013	68	0
2014	135	0
2015	132	0
2016	242	26
2017	141	52
2018	148	63
2019	174	56
2020	67	2
2021	147	31
2022	204	94
2023	286	87

Table A3.3. Total number of spoonbills measured for body condition and resighted in their first winter, per migratory behaviour and year of birth (n_{Chicks_W} = 105).

		Number of ecological barriers crossed		
Year of birth	Recorded in winter	None	Single	Multiple
2009	1	0	1	0
2010	6	4	1	1
2011	4	2	1	1
2012	6	4	2	0
2013	3	0	0	3
2014	4	1	1	2
2015	9	1	2	6
2016	3	1	2	0
2017	8	3	4	1
2018	9	0	6	3
2019	5	0	0	5
2020	1	0	0	1
2021	10	4	2	4
2022	15	1	5	9
2023	21	4	5	12
Total	105	25	32	48

Table A3.4. Summary of a general linear mixed model analysis of the effect of season (*First_Obs*) on breeder's age, with a 95% confidence interval ($n_{Breeder}$ = 451; n = 968); and the effect of season (*Laying_day_Br*) on breeder's age, with a 95% confidence interval ($n_{Breeder}$ = 54; n_{Nest} = 49; n = 59).

Model	**Coefficient**	**Estimates**	**Standard Error**	***t*-value**	***p*-value**	***2.5%***	***97.5%***
First_Obs ~ Age + Year	*(Intercept)*	0.74	0.20	3.71	< 0.001	0.32	1.17
	Day	-0.08	0.02	-4.72	< 0.001	-0.12	-0.05
Laying_day_Br ~ Age	*(Intercept)*	1.29	0.41	3.14	< 0.001	0.47	2.11
	Age	-0.16	0.05	-3.28	0.002	-0.26	-0.06

Table A3.5. Summary of a general linear mixed model analysis of the effect of season (*Ring_day*; scaled) in body condition (obtained through the SMI), with a 95% confidence interval ($n_{BC\_SMI} = 2382$; Model 2 Table 1).

Coefficient	Estimates	Standard Error	*t*-value	*p*-value	*2.5%*	*97.5%*
(Intercept)	1405.67	6.41	219.32	< 0.001	1392.95	1418.81
Ring_Day	-23.45	5.60	-4.19	< 0.001	-34.52	-12.01

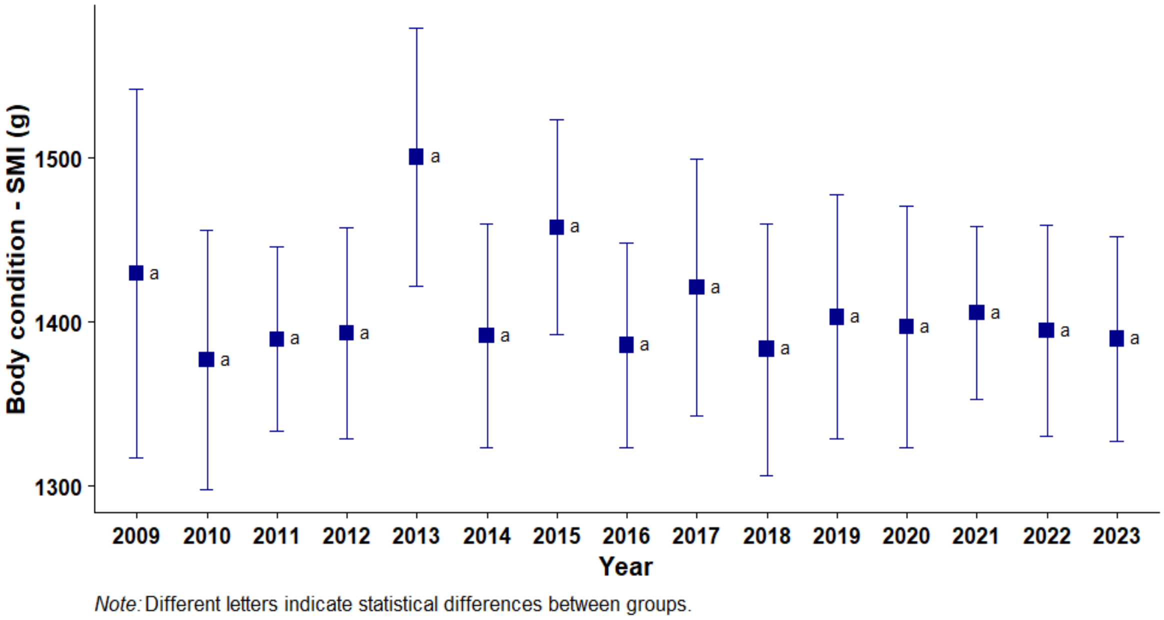

Fig. A3.2 – Post-hoc comparison of estimated marginal mean of body condition (SMI, g) between years (2009 to 2023). Vertical lines indicate 95% confidence, and a Sidak correction was applied ($n_{BC\_SMI} = 2382$; Model 4).

Table A3.6. Summary of a general linear mixed model analysis of the effect of year (2016 to 2023) on body condition (obtained from the *BC_P8* dataset), with a 95% confidence interval ($n_{BC\_P8} = 411$; Model 4, Table 2).

Coefficient	**Estimates**	**Standard Error**	***t*-value**	***p*-value**	***2.5%***	***97.5%***
(Intercept)	1.02	0.02	54.12	< 0.001	0.99	1.06
2017	0.02	0.02	0.78	0.434	-0.03	0.06
2018	-0.00	0.02	-0.03	0.980	-0.05	0.04
2019	0.03	0.02	1.19	0.236	-0.02	0.07
2020	-0.21	0.07	-2.96	0.003	-0.35	-0.07
2021	-0.01	0.03	-0.23	0.820	-0.06	0.05
2022	0.03	0.02	1.26	0.209	-0.02	0.07
2023	0.02	0.02	1.11	0.269	-0.02	0.07

This chapter is under review by Science of the Total Environment

CHAPTER 4

Presence and potential impact of artificial materials in the nests of a colony-breeding waterbird

Hugo R. S. Ferreira, Ana C. Hadden, Jocelyn Champagnon, Tamar Lok, Marion Vittecoq, and José A. Alves

Spoonbill nests lined with artificial material, Camargue, 2022.
This species belongs to the order Pelecaniformes, which is notorious for collecting materials from older nests or conspecifics.

Presence and potential impact of artificial materials in the nests of a colony-breeding waterbird

Abstract

Despite the vital importance of wetlands globally, these habitats have increasingly received artificial materials, such as plastics, which can influence the wildlife these habitats support. We monitored the occurrence of artificial materials in Eurasian spoonbill nests in the Camargue wetland in Southern France during two breeding seasons (2021-2022), and investigated their potential function by associating their presence with breeder age (proxy for experience) and hatching success. In our study, 41% of the nests contained at least one artificial material ($n = 439$), usually plastic of sheet-like shape and white-transparent colours. Throughout the breeding season, the proportion of artificial materials in the nest lining increased, coinciding with a decrease in natural materials (i.e., vegetation). A higher proportion of natural materials was detected during the egg phase compared to other phases of nest development, suggesting that these materials may have a thermoregulatory function during incubation. Our results did not support a correlation between the proportion of artificial materials and breeder experience, nor with hatching success. This study recorded the use of sheet-like plastics as a lining material by a colony-breeding waterbird. Further studies (e.g., physiological through necropsy or fine temperature nest assessment) may disentangle the benefits and adverse effects of such materials on waterbird breeding success.

Keywords/phrases: *Platalea leucorodia*; nest lining; nest function; plastic pollution; Mediterranean.

Introduction

The importance of wetlands for biodiversity and the value of the ecosystem services they provide are recognized worldwide (Assessment, 2005; Corcoran, 2010; Keddy, 2010; Tiner, 1989). Nonetheless, it is estimated that 87% of the world's wetlands were lost since 1700, and that many of the remaining wetlands are either degraded or currently under severe anthropogenic pressure (Davidson, 2014; Gardner and Finlayson, 2018). The increasing influx of artificial materials into the general environment, in combination with their slow rate of degradation, is one of the main threats for natural ecosystems worldwide (Galgani et al., 2013), including wetlands. Plastic pollution in particular has become such a challenge that the United Nations Environment Programme (UNEP) has classified it as a critical environmental issue (UNEP, 2014, 2011). However, despite global alerts and efforts to reduce societal dependency on (single use) plastics (UNEP, 2016) and to remove them from the environment (Jain, 2017), their spread and abundance in the natural world continues to increase (Borrelle et al., 2020; Geyer et al., 2017).

Artificial materials are solid man-made objects (Barnes et al., 2009; Eriksen et al., 2014) of different types (e.g., fibre, metal, paper, plastic, rope, and rubber). Invariably and despite global recycling efforts, many are incorrectly disposed and often find their way into the natural environment. Plastics are the most common type of debris in the world (Browne et al., 2015), and can be further categorised according to their original purpose into industrial plastics (e.g., nurdles) and user plastics (e.g., sheet-plastics – plastic bags and threadlike plastics – rope) (Franeker and Meijboom, 2007; Provencher et al., 2017). Consequently, interactions between wildlife and artificial materials have been increasingly reported. For example, artificial materials have been found in the digestive tract of several species of marine birds (e.g., *Charadriiformes*, *Pelecaniformes*, and *Procellariiforme*s), mammals (e.g., *Mysticeti*, *Otariidae*, and S*irenia*) and turtles, (Kühn and van Franeker, 2020; Laist, 1997), and in some cases, they have been shown to condition some species development and behaviour (e.g., Red phalarope – *Phalaropus fulicarius,* Connors and Smith, 1982; Derraik, 2002; Gregory, 2009). Additionally, an increasing number of reports indicate that chemical components in artificial materials can have long-term effects on animal physiology (Derraik, 2002; Kühn and van Franeker, 2020; Laist, 1997). The presence of artificial materials in nests has been reported across several avian groups, including land birds (e.g., Hanmer et al., 2017; Suárez-Rodríguez and Garcia, 2017; Townsend and Barker, 2014) and seabirds (e.g., de Souza Petersen et al., 2016; Witteveen et al., 2017). Yet, detailed information regarding the occurrence of artificial materials on numerous other avian groups remains unknown (Jagiello et al., 2019; Rodríguez et al., 2023; Tavares et al., 2016, 2017).

Nests are comprised of four main sections: attachment (composed by materials responsible for the attachment of the nest to its substrate), outer layer (decorative), structural layer (support of the structure), and lining (to protect the eggs) (Hansell, 2000). The materials that usually make up the shape of the nest and provide its structural support are considered as structural materials, whereas the lining materials are typically associated with the creation of a suitable microclimate within the nest (Hansell, 2000, 2005). And the use of artificial materials in nests, both for structural and lining purposes, tends to be associated with the scarcity or absence of natural materials in the vicinity of nesting sites (Antczak et al., 2010; Hiemstra et al., 2021; James Reynolds et al., 2019; Lavers et al., 2013; Witteveen et al., 2017). This suggests a potential trade-off between the time and energy spent searching for natural materials and the collection of more readily available and easily found artificial materials (Antczak et al., 2010). For example, in South Korea, 71% of the nests in a colony of Black-faced spoonbill (*Platalea minor*) were reported to contain some type of plastic material in 2010 (Choi et al., 2015). However, when natural materials were provided at nesting sites, the proportion of nests containing plastic materials halved across the subsequent years (2011 – 37%; 2012 – 33%) (Choi et al., 2015). The presence of specific artificial materials in nests could also be linked to the similarity with the shape of natural materials used to form and line the nests. The Brown noddy (*Anous stolidus*), mostly collects rope and rope-like materials to build its nests, potentially due to the similarity between these materials and elongated fragments of natural materials such as twigs (Ryan, 2020).

Nest characteristics have a key role in determining breeding success (Mainwaring et al., 2014; Moreno et al., 1995) and the presence of artificial materials (e.g., fishing nets and gears) is known to increase nestling mortality due to entanglement or ingestion (Lavers et al., 2014; Luna et al., 2018; Ryan, 2018; Seacor et al., 2014; Votier et al., 2011). Furthermore, the proportion and type of artificial materials in the nest could potentially compromise its functional performance (e.g., camouflage, structural integrity, and thermoregulation), which could in turn, impact fitness-related traits (e.g., hatching, or fledging success), with potential cascading effects at the population level, if the use of artificial materials is widespread across the population (Deeming and Reynolds, 2015; Thompson et al., 2020). Nevertheless, some authors have proposed that artificial materials may be favoured over natural materials in certain contexts. As different types of artificial materials contain very specific properties, these could potentially benefit nests of different species, specifically: i) durability and malleability - for example, the use of plastic for strengthening the nest structure was shown to play an important role in protecting eggs and nestlings of the Great grey shrike (*Lanius excubitor*) against harsh weather conditions in early spring (Antczak et al., 2010); ii) chemical components - discarded cigarette butts retain substantial amounts of nicotine and other compounds, which may act as ectoparasite repellents (Suárez-Rodríguez et al., 2013). These are actively selected by the House finch (*Haemorhous mexicanus*) (Suárez-Rodríguez and Macías Garcia, 2017) and were seen to improve breeding success, despite the potential for long-term toxic damage (Suárez-Rodríguez and Macías Garcia, 2014); iii) visibility/mate attraction - in Satin bowerbirds (*Ptilonorhynchus violaceu*s), bower decoration with similarly coloured bottle tops and straws was shown to be a decisive factor in mate choice (Borgia, 1985). Although these structures are not nests, Black kites (*Milvus migrans*) do use plastic in the nest structure to likely signal the quality of their nests (Sergio et al., 2011); iv) availability - the wider availability of artificial materials in the nesting area might reduce search costs for nest materials and increase the speed of nest building (Antczak et al., 2010).

Artificial materials can enter coastal wetlands through direct input from surrounding urban settlements or via influx from waves, tides and rivers that collect such materials along their course (Geyer et al., 2017; Koehler et al., 2015; Lebreton et al., 2017). The Camargue, situated along the Mediterranean Sea in Southern France, is a semi-natural region of 180,000 ha making it the largest wetland in France (Galewski and Devictor, 2016; Roche et al., 2009). It consists of a mosaic of different habitats, with a complex and diverse land use, with some areas being designated as nature reserves while others serve agriculture, fishing, hunting, industry and tourism purposes (Blondel et al., 2013). Additionally, it is an important nesting site for several migratory waterbird species of high conservation value (Fraixedas et al., 2019), thus providing an opportunity to assess the impact of anthropogenic pressures on the presence and type of artificial materials in waterbird nests. The Eurasian spoonbill (*Platalea leucorodia*, hereafter spoonbill) is a waterbird species that regularly breeds in Camargue, where it forms large colonies (Champagnon and Kralj, 2023). Furthermore, its relatively long breeding season (i.e., from February to early August) and accessible colonies make it an ideal candidate to explore the occurrence and possible function of artificial materials in waterbird nests. A total of four different islets in Camargue were sampled and monitored to: i) determine the presence and type of artificial materials in spoonbill nests; ii) explore the use of artificial materials as a substitute to natural materials and how this varies in relation to season, breeding phase, age of breeders, and varying distance to main human settlements; and iii) assess the potential impact of artificial materials on hatching success. We predict that nests closer to settlements will have a higher abundance of artificial materials. Furthermore, we predict that due to the likely decrease in the availability and quality of natural nesting materials (e.g., due to the flowering period and vegetation dryness), the number of artificial materials in nests will increase throughout the season. During the incubation period, we predict that there will be a higher amount of lining materials (both artificial and natural), which are likely to improve nest (and thus egg) temperature regulation and potentially increase the hatching success.

Material and Methods

Study population and site

The Eurasian spoonbill is a colonial waterbird that breeds in wetland areas, either on the ground, on islands or dikes, in reed beds, or in trees, with nearby access to shallow open water or salt ponds (Hancock et al., 2010; Svensson et al., 2023). This species constructs its nest using branches and stems, lining it with grass and leaves (Isenmann et al., 2010; Matheu et al., 2020). In Camargue, this species breeds on the ground in small islets with abundant shrub and herb vegetation (Kayser et al., 2008). As with other bird species (Peralta-Sanchez et al., 2010; Wimberger, 1984), spoonbills tend to replenish their nests with new material throughout the season, particularly during the incubation period.

During the breeding seasons of 2021 and 2022, we conducted fieldwork at nine different colonies across four different islets of Camargue, with distances ranging from 2 to 29 km between each islet. Seven of the nine colonies were situated on the islets Banaston and Besson in the Sensitive Natural Area of the "*Etang des Impériaux*" (N43°28, E4°28, Fig. 1), close to Saintes-Maries-de-la-Mer, a small touristic coastal town of more than 2000 inhabitants, which is highly visited during spring and summer months (Badone 2008). The two remaining colonies were in Galère and Vaisseau, which are located within a privately managed area of operational saltworks (N43°22, E4°39, Fig. 1), at a greater distance from Salin-de-Giraud, another urban settlement of approximately 2000 inhabitants. The colonies on the saltwork islets were considerably smaller (fewer nests) than those in *Impériaux* (Appendix: Table A4.1). Fishing, hunting, and tourist activities may result in the introduction of artificial materials into the environment in both areas.

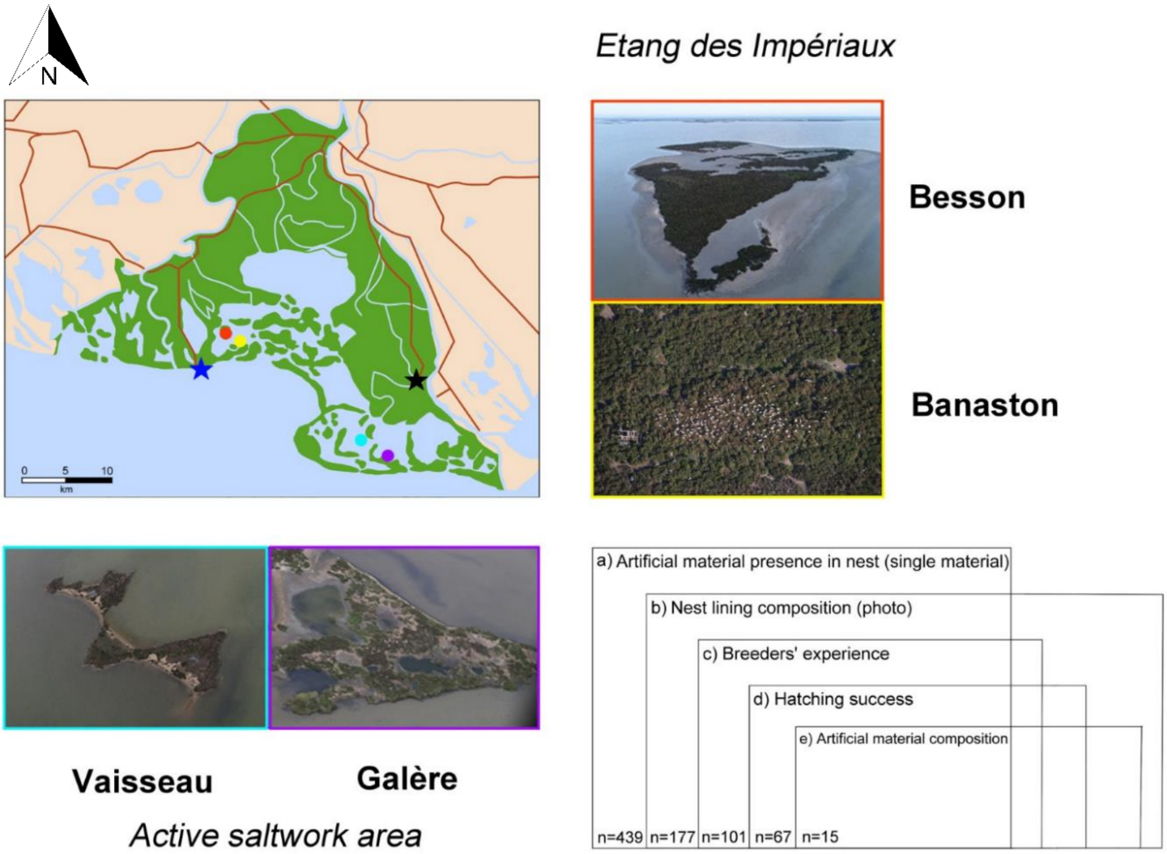

Fig. 1 – Map of Camargue area in green and location of the four different islets where spoonbill nests were sampled. At *Etang des Impériaux*: Islet of Besson (in red colour; ©Antoine Arnaud / Tour du Valat) and Islet of Banaston (in yellow colour; ©Yves Kayser / Tour du Valat). In the saltworks area: Islet of Galère (in purple colour; ©Yves Kayser / Tour du Valat) and Islet of Vaisseau (in blue colour; ©Yves Kayser / Tour du Valat). Rectangular schematic inset represents the different surveys conducted in this study and total number of nests sampled is described per survey. Blue star – Saintes-Maries-de-la-Mer; Black star – Salin-de-Giraud. Rectangles that are not contained within the taller ones include nests that

were not considered in the other surveys (e.g., all nests in e) were also surveyed for b), but only some nests of e) were also surveyed for d) and c)).

These islets are in close proximity to, or covered by, a vast area of saltmarshes which encompass a total area of 10,000 ha in Camargue (Blondel et al., 2013; Marnotte and Carrara, 2006; Médail, 2018). The main vegetation types identified in the monitored nests were consistent with the dominant perennial plant species present in the area: *Halimione portulacoides* (hereafter *Halimione*); *Sarcocornia fruticose* (hereafter *Sarcocornia*); and *Suaeda vera* (hereafter *Suaeda*). However, a comprehensive identification of all the vegetal material was not carried out.

Since 2008, the population of spoonbills in Camargue has been subject to a long-term monitoring programme by the Tour du Valat (Blanchon et al., 2010). This programme has enabled the identification of previously marked individuals (i.e., marked as chicks with a PVC ring), thereby allowing for the determination of their age.

Artificial material presence in nest (single material)

During early egg incubation (i.e., approximately two weeks after egg laying to limit disturbance), 439 nests distributed across seven out of the nine monitored colonies (Appendix: Table A4.1) were visually examined to determine the presence of at least one artificial material. Spoonbills can display highly asynchronous breeding and there may be months between earliest and latest laying dates in the same breeding site (Aguilera, 1990). In Camargue, the breeding season is quite extended and characterized for having several breeding peaks (within the same islet or in other islets), allowing to separate the different peaks spatially and temporarily into distinctive cohorts (henceforward, colonies). Therefore, the seven colonies monitored for this assessment were surveyed at different times during the season. Only a subset of nests from each colony was considered (for further details regarding colony size, type of survey and survey period, refer to Appendix: Table A4.1). To avoid disturbance at the breeding site, this survey was conducted as swiftly as possible and only once during the initial incubation period of each colony.

Nest lining composition (photo)

To assess the type of materials (both artificial and natural) used in nest lining in different colonies throughout the season, we randomly selected nests and monitored them until the respective chicks fledged. We followed a methodology adapted from the study of Ryan (2020) on the presence of plastics in Brown noddy nests. Number of nests monitored since incubation at each colony and number of photos taken per nest varied according to nest failure (mainly due to predation), nests not having a subsequent visit, limited time at the colony, and colony size. To field test the protocol and due to other surveys being conducted at the same time, the first colony surveyed (Besson 2021) had considerably more nests sampled (n_{Nests} = 71) compared to other colonies. On each visit, nests were vertically photographed twice (two replicates) at a height of approximately one metre above the nest, resulting in a total of 870 photos from 177 different nests (Banaston: n_{Nests} = 54, n_{Photos} = 360; Besson: n_{Nests} = 99, n_{Photos} = 382; Galère: n_{Nests} = 14, n_{Photos} = 54; Vaisseau: n_{Nests} = 10, n_{Photos} = 74), which were individually marked with two small flags. The nests monitored in this survey were not necessarily included in the previous "*Artificial materials visual presence (single material)*" survey. Subsequently, each photo was analysed using the point-count CPCe 4.1 software (Coral Point Count with Excel extensions; Kohler and Gill, 2006), which randomly generates sample points within the limitation of the nest lining defined by the user. This sampling method developed by Dumas et al. (2009) and adapted by Thompson et al. (2020), involves the delineation of a square border along the outer edge of the nest photo, incorporating the nest cup and a part of the outer edge. Thus ensuring, an accurate representation of the lining. The space within the created border was converted to a 3 x 3 squares grid, and six points were generated in each grid square, resulting in 54 random points per photo. We performed an exploratory analysis to determine the appropriate number of random points required to accurately reflect the proportion of artificial and natural materials in the nest lining. In short, 15 photos were randomly selected, and total point sample sizes of 27, 54, and 72, were randomly generated on the selected photos and the material under these points classified. The classification was based on colour, shape, and consistency, with materials divided into two major categories (Galgani et al., 2013; Provencher et al., 2017): natural materials (feathers, *Sarcocornia*, *Halimione*, *Suaeda*, and other plant material) and artificial materials (marking flags, papers, user plastics, ropes or strings, and others). Based on this preliminary analysis, 54 points were determined to be a reasonable compromise between processing time and accurate representation of the materials present in the nest lining. When increased to 72 points, the proportion of artificial materials in the nest lining did not change substantially. Points corresponding to other materials (chicks, eggs, nest identification flags, and unknown elements) were subtracted from the total, as these are not lining materials and could skew the surface density estimate of all other materials of interest. For each photo, the percentage of artificial and natural materials of each type was calculated. The frequency of occurrence (FO) of each material across both nest replicas was then averaged and each unique nest/visit was assigned a single mean value of FO for each type of material. This was done to avoid replication, account for variation across both replicates, and obtain a more reliable representation of the nest lining (Thompson et al., 2020).

Contrary to the *Sarcocornia* and *Suaeda* plant, which possess small leaves and are likely used as structural components of the nest due to their elongated shape, *Halimione* contains lanceolate or linear-lanceolate leaves (Aellen, 1938; Lamare and Pavon, 2021; Marnotte and Carrara, 2006; Thomas et al., 2018) that are likely used as lining material. In fact, *Halimione* fragments appear to be placed at the centre of the nest during the incubation period (Appendix: Fig. A4.1), suggesting a thermoregulation role within the nest. Therefore, and due to scarcity of the remaining vegetal materials in the nest lining, *Halimione* was identified as the main natural lining material.

Artificial material composition

To quantify the frequency of occurrence (FO) and the type of artificial materials composing the nest structure, 15 nests (out of 177) were randomly selected from the islets of *Impériaux* to be weighed and decomposed (Appendix: Table A4.2). To avoid any disturbance to the colonies, this survey was carried out once juveniles had left the islets and no active nests were present. The nests were collected, placed in a bag, and weighed using a dynamometer (±25 g). All the artificial materials were then separated from the natural ones (e.g., branches, leaves, and feathers) *in situ* and collected for examination at the laboratory. In the laboratory, the total mass of the artificial materials for each nest was measured (±1 g) and each material was characterized and classified based on Galgani et al. (2013) and Provencher et al. (2017) classifications, taking into account the colour, type of material, and shape of the material ($n_{Materials} = 423$).

Breeders' experience

Since 2008, more than 3000 spoonbill chicks have been ringed with an engraved PVC ring allowing us to individually identify marked birds and to discern their age. Camera traps which took photos every ten minutes, were deployed in several nests, and regularly rotated to associate marked breeders with their nests. In total we were able to identify 121 marked breeders associated with 101 (out of 177) photographed nests. Some marked birds were associated with multiple nests ($n_{Ind} = 13$), and in 34 nests both breeders were marked.

Hatching success

To test whether the presence of artificial materials in the nest was correlated with hatching success, the number of eggs that hatched successfully or not was recorded for each nest. Due to the disappearance of nest identification flags, predation by Eurasian wild boar (*Sus scrofa*) or too long period between visits (i.e., when the number of eggs and chicks in the nest was less than the number of eggs counted during the previous visit, which prevented us from distinguishing between the disappearance of eggs and the death of successfully hatched chicks), hatching success could not be determined for 114 of the 177 nests photographed. These were therefore discarded, leaving a total of 63 nests for this analysis.

Statistical analysis

We used generalized linear mixed-effects model (*GLMM*; package*: lme4*, Bates et al., 2015) with a binomial error structure and a logit link function, in an information-theoretic model selection framework (Burnham and Anderson, 2003) to determine the relationship between nest lining and the variables of interest: spatial (site); temporal (breeder age, nest development phase, season, and year). Two different response variables were considered: i) artificial materials, how many points in each photo were classified as artificial materials and how many were not; ii) *Halimione*, how many points in each photo were classified as *Halimione* and how many were not.

To explore the usage of artificial materials as a substitute to natural materials, seasonality and spatial distribution were considered. Despite the dominant perennial plant species of the area being available all year round (*pers. obs.*; Aellen, 1938; Marnotte and Carrara, 2006), we considered seasonal variability because of the dryness of the area, which could affect the quality of the vegetation (e.g., thermoregulation potential or colour, spoonbills appear to collect mainly green vegetation). Furthermore, due to the flourishing of *Halimione*, from June to October (Aellen, 1938; Marnotte and Carrara, 2006), the detectability (i.e., during our photo assessment, no *Halimione* flowers were detected) and quality of this plant could also change. Thus, to test for a seasonal effect due to a possible diminishing attractiveness of *Halimione* and an increase in available artificial debris due to the holiday season, Julian date was scaled and considered as a continuous fixed effect (*Day* – Julian day). Due to the proximity of some islets to highly touristic areas (Banaston and Besson) and the potential differences in material availability in the immediate surrounding environment, *Site w*as considered as a four-level fixed effect (Banaston, Besson, Galére and Vaisseau).

To test whether artificial materials and *Halimione* e could have a role in the thermoregulation of the nest, we considered the development phase of the nest (*Phase*) as a fixed effect of two levels (egg versus chick, when at least one egg hatched), according to the state of the nest at the time of monitoring. Finally, *Year* was considered as a fixed effect of two levels (2021 and 2022), due to possible differences in abiotic conditions and materials availability between seasons. Nest identity (*Nest*) was included as a random term to account for the same nest being sampled at several moments throughout the season. Thus, we obtained the following equation as the initial model:

$$Y_i \sim B(n_i, \pi_i)$$

$$logit(\pi_i) \; = \; Day_i + Site_i + Phase_i + Year_i + Nest_i$$

$$Nest_i \sim N(0, {\sigma_{Nest}}^2)$$

(equation $_{1:}$ artificial material; equation $_{2:}$ *Halimione*)

Where Y_i is the number of samples with artificial materials in nest *i*, n_i is the total number of samples in nest *i*, and is the probability of artificial lining within nest *i*. While in equation $_2$, Y_i is the number of samples with *Halimione* vegetation in nest *i*, n_i is the total number of samples in nest *i*, and is the probability of *Halimione* lining within nest *i*.

The different models developed were ranked and selected according to the Akaike´s Information Criterion adjusted for small sample size (*AICc*) (Anderson and Burnham, 2002). When there were multiple models within two AICc points of the top-ranking model, the model with the fewest parameters was selected (i.e., the most parsimonious model, Anderson and Burnham 2002). Once the most parsimonious model was selected, we built a forest plot to represent the odds ratio that each point on the photo corresponds to artificial materials (or *Halimione*) in response to the different variables. Using the *emmeans* package (Lenth et al., 2024), subsequent pairwise Tukey HSD post-hoc test comparisons were conducted to the most parsimonious model to explore differences between the marginal means of each group. A Sidak correction was applied, which adjusts for the family-wise error rate across all tests and provides a more conservative control for Type I errors (Sidak, 1967).

To test if bird experience affects the type of material lining the nest, age (*Age,* numerical variable) was considered as a continuous variable according to the breeder's age. To account for the fact that multiple observations originate from the same nest or individual, we considered including *Nest* and *Breeder* as random intercepts. However, the inclusion of *Breeder* as a random effect led to singular fit, which indicates an over fitted model, likely due to a small number of individuals with multiple nests ($n_{Breeder} = 13$), and thus *Breeder* was removed. The linear mixed model containing *Age* as a fixed effect (equation $_3$) was then compared to a null model through an analyse of variance (ANOVA) test.

$$Y_i \sim B(n_i, \pi_i)$$

$$logit(\pi_i) \;=\; Age_i + Nest_i$$

$$Nest_i \sim N(0, {\sigma_{Nest}}^2)$$

(equation $_{3:}$ artificial material; equation $_{4:}$ *Halimione*)

Where Y_i is the number of samples with artificial materials in nest *i*, n_i is the total number of samples in nest *i*, and is the probability of artificial lining within nest *i*. While for equation $_4$, Y_i is the number of samples with *Halimione* vegetation in nest *i*, n_i is the total number of samples in nest *i*, and is the probability of *Halimione* lining within nest *i*.

To test the potential impact of nest artificial materials and *Halimione* FO on hatching success, further models were tested. In equation $_5$, a binomial variable of hatching success was considered as the response variable and an interaction of the FO of both artificial materials and *Halimione* in the nest lining as the fixed effect. The interaction was included to see if the different materials impacted the nests differently. The same process as for the previous equations was carried out.

$$Y_i \sim B(n_i, \pi_i)$$

$$logit(\pi_i) \; = \; Artificial_i \times Halimione_i + Nest_i$$

$$Nest_i \sim \; N(0, {\sigma_{Nest}}^2)$$

(equation $_{5:}$ hatching success)

Where Y_i is the number of samples with hatched eggs (hatching success) in nest *i*, n_i is the total number of samples in nest *i*, and is the probability of hatching within the nest *i*. In a preliminary analysis, the two variables showed limited collinearity (433) = -0.23, $p < 0.001$, which allowed this equation to be tested.

All analyses were carried out in the software R version 4.2.1 (R Core Team, 2022) and plots were generated using the packages *ggplot2* (Wickham, 2016) and *sjPlot* (Lüdecke et al., 2023). Our linear mixed models were estimated using the ML and Nelder-Mead optimisers via the *glmer* function in the in "*lm4*" package (Bates et al., 2015).

Results

Artificial material presence, characterization, and nest composition

Visual inspection of nests at the field sites revealed the presence of artificial materials in all colonies surveyed. On average 41% (±19% SD, range 17-69%) of the monitored nests (n_{Nests} = 439) contained at least one artificial material (Appendix: Fig. A4.2). While the point-count assessment of the photos (n_{Nests} = 177) revealed that 78% of the nests had some degree of artificial lining at some point during their use.

When considering the 15 decomposed nests, the total mass proportion of artificial materials varied between 0.1% and 2.8% (Appendix: Table A4.2), representing a minor proportion of the nest total mass (FO $_{Mean\ nest\ mass}$: 1.4 ± 0.87% SD; n_{Nests} = 15). The decomposed nests were mainly composed of dried vegetation. A total of 423 fragments of artificial materials were found (Appendix: Fig. A4.3 and A4.4). Most of these materials were plastics (FO $_{Mean\ plastic}$: = 56 ± 18% SD, range 20-88%, $n_{Materials}$ = 259) and paper (FO $_{Mean\ paper}$ = 35 ± 19% SD, range 0-67%; $n_{Materials}$ = 121). There was a higher occurrence of materials with either a transparent colour (FO $_{Mean\ transparent}$ = 22 ± 18% SD, range 0-50%; $n_{Materials}$ = 123) or a light-coloured shade (FO $_{Mean\ white}$ = 33 ± 28% SD, range 0-100%, $n_{Materials}$ = 111; cream: FO $_{Mean\ cream}$: 17 ± 26% SD, range 0-75%, $n_{Materials}$ = 51).

Nest lining composition

The nest lining was found to contain an average of 6% (±8% SD, range 0-48%) of artificial materials and 26% (±21% SD, range 0-82%) of *Halimione*, based on the photos taken. The FO of *Halimione* on the nest lining decreases after around 21 days of incubation, while the FO of artificial materials remains stable (Fig. 2).

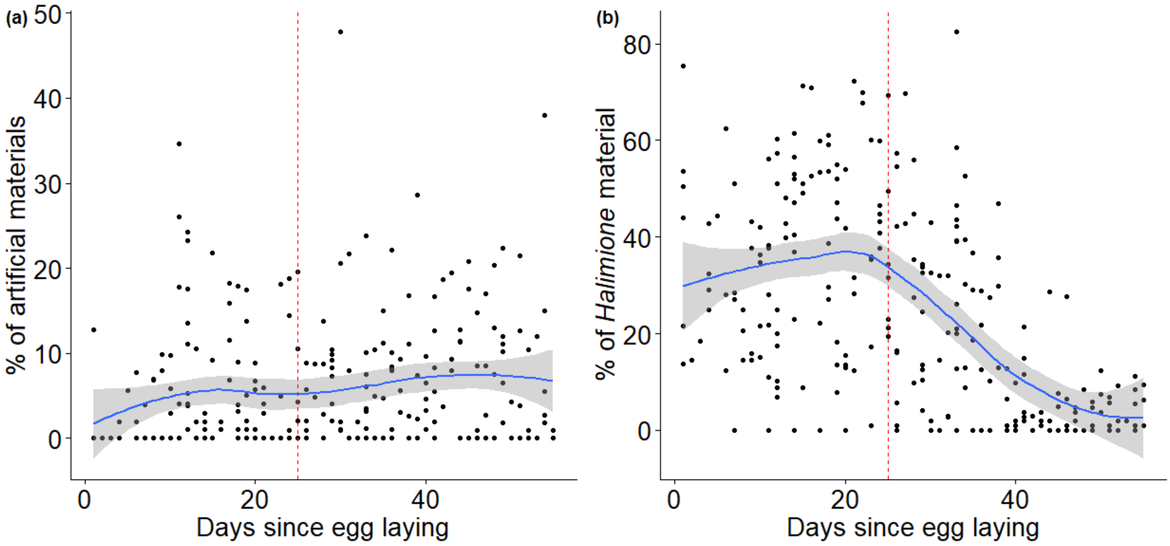

Fig. 2 – (a) Artificial materials FO in the nest lining on relation to the nest development phase with 95% confidence intervals (n_{Photos} = 259; n_{Nests} = 78). (b) *Halimione* FO on the nest lining in relation to the *Day* of the nest with 95% confidence intervals (n_{Photos} = 259; n_{Nests} = 78). The red dotted line indicates 25 days of incubation, the day when usually spoonbills egg hatch. Shaded-grey area represents a confidence interval of 95%.

Despite the inclusion of the variables *Year* and *Nest* development phase (*Phase*) in two of the most competitive models explaining the presence of artificial materials (equation $_1$), these variables were not retained in the most parsimonious model. Nevertheless, this model included a seasonal (*Day*) effect (Model 2, Appendix: Table A4.3), meaning that the odds of encountering artificial materials lining the nest increased as the season progressed (*Beta* = 0.27, 95% CI [0.16, 0.37], $p < 0.001$; Fig. 3).

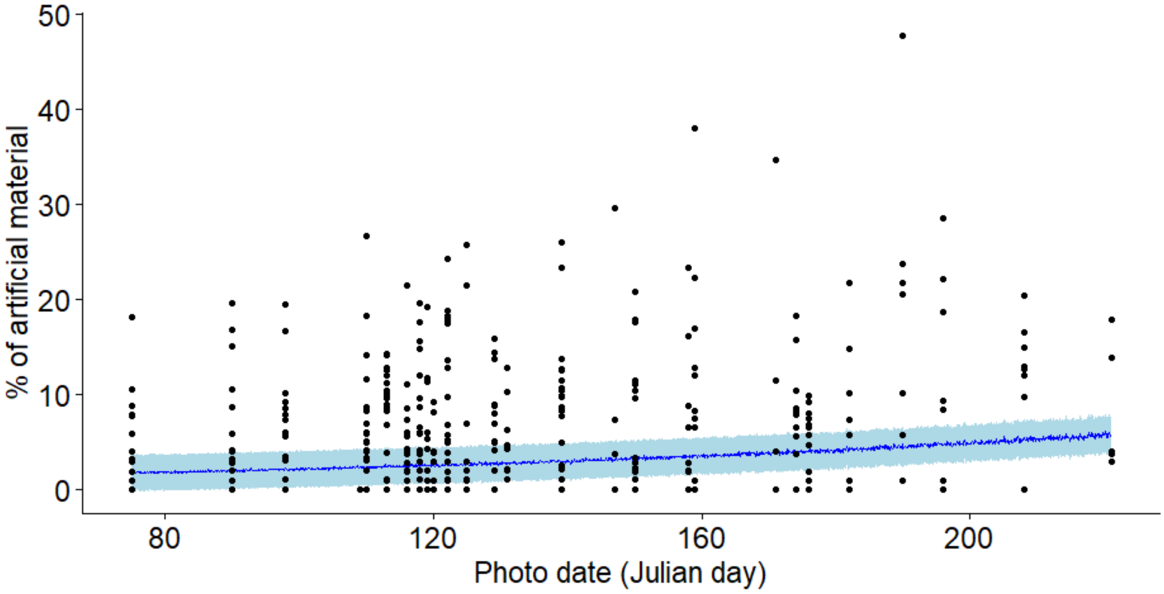

Fig. 3 – Predicted variation in artificial material lining over the season according to the most parsimonious model (n_{Photos} = 435; n_{Nests} = 177; Appendix: Table A4.3, Model 2). Black dots indicate the actual proportion of artificial material and the shaded-blue area a standard error of ±1.8 %.

When considering *Halimione* lining as the response (equation 2), the model containing all variables was the most parsimonious model ($df = 8$, $AIC_c = 5106.7$, *weight* =1; Appendix: Table A4.4). Contrary to the artificial materials, the odds of having *Halimione* in the nest lining decreases throughout the season (Fig. 4).

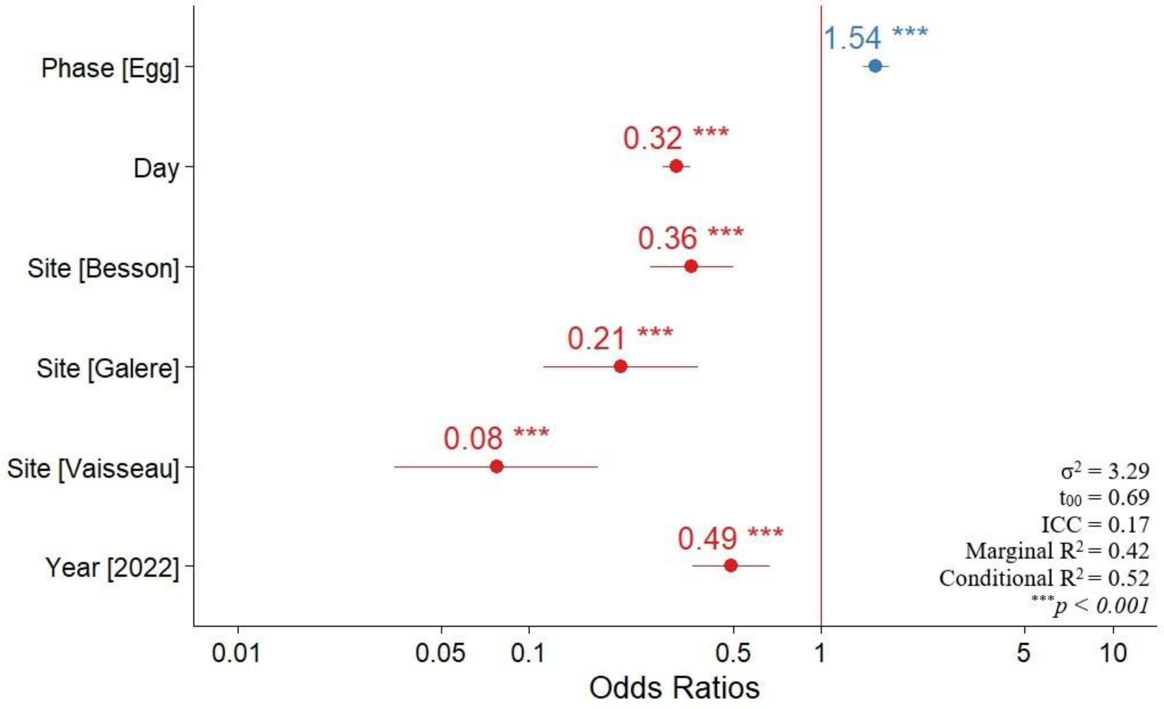

Fig. 4 – Odds ratios of a lining material being *Halimione*: as the season progresses (Day); between nest development phase (chick – Reference and egg); site (Banaston – Reference, Besson, Galère and Vaisseau); and year (2021 – Reference and 2022). Red colour represents lower odds of a point being *Halimione* when compared to the reference level, while blue colour represents higher odds. The "neutral" line (red vertical line) indicates no effect when intercepted. Horizontal lines indicate 95% confidence intervals. For details check Appendix: Table A4.5.

Abbreviations: σ^2 – Population variance; $^{\tau}00$ – Variance between nests; ICC – Intraclass correlation coefficient; ^{n} Nests –Number of nests; R^2 – r-squared.

There is also a spatial difference in nest lining, with Banaston being the site with the highest odds of having *Halimione* when compared to the other islets (Fig. 5). As for the nest development phase, during the egg phase there is higher probability of having *Halimione* lining than during chick phase.

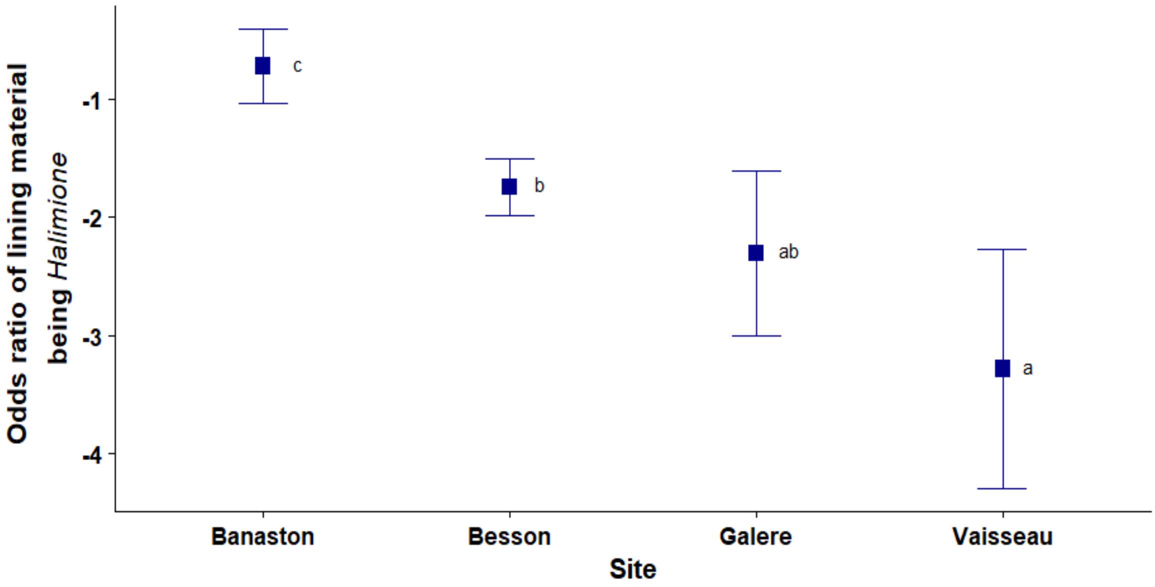

Fig. 5 – Post-hoc comparisons of estimated marginal mean of percentage of *Halimione* lining the nests between sites. Vertical lines indicate 95% confidence, and a Sidak correction was applied. If two or more means share the same grouping symbol, then these are not significantly different (n_{Photos} = 435; n_{Nests} = 177; Appendix: Table A4.6, Model 1).

Breeder's age was not found to be significantly associated with the proportion of artificial materials or *Halimione* present in the nest lining. A pairwise comparison between a null model and a model containing *Age* (equation $_3$), showed no significant relationship between breeder´s age and amount of artificial material lining the nests [F (1, $n_{Breeder*Nest}$= 357) = 0.002, p = 0.967]. Likewise, when considering haliomione lining, no significant relation was detected [F (1, $n_{Breeder*Nest}$ = 357) = 0.076, p = 0.078].

Hatching success

The proportion of artificial materials or *Halimione* in the nest lining was not correlated with hatching success (equation $_5$), with the null model being the most parsimonious (Appendix: Table A4.6, Model 2).

In Table 1 a summary of all the significant variables present in the different parsimonious models are highlighted per equation.

Table 1. Summary of significant fixed effects ($p < 0.05$; highlighted in "X" blue bold), in different fitted GLMMs. If no variable was highlighted, the null model was the most parsimonious model. Variables identified with an "0" were tested but retained in the final model. Variables identified with an "-" were not included. For details in model selection consult Appendix: Table A4.3, A4.4, A4.6, A4.7, and A4.8.

Equation	**Response (probability of)**	***Age***	***Artificial material***	***Day***	***Halimione***	***Phase***	***Site***	***Year***
1	*Artificial lining*	-	-	**X**	-	0	0	0
2	*Halimione lining*	-	-	**X**	-	**X**	**X**	**X**
3	*Artificial lining*	0	-	-	-	-	-	-
4	*Halimione lining*	0	-	-	-	-	-	-
5	*Hatching*	-	0	-	0	-	-	-

Discussion

In our study, 41% of nests contained at least one artificial material. This finding supports our initial prediction of a widespread presence of artificial materials in spoonbill nests. In Camargue, spoonbills appear to prefer plastic materials with a sheet-like shape (61%) and white-transparent colours (68%) over other artificial materials. Our results support the hypothesis that artificial materials are being used as a substitute for natural materials. This is suggested by the increasing use of artificial materials throughout the season, which coincided with a decrease in the proportion of *Halimione* in the nest lining. Surprisingly, there was no significant spatial variation in the proportion of artificial materials in the nest lining between sites. Nevertheless, a significant spatial variation was found when considering *Halimione* lining. Similarly, no differences were found in the proportion of artificial materials in the nest lining between development phases (chick and egg), but a higher amount of *Halimione* was found in the egg phase. Contrary to our predictions and independently of the material considered, breeder experience did not influence nest lining composition. Finally, our findings suggest that nest lining had no significant effect on hatching success, regardless of the material used.

Presence and type of artificial materials

On average, 41% of nests were found to contained at least one artificial material during visual inspection. Nevertheless, detailed examination of photos revealed that 78% of the nests surveyed (139 out of 177) had some degree of artificial material at some point. The frequency of occurrence of artificial materials in the nests of different waterbird species and colonies has been reported to range from 4 to 80% (Battisti, 2020; Hartwig et al., 2007; Tavares et al., 2016; Votier et al., 2011; Witteveen et al., 2017). The considerable variation in percentages is likely due to differences in breeding ecology between monitored species or populations, with a higher occurrence of artificial plastics possibly being associated with nests being reused over the years (Thompson et al., 2020). Generally, spoonbills build a new nest each year (*pers. obs.*) and, like other Pelecaniformes, tend to use materials collected from conspecific nests (Grant et al., 2018; Nelson, 2006).

Recent studies suggest that the use of photos may be an effective intermediate solution to the precision-disturbance trade-off, allowing for a systematic and permanent representation of the nest lining, while considerably reducing disturbance to the colony (Rodríguez et al., 2023; Ryan, 2020). This is supported by our subsample of decomposed nests, which confirmed that artificial materials represent only a small proportion of the total nest mass (mean frequency of proportional mass: 1.4 ± 0.2% SE). Thus, although present in most nests, the mass of artificial material is relatively small. Therefore, it is unlikely that these materials are used as fundamental structural layers of the nest, as they seem to be mainly present in the centre of the nest, incorporated in the nest lining. Additionally, it means that photos of the nest lining are likely to provide a reliable representation of the use of artificial materials by spoonbills, while avoiding disturbance.

Examination of 15 decomposed nests revealed that most of the artificial material incorporated into the nests corresponded to sheet-like plastic of white-transparent colour, which are likely to have originated from human waste. Similar types of material were also found in the nests of other waterbird species, such as White stork (*Ciconia ciconia*, Jagiello et al. 2018), Herring gull (*Larus argentatus*, Thompson et al. 2020) and Kelp gull (*Larus dominicanu*s, Witteveen, Brown, and Ryan 2017). Due to their shape and colour, it is unlikely that the plastics used were mistaken for natural materials such as branches. Furthermore, spoonbills are not known to eat food wrapped in plastic, as some gull species do (Battisti 2020). In the Wadden Sea, the loss of a ship container resulted in the contamination of the spoonbill breeding area with small pieces of plastic. However, no macro plastics (>20–100 mm) were detected in the regurgitates of spoonbills (Foekema et al., 2021). It is therefore unlikely that Camargue spoonbills inadvertently collect sheet-like plastics at a higher rate than other artificial materials.

Role of lining materials

Our results indicate that the proportion of artificial materials in the nest lining increased towards the end of the breeding season, while the proportion of *Halimione* decreased. This suggests a replacement of *Halimione* by artificial materials throughout the season, as was initially hypothesised.

Surprisingly, despite the nests at the *Impériaux* (Besson and Banaston) being closer to the city of Saintes-Maries-de-la-Mer, and presumably having higher availability of artificial materials, they had the highest proportion of *Halimione* lining. Furthermore, the significant difference between the islets of Banaston and Besson, which are only two kilometres apart, suggests that spoonbills collect *Halimione* at the immediate vicinity of the colony (i.e. on the islets). Thus, the striking absence of spatial differences in the proportion of artificial materials in the nest lining, indicates that spoonbills tend to collect artificial materials when building or replenishing their nest, probably away from the breeding islets. This behaviour has previously been documented in Great tits (*Parus major*), which appear to actively seek out artificial materials even when they are uncommon in the area (Hanmer et al., 2017; Surgey et al., 2012). However, the availability of materials in proximity to the breeding sites was not assessed, and thus, an opportunistic source of artificial materials or an unknown reason for a localised absence of *Halimione* cannot be ruled out. For instance, the progressive increase in artificial lining may be connected to an accumulation of waste in addition to the influx of new materials (i.e., brought to the nest by breeders), rather than a decreasing availability of natural materials. Nevertheless, due to the many human activities in Camargue (e.g., agriculture, ecotourism, fishing, and settlements), different types of artificial materials are easily found everywhere. Therefore, given the wide range of activity of spoonbills, which can reach up to 50-60 km from their nesting site (Pigniczki et al., 2016; Tenan et al., 2017), it is unlikely that there is a lack of artificial materials. Furthermore, a recent study of a gull species (Yellow-legged gulls – *Larus michahellis*) with a range similar to that of spoonbills in the Camargue found no significant differences in plastic availability between sites (Almeida et al., 2023), suggesting these materials are equally widespread across the region, being therefore readily available anywhere.

Green vegetation materials are included in the nests of several bird species and are considered to play a role in microclimate regulation (Igic et al., 2009; Wimberger, 1984). When plotting the estimated nest development phase (in days since egg laying started), in relation to the proportion of *Halimione* lining, a clear decrease in *Halimione* was observed at around 21 days. As spoonbills' eggs hatch at around 25-26 days (Lok et al., 2014), this suggests a potential role of *Halimione* leaves in nest thermoregulation during the egg phase (for nests initiated at any time during the breeding season). Indeed, there is higher odds of encountering *Halimione* lining during egg phase than during chick phase (for nests initiated at any time during the breeding season). However, this was not the case for sheet-like plastic materials, despite these are also having thermoregulatory properties (Thompson et al., 2020). This could be explained by a fundamental difference between artificial and natural materials. After incubation, it appears that breeders stop replenishing the nest with new material, possibly due to different microclimate requirements (i.e., within the nest) between egg and chick phases, and to reduce their energy costs (Ar and Sidis, 2002; Dawson et al., 2011; Lambrechts et al., 2012; Mainwaring et al., 2014; McGowan et al., 2004; Webb, 1987). Consequently, it is possible that vegetation materials present in the nest will rapidly dry out, whereas artificial materials may remain intact in the nest until removed by wind or other birds (Marchant et al., 1990; Thompson et al., 2020). In addition, unlike other species such as the Herring gull, sheet-like plastics were mainly found in the centre of nests, rather than at the periphery, suggesting that this type of material may be more frequently used during the incubation phase. Therefore, it is possible that artificial materials may have a role in regulating nest temperature, despite the lack of significant differences in artificial lining between nest development phases.

The composition of nest lining does not seem to be influenced by breeder experience. However, male spoonbill are thought to be primarily responsible for nest building (Aguilera, 1990). In this study we were not able to sex the breeders. Further data collection, considering the age of male through genetic sampling at the time of ringing may in the future be used to further test this. Alternatively, as no effects on hatching success were found, there is no reinforcement for experienced birds to add more artificial materials to their nests as they age, thus explaining the pattern observed here.

Potential impact of lining materials

It is worth nothing that in order to test the potential role of lining material in nest thermoregulation, we used seven Onset Computer HOBOware (Onset Corporation, Borne, MA) thermal loggers to measure nest temperature and humidity. Loggers were placed within the nest and near its surface. However, after the loggers were deployed, spoonbills continued to replenish their nests, sometimes significantly increasing the size of the nest, and moving the eggs away from the loggers. Consequently, temperature recorded by loggers did not represent the temperature experienced by the eggs, and no data analysis was carried out. Therefore, we recommend the use of temperature loggers embedded in fake eggs (e.g., Hope et al. 2018) to further investigate the relationship between lining material and nest temperature.

In this study we did not test the impact of artificial materials on the presence of parasites and pathogens, due to the biocidal effects of volatile secondary compounds such as hydrocarbons (e.g., monoterpenes and isoprene - Clark 1991; Brouwer and Komdeur 2004; Dubiec, Góźdź, and Mazgajski 2013). Given the high incidence of small parasites opportunistically noted in Galère, it would be of interest to test the association between lining material used and the presence of parasites in spoonbill nests. Finally, although our study did not show a clear negative impact of the presence of artificial materials on hatching success, there is a possibility that long-term consequences may result from contaminants present in artificial materials (e.g., biphenol A - Zalko et al. 2011; Verlis, Campbell, and Wilson 2014; Provencher et al. 2017). When in contact with bird skin (Provencher et al., 2017; Verlis et al., 2014), some contaminants could potentially interfere with individuals' physiology, causing negative impacts on behaviour, reproduction and survival (Herzke et al., 2016; Lavers and Bond, 2016; O'Hanlon et al., 2017; Teuten et al., 2009). Thus, the collection of complementary data could potentially shed light on the impact of lining materials on chick growth and survival. Nevertheless, our results showed that this effect is probably not significant or too small to be detected, at least in Camargue, where breeding success is generally high (Champagnon et al., 2019) and mainly impacted by predation events such as those caused by wild boars (Champagnon et al., 2021).

It is also noteworthy that, despite the high incidence of artificial materials in spoonbill nests, there are no documented cases of mortality due to entanglement or suffocation of chicks or adults by nest material in Camargue. However, to further assess the costs and benefits of the use of artificial materials, an experimental approach is recommended (e.g., to control the availability of materials, or to assess the impact of different materials in nest temperature). Despite the presence of plastic in nests being potentially a useful indicator of plastic pollution (Bond et al., 2012; Jagiello et al., 2019; Kershaw et al., 2019; O'Hanlon et al., 2019; Tavares et al., 2016), the lack of spatial variation in the amount of artificial materials used, combined with the fact that spoonbills seem to actively collect certain types of plastic, suggests that other species may be better sentinels of plastic pollution in wetland nesting sites. Nevertheless, the abundance of artificial materials found in a protected area such as Camargue reinforces the need for long-term monitoring programmes. These programmes allow spatial and temporal comparisons that are essential to understand how animals respond to adverse and increasing anthropogenic influences (e.g., recognition and use of artificial materials as beneficial nesting material) that show no signs of slowing down. Such insights are fundamental for establishing a baseline to mitigate the negative impacts of such materials in the environment (Avery-Gomm et al., 2018; Jagiello et al., 2019; Sergio et al., 2011).

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Ethics approval

All fieldwork procedures were compliant with applicable animal welfare regulations by the Centre de Recherches sur la Biologie des Populations d'Oiseaux (Museum National d'Histoire Naturelle, [https://crbpo.mnhn.fr]), programme personnel 580.

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Appendices 4

Table A4.1. Description of the nine colonies surveyed by year, as well as information regarding the total number of nests, total number of surveyed nests and survey period.

Colony	**Year**	**Number of nests (Total)**	**Number of nests surveyed**		**Survey period**
			Presence	**Photos**	
Besson	2021	147	147	71*	20/4 - 5/5
Banaston	2021	46	36	14	23/4 - 27/5
Galère	2021	16	13	14	25/6 - 1/7
Besson_1	2022	236	-	20	16/03 - 26/4
Banaston_1	2022	121	89	20	19/4 - 8/6
Banaston_2	2022	46	P	10	9/5 - 7/6
Besson_2	2022	102	102	8	7/6
Banaston_3	2022	41	-	10	23/6
Vaisseau	2022	14	6	10	9/7 – 9/8

Note: Differences in surveyed period are related to the time when the colony was detected and predation events that made the colony fail. *First colony surveyed, which a larger number of nests were selected to test the protocol and due to other surveys being conducted at the same time as our project.

Table A4.2. Total nest mass, artificial materials mass, and proportion (%) of nest total mass.

Nest	Year	Mass (nest, ±25 g)	Artificial materials mass (total, ±1 g)	Artificial materials (%)
1	2021	3450	58	1.7
2	2021	700	8	1.1
3	2021	3800	68	1.8
4	2021	1000	17	1.7
5	2021	3900	106	2.7
6	2021	900	7	0.8
7	2021	1400	24	1.7
8	2021	1000	6	0.6
9	2021	3300	84	2.5
10	2022	1675	27.8	1.7
11	2022	1300	9	0.7
12	2022	2100	1.4	0.1
13	2022	2200	4.4	0.2
14	2022	1200	9.6	0.8
15	2022	3100	86.7	2.8

Table A4.3. Generalized linear mixed model selections for proportion of artificial materials in the nest lining for combined 2021-2022 breeding seasons (n_{Nests} = 177). *Nest* is included as a random variable. Models were ranked according to the Akaike, and the most parsimonious model is indicated in bold.

Number	**Model**	***df***	**AIC$_c$**	**ΔAIC$_c$**	**Akaike weight**
1	*Day + Year*	4	3084.3	0.0	0.4
2	***Day***	**3**	**3084.7**	**0.4**	**0.3**
3	*Day + Phase + Year*	5	3086.0	1.7	0.2
4	*Day + Phase*	4	3086.3	2.0	0.1
5	*Day + Site*	6	3089.3	4.9	0.0
6	*Day + Site + Year*	7	3089.7	5.4	0.0
7	*Day + Phase + Site*	7	3090.8	6.5	0.0
8	*Day + Phase + Site + Year*	8	3091.2	6.9	0.0
9	*Phase + Year*	4	3098.9	14.6	0.0
10	*Phase*	3	3100.6	16.3	0.0
11	*Phase + Site*	6	3102.9	18.6	0.0
12	*Site + Phase + Year*	7	3103.5	19.2	0.0
13	*Year*	3	3104.5	20.2	0.0
14	*Null*	2	3106.8	22.5	0.0
15	*Site*	5	3108.8	24.5	0.0
16	*Site + Year*	6	3108.9	24.6	0.0

Abbreviations: *Day* – day of the season; *Phase* – nest development phase.

Table A4.4. Generalized linear mixed model selections for proportion of *Halimione* in the nest lining for combined 2021-2022 breeding seasons (n_{Nests} = 177). *Nest* is included as a random variable. Models were ranked according to the Akaike, and the most parsimonious model is indicated in bold.

Number	Model	*df*	AIC$_c$	ΔAIC$_c$	Akaike weight
1	***Day + Phase + Site + Year***	**8**	**5106.7**	**0.0**	**1.0**
2	*Day + Phase + Site*	7	5124.2	17.5	0.0
3	*Day + Phase + Year*	5	5169.2	62.4	0.0
4	*Day + Site + Year*	7	5170.5	63.8	0.0
5	*Day + Phase*	4	5172.1	65.3	0.0
6	*Day + Site*	6	5188.7	81.9	0.0
7	*Day + Year*	4	5224.7	118.0	0.0
8	*Day*	3	5226.0	119.3	0.0
9	*Site + Phase + Year*	7	5590.3	483.6	0.0
10	*Phase + Site*	6	5600.2	493.4	0.0
11	*Phase + Year*	4	5738.6	631.8	0.0
12	*Phase*	3	5747.6	640.9	0.0
13	*Site + Year*	6	6815.8	1709.1	0.0
14	*Site*	5	6845.5	1738.8	0.0
15	*Year*	3	6998.0	1891.3	0.0
16	*Null*	2	7012.6	1905.8	0.0

Abbreviations: *Day* – day of the season; *Phase* – nest development phase.

Table A4.5. Odds ratio of a point in the nest corresponding to *Halimione* between egg development phase (chick – Reference and egg), site (Banaston – Reference, Besson, Galère and Vaisseau) and between year (2021 – Reference and 2022).

Predictors	***Odds Ratios***	***Confidence Intervals***	***p***
Day	1.31	1.18 – 1.45	< 0.001
Banaston	*Reference*		
Besson	0.36	0.26 – 0.50	< 0.001
Galère	0.21	0.11 – 0.38	< 0.001
Vaisseau	0.08	0.03 – 0.17	< 0.001
Chick	*Reference*		
Egg	1.54	1.39 – 1.71	< 0.001
2021	*Reference*		
2022	0.49	0.36 – 0.67	< 0.001
Random Effects			
σ^2	3.29		
τ_{00} Nest	0.69		
ICC	0.17		
^{n} Nests	177		
Observations	435		
Marginal R^2 / Conditional R^2	0.417 / 0.518		

Table A4.6. Generalized linear mixed model selections explaining hatching success in response to type of material in the nest lining (artificial or *Halimione*) for combined 2021-2022 breeding seasons ($n_{Nests} = 67$). *Nest* was included as a random variable. Models were ranked according to the Akaike, and the most parsimonious model is indicated in bold.

Number	Model	*df*	AIC$_c$	ΔAIC$_c$	Akaike weight
1	*Halimione*	***3***	284.0	0.0	0.4
2	***Null***	***2***	**284.4**	**0.4**	**0.3**
3	*Halimione + artificial*	*4*	286.0	1.9	0.1
4	*artificial*	*3*	286.5	2.4	0.1
6	*Halimione + artificial*	*5*	288.0	4.0	0.1

Fig. A4.1 – (a) Nest containing a considerable proportion of *Halimione* (© Hugo Ferreira/Tour du Valat). (b) Nest containing a considerable proportion of artificial (© Hugo Ferreira/Tour du Valat).

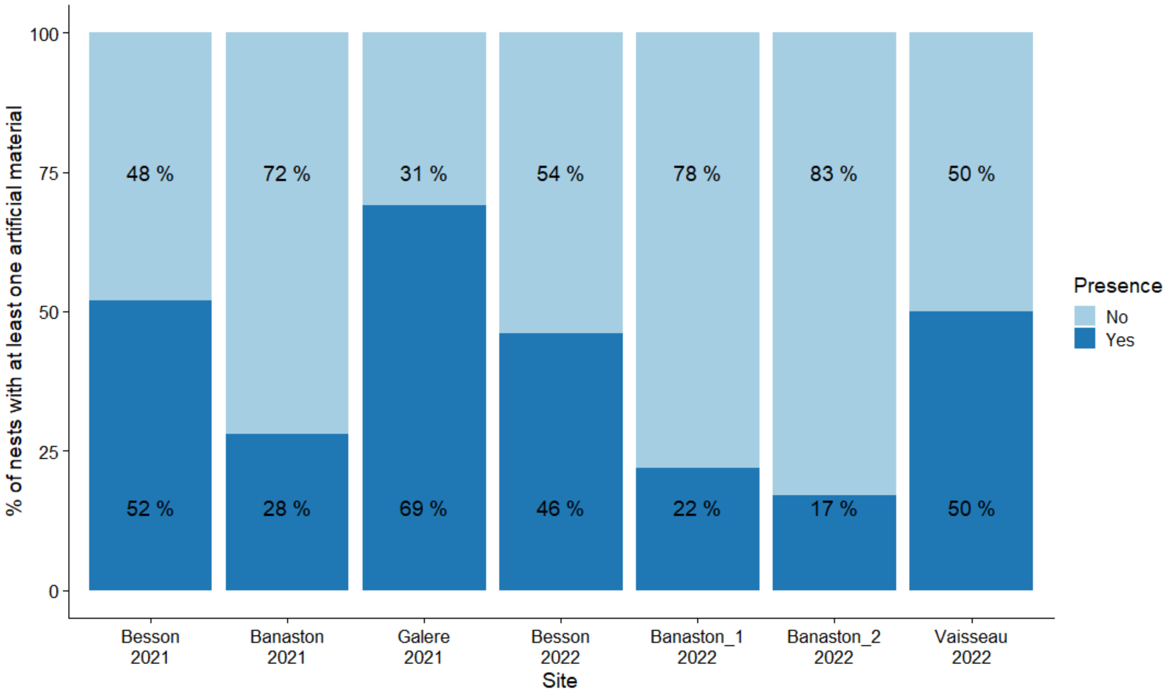

Fig. A4.2 – Variation in proportion of nests containing at least one artificial material per group and year. The total number of nests per category is described at the centre of each column.

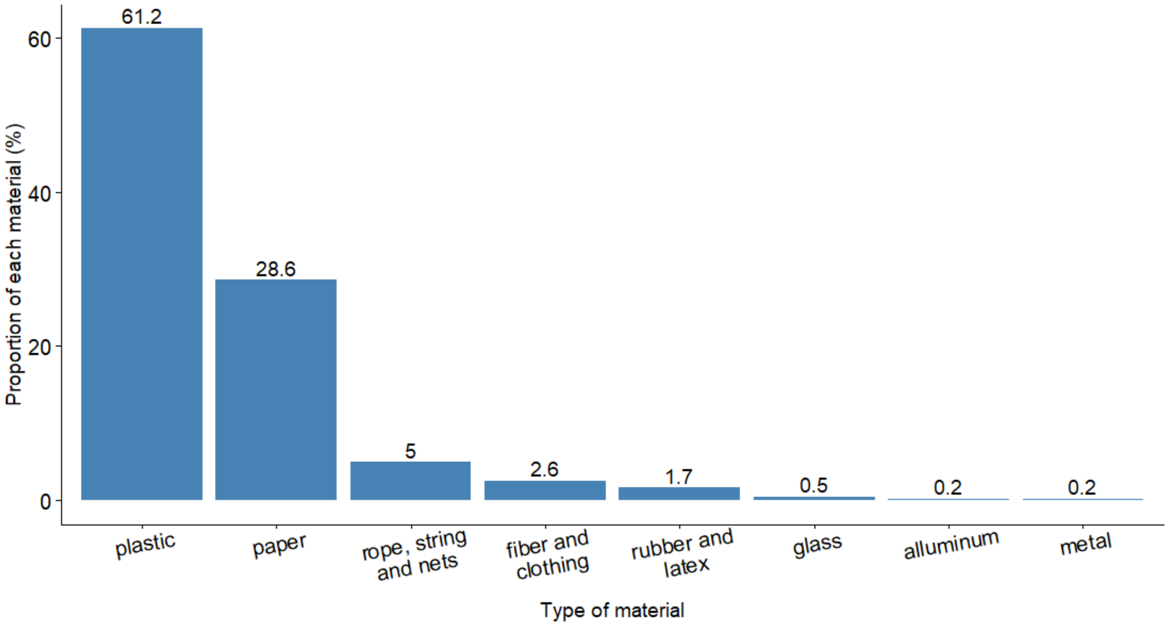

Fig. A4.3 – Variation in relative abundance (% of all artificial materials) of different types of artificial materials found in the decomposed nests (n_{Nests} = 15 nests; $n_{Materials}$ = 423).

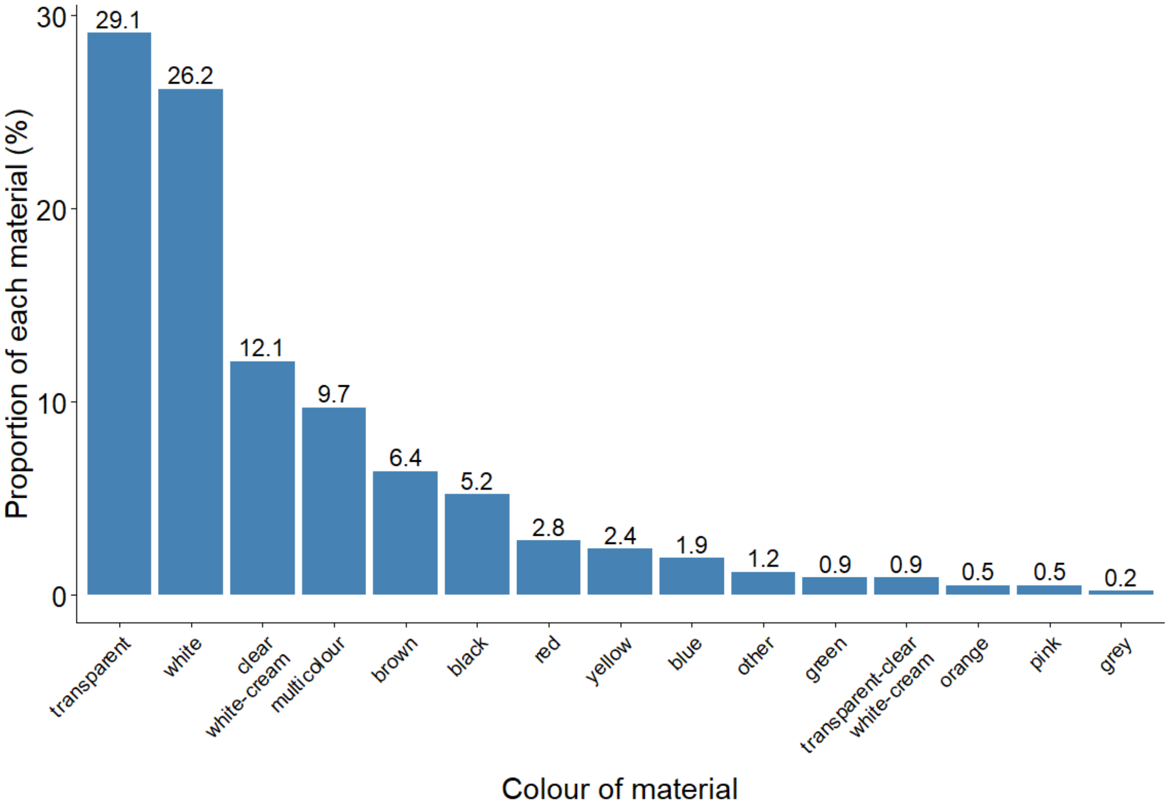

Fig. 4.4 – Variation in relative abundance (% of all artificial materials) of different colours of artificial materials found in the decomposed nests (n_{Nests} = 15 nests; $n_{Materials}$ = 423).

This chapter is under review byLandscape Ecology.

CHAPTER 5

Role of protected areas for a colonial-breeding waterbird in a fragmented landscape throughout its annual cycle

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Vigueirat National Nature Reserve, Camargue, 2018

In this strongly protected area of 1,200 ha, water levels are actively managed to provide optimal conditions for certain waterbird species, considering climatic conditions, the annual cycle, and the biology of the species targeted.

Role of protected areas for a colonial-breeding waterbird in a fragmented landscape throughout its annual cycle

Abstract

Throughout their annual cycle and life stages, animals depend on a variety of habitats to meet their vital needs. However, habitat loss, degradation, and fragmentation, are making it increasingly difficult for mobile species such as birds to find suitable habitats. Wetlands are highly productive systems of great importance to many animals, but their continued degradation threatens their capacity to support different species, including waterbirds. In this context, waterbirds are likely to benefit not only from the creation and management of protected wetlands, but also from the existence of anthropogenic wetlands, managed for economic or recreational activities. Here, we tracked 91 Eurasian spoonbills of different ages through their annual cycle in a highly fragmented landscape in Southern France. In this study, we show that privately managed wetland areas play a complementary role to strongly protected wetland areas: they are likely to provide suitable foraging habitat for spoonbills (and other waterbirds) that may be depressed in strongly protected wetland areas at certain periods of the year. This study illustrates how spoonbill, a moderately specialized species, is benefiting from current global changes due to its ability to use suitable habitats in fragmented landscapes even if artificial. Nevertheless, reliance on privately managed wetland areas may have serious consequences for species that are highly dependent on them, and thus, habitat management promoting natural conditions may be essential to maintain species resilience. It is therefore essential to understand how specific management actions may affect waterbird presence and habitat use, not only to enhance the effectiveness of conservation efforts, but also to promote wetland connectivity and species resilience, particularly in fragmented landscapes.

Keywords/phrases*:* *Platalea leucorodia;* areas of strong protection; hunting pressure; Nature Reserves; water management; tracking data.

Introduction

Animals often rely on different habitats to fulfil their vital needs (e.g., breed, feed, moult, and shelter), however habitat requirements for specific functions are highly variable (i.e., according to species biology) and often change throughout the annual cycle and lifetime (Johst et al., 2001; Ouin et al., 2004; Pope et al., 2000). Due to habitat loss, degradation and fragmentation, the ability of even highly mobile species like birds to find areas with suitable habitats is increasingly hard (Freemark and Merriam, 1986; MEA, 2005; Piersma et al., 2016; Taylor and Stutchbury, 2016). The designation, management, and restoration of protected habitats and areas are therefore considered essential for the sustainability of highly mobile species in these patchy and complex landscapes (Braun et al., 1978; Dobkin et al., 1998; Geldmann et al., 2019, 2013; Leberger et al., 2020; Manning et al., 2011; Murray and Hamilton, 2010; Weller, 1999).

Wetlands are one of the most degraded habitats worldwide, with an estimated loss of 87% since the 1700s, displaying rates that supersede forest loss threefold (Convention on Wetlands et al., 2021). Wetlands are also highly productive systems with great importance for many animals throughout their annual cycle (Corcoran, 2010; Keddy, 2010; Lévêque et al., 2005; MEA, 2005; Tiner, 1989). However, their severe and continuous degradation compromises not only their capacity to host different species (including waterbirds), but also the ecosystem services they provide (Okes et al., 2008; Platteeuw et al., 2010). Surprisingly, despite the negative scenario, several waterbird species in Western Europe have been expanding and recolonizing their historical distribution range in recent decades (e.g., Common crane, *Grus grus* – Guzmán et al., 1998; Glossy ibis, *Plegadis falcinellus* – Santoro et al., 2019; Greater flamingo, *Phoenicopterus roseus* – Johnson and Cézilly, 2009; Dalmatian pelican, *Pelecanus crispus* – Catsadorakis et al., 2015). Some species are known to have benefited from the creation of protected areas in wetlands, such as Whooper swans (*Cygnus cygnus*), which have a higher survival rate inside protected areas than outside (Soriano-Redondo et al., 2023). Similarly, tracking of dabbling ducks in California revealed rapid adjustment to disturbance through increased use of protected areas (McDuie et al., 2021). Yet, some species are likely to benefit from additional actions besides the creation of protected areas, such as strengthened environmental legislation (Rodrigues et al., 2023; Wetlands International, 2016). For instance, in addition to measures to mitigate colony disturbance from anthropogenic influence (e.g., aircrafts) and predators (e.g., Yellow-legged gulls, *Larus michahellis*), breeding flamingos have benefited from several targeted management and conservation actions to counter erosion (i.e., caused by sea level rise) and the lack of suitable nesting islands (Johnson and Cézilly, 2009). Furthermore, besides the different conservation measures, some species may have benefited indirectly from other measures or factors, such as new food sources (e.g., proliferation of the Red-swamp crayfish – *Procambarus clarkii*, Correia, 2001; Poulin et al., 2007; garbage dumps, Plaza and Lambertucci, 2017). Likewise, the existence of anthropogenic wetlands managed for economic or recreational activities (e.g., agriculture and hunting) can provide food for some waterbird species (Alonso et al., 2008; Hamza et al., 2015; Johst et al., 2001; Li et al., 2015). For instance, in regions of intensive rice cultivation, rice fields provide a suitable habitat for waterbirds at different points of their annual cycle (Acosta et al., 1996; Alves et al., 2010; Elphick and Oring, 1998; Fasola, 1996; Hobaugh et al., 1989; Vansteelant, 2023). In the case of hunting areas during non-breeding period, managers artificially control water levels to promote aquatic plant productivity and create ecological niches for waterfowl prey (e.g., seeds, small fish, invertebrates) (Isola et al., 2000; Tamisier et al., 1995). Thus, to further promote wetland birds' recovery and resilience, it is important to gain a detailed understanding of their habitat use in areas that offer multiple wetland habitats under varying management regimes.

While habitat selection and use by highly mobile bird species has been extensively studied (Fuller, 2012), studies were until recently limited by biased observational efforts in space and time (Brown et al., 2013; Graf et al., 2015). The emergence of tracking and other biologging technologies, such as GPS tags (Cagnacci et al., 2010; Wilmers et al., 2015), allows not only the collection of highly detailed information on habitat use, but also for the additional understanding of habitat functional roles, i.e. the main activity carried out in each habitat (e.g., foraging or roosting) (e.g., Ewing et al., 2018; Rodrigues et al., 2023; Wakefield et al., 2009). It is therefore currently possible to identify species needs in terms of specific habitats, understand how areas under different land management regimes or protection levels are used, and use this information to develop and test the efficiency of targeted management objectives (Allen and Singh, 2016; DeFries et al., 2007; He et al., 2019; Kämpfer et al., 2023; McDuie et al., 2021).

The Eurasian spoonbill (*Platalea leucorodia*, hereafter spoonbill) is a long-lived migratory waterbird, distributed from the East-Atlantic Coast to Southeast Asia (Triplet et al., 2008). In Europe, spoonbills have three distinct flyway populations (Champagnon et al., 2019b). Currently, the East Atlantic Flyway population is steadily increasing in several breeding sites, in contrast to the Central European and Southeastern European flyways populations, which are experiencing stable and declining trends, respectively (Champagnon and Kralj, 2023). Spoonbills are dependent on shallow water to feed, where they tactically forage on small fish and invertebrates, sweeping their bills from side to side in the water column (Cramp and Simmons, 1977; Hancock et al., 2010). Since 1998, spoonbills have been breeding in Camargue (Blanchon et al., 2019), with the population increasing to more than 400 pairs by 2021 (Champagnon and Kralj, 2023). Camargue is a wetland of international importance, according to the Ramsar Convention, that benefits from protection measures in its entire geographical area through overlapping international, national and regional protection statuses (Vallecillo et al., 2023), resulting in spatial variation on the level of protection, i.e. moderate or strong (according to international land protection and management categories; see methods). In general, the population of spoonbills in Camargue does not nest in areas that are strongly protected (Chapter 3 and 6). Furthermore, although areas of strong protection tend to be highly undisturbed, they may not hold the highest abundance of food resources in comparison with privately managed agricultural fields and wetlands (Central Valley Joint Venture, 2006), particularly when management in protected areas prioritizes other taxa (e.g., Mediterranean grasslands habitat or Odonata community). Currently, there is a growing number of resident spoonbills that also winter in Camargue, consisting of ca. 250 individuals in recent years (Moussy et al., 2023), which highlights the year-round importance of this wetland for spoonbills. Thus, assessing how spoonbills thrive in this a major wetland with multiple land uses and habitats, provides a unique opportunity to explore and gain a detailed understanding of the functional habitat use across multiple life stages of this waterbird species.

Here we investigated habitat use of spoonbills within an extensive and heterogeneous area and how it varies across the annual cycle and for different age classes. Between 2016 and 2023, we fitted 96 spoonbills with GPS tags and tracked their movements in Camargue throughout their annual cycle. We first (i) assessed the general relevance of areas with different protection levels in Camargue for the spoonbill population. We predict a lower proportion of birds in areas of strong protection, as food abundance may be higher in areas of moderate protection. We then (ii) explored how the use of strongly protected areas changes seasonally throughout the annual cycle (i.e., breeding *vs.* early dispersal *vs*. late dispersal *vs*. wintering). We predict that during breeding, spoonbills will spend considerably more time in the colonies, which are located outside strongly protected areas. Furthermore, due to the occurrence of hunting disturbance in moderately protected areas (Article 7, European Commission, 2008) during the late dispersal and wintering periods, we also predict a higher use of strongly protected areas during these periods. Subsequently, (iii) we investigated the importance of strongly protected areas for different age classes (juvenile *vs*. immature *vs*. adult). Due to their accumulated experience of using the Camargue landscape and associated levels of disturbance, we predict that strongly protected areas will be mainly used by adults. Additionally, due to their higher exploratory behaviour, competition, and inexperience in foraging, immature birds often forage across larger areas (Grecian et al., 2018; Huyvaert and Anderson, 2004; Pettex et al., 2019; Votier et al., 2011; Zango et al., 2020), and consequently will likely display a dispersive behaviour and higher use of less (i.e. moderately) protected areas. Finally, (iv) we presented spatially, and temporarily explicit information of protected area use across periods for the three age classes. This showed which areas were used by spoonbills and when, allowing the presence of spoonbills in these areas to be indirectly linked to specific management actions.

Material and Methods

Study area and population

Camargue extends over an area of 180,000 ha and comprises a diverse mosaic of habitats, including natural and semi-natural wetlands, two important salt pans, rice fields, and other agricultural areas (Blondel et al., 2013; Galewski and Devictor, 2016). It encompasses a complex diversity of management techniques and stakeholders, involved in the administration of areas under different legal regimens (e.g., national, private, and regional reserves) and different land uses (e.g., farming, salt pans, and waterfowl hunting areas) (Galewski and Devictor, 2016). The existing types of protection are diverse and overlapping, ranging from conventional and regulatory protection to protection through land ownership, and compliance to European or international laws and conventions (see Table 1 and Fig. 1 for further details and a breakdown of the types of protection). Hereafter, in order to standardize the different types of protection, we consider all the areas that contain one of the first four categories of the International Union for Conservation of Nature protected area classification (IUCN, 1994) to belong to strongly protected areas, encompassing 26% of the study area.

Table 1. Protected areas covered by the study area according to Lefebvre and Moncorps (2010). The types correspond to the type of protection: A – statutory; B – property-based; C – conventional; D – under a European or international law. The level of protection corresponds to the category considered for this study: moderate or strong.

Protected area classification	**IUCN categories**	**Protection type**	**Level of protection**	**Surface area (ca. ha)**
Camargue National Nature Reserve	I – IV	A	Strong	14,127
Vigueirat National Nature Reserve	I – IV	A	Strong	1,200
“Site classé” (1)	III	A	Strong	14,150
Arrêté de protection de biotope (2)	IV	A	Strong	788
Mahistre & Musette Regional Nature Reserve	IV	A	Strong	263
Scamandre Regional Nature Reserve	IV	A	Strong	148
Tour du Valat Regional Nature Reserve	IV	A	Strong	1,865
“Conservatoire du Littoral” dependencies (3)	IV – V	B	Strong	29,497
Camargue Regional Nature Park	V	C	Moderate	99,849
Espaces naturels sensibles (4)	V	B	Moderate	3,851
“Sites inscrits” (2)	V – VI	A	Moderate	108,678
Camargue Ramsar Site	(6)	D	Moderate	126,288
Camargue/Delta du Rhône Biosphere Reserve	(6)	D	Moderate	193,021
Special Protection Areas (Natura 2000) (5)	(6)	D	Moderate	243,187
Special Areas of Conservation (Natura 2000) (5)	(6)	D	Moderate	163,502

(1) *Protection under the laws of 21 April 1906 and 2 May 1930 (articles L. 341-1 to 22 of the French Environment Code).*

(2) *Protection system created by decree no. 77-1295 of 25 November 1977 (codified in the French Environment Code in articles L. 411-1, L. 411-2, R. 411-15, R.411-16 and R.411-17).*

(3) *Name of the areas included: Bois de Tourtoulen; Camargue Gardoise; Domaine de Rousty; Embouchure du Petit-Rhône; Étangs et Marais des Salins de Camargue; La Palissade; Domaine des Grandes Cabanes du Vaccarès; Marais du Vigueirat; Sainte-Cécile; Vaccarès.*

(4) *Name of the areas included: "Étangs des Impériaux ; Malagroy & Consecanières"; "Domaine du Ménage" ; "Château d'Avignon"; "Grandes Cabanes du Vaccarès"; "Clos de la Royalette".*

(5) *SPA & SAC Natura 2000 sites are respectively designated under the Birds and the Habitats Directives.*

(6) *IUCN category not attributable due to the absence of a defined legal status in France (Ramsar, Biosphere reserves) or because management is too heterogeneous (Natura 2000).*

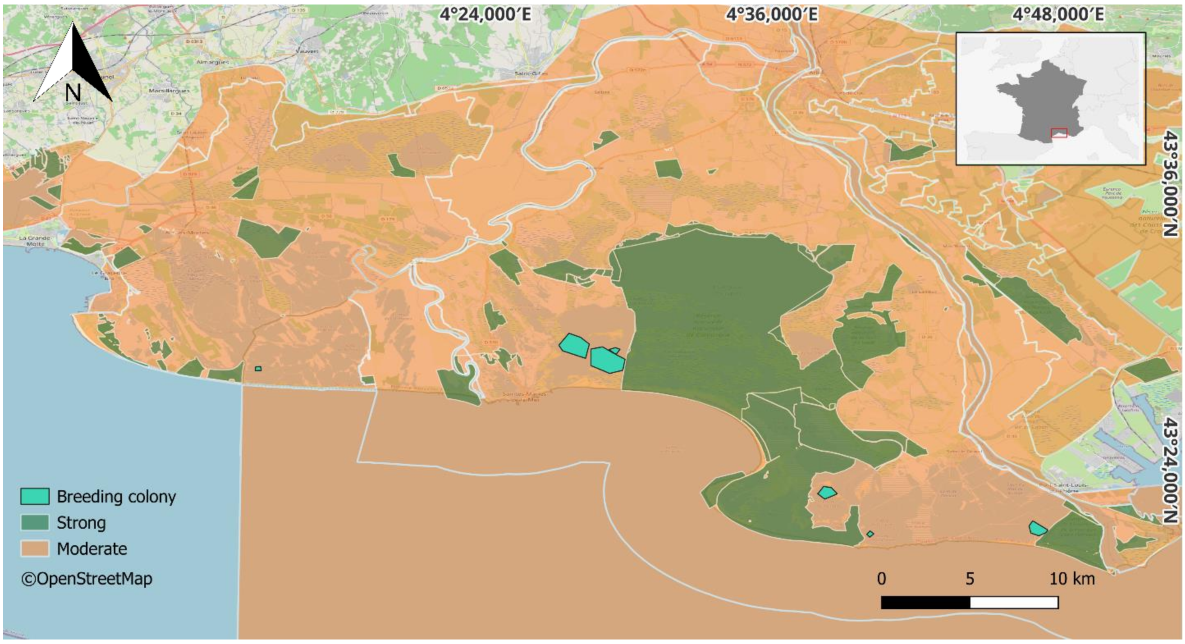

Fig. 1 – Map of the Camargue region along the Mediterranean coast of France, highlighting areas of moderate (orange) and strong protection (dark green). Areas were classified based on the IUCN categories stated in Table 1. The main breeding colonies in Camargue (and where GPS tags were deployed) are also shown (light green) and located within areas of moderate protection. White lines and polygons represent the delineations of the areas described in Table 1.

A total of 94 chicks (Appendix, Table A5.1 and Fig. A5.1) were captured in the colonies during the breeding seasons of 2016 to 2023 (Appendix, Table A5.1 and Fig. A5.1). Chicks were captured by hand during their pre-fledging period (ca. 28-33 days) and individually fitted with solar-powered GPS/accelerometer GSM tags (Druid, www.druid.tech; Ecotone, www.ecotone-telemetry.com; Ornitela, www.ornitela.com). Additionally, two breeding birds were captured using a noose trap deployed at the nest and subsequently tagged, increasing the total number of individuals initially considered for this study (*n* = 96). All the tags (except two that were attached directly to the leg of the chicks), were attached using a Teflon ribbon backpack harness (Kölzsch et al., 2016; Thaxter et al., 2014) (Appendix, Table A5.1). The body weight (*g*) of the chicks was recorded using a Pesola spring balance (±10 *g*). The total combined weight of the tags (25 *g*), harness, and PVC engraved ring (for visual individual identification of marked birds at a distance) was ca. 36 *g*, thus below the 3% threshold of the body weight of the tagged spoonbills (mean body mass ± SD = 1625 ± 186 *g*, *range* = 1200-2120 *g*, *n* = 95; one individual was not weighed, see Appendix, Table A5.1 for details) (Casper, 2009; Phillips et al., 2003). During the capture and GPS fitting procedures, birds were handled with the utmost care by qualified and trained ringers validated by the French national ringing scheme (CRBPO, Programmes personnels PP580 and PP1190 MigraLion).

Data collection and selection

Tags were programmed to record a GPS fix every 10 mins whenever possible (with an associated error of ≤6 m) but due to battery saving the frequency of data acquisition may decrease to every 6 hours: GPS fix frequency on average for Druid and Ornitela tags = 14.3 min ± 1.6 SE; on average for Ecotone tags = 408.8 mins ± 77.6 SE. Data were filtered to include only GPS fixes within the defined Camargue area (from 43°19’N to 43°42’N and from 4°06’E to 4°54″E; Fig. 1), resulting in the exclusion of four individuals with no GPS fixes recorded in Camargue. To reduce uncertainty, only GPS fixes that used at least four satellites for geo-positioning were retained. In the case of four individuals (Appendix, Table A5.1: APVA; ATTL; FBZA; FBZB), no information on the number of satellites used was available so all data were included. For each spoonbill, the first GPS fix considered here corresponds to the first GPS fix after each individual had spent a complete day outside the breeding colony. This filter was applied to ensure that GPS fixes of chicks prior to fledging were excluded, as their movement is constrained to the colony. In the case of the two adults, all fixes recorded since the tags were fitted to the individual were considered. The last recorded GPS fix corresponds either to the start of the early dispersal period of 2024 (15th of May) (*n* = 30), a mortality event (*n* = 36), tag failure (*n* = 3) or because individuals moved into an area of poor GSM coverage, and their fate is unknown (*n* = 27).

Spoonbills in Camargue breed over a relatively long period with egg-laying occurring between February and June (Blanchon et al., 2019; Chapter 2). We considered the start of the breeding period as the 15th of February and individuals were categorized in age classes according to the date associated with each GPS fix: (i) juvenile, all the GPS fixes since the individual fledged to the start of the next breeding period; (ii) immature, all the GPS fixes between the start of the second breeding period and the start of the fourth one; (iii) adult, all GPS fixes after the start of the fourth breeding period and all GPS fixes of the two individuals originally tagged as breeding adults. Although spoonbills have delayed maturity and are considered to recruit in their fourth calendar year (Cramp and Simmons, 1977), a low proportion of breeders can breed at two years old (third calendar year; Bauchau et al., 1998; Champagnon et al., 2019a). Three of the tracked individuals were seen at the colony and displaying breeder behaviour during their third calendar year, so for this study we considered individuals to be adults (breeders) at the start of their fourth breeding period. In total, 89 different juveniles were considered for this study; 19 of those birds also provided data as immatures; and seven of those further provided data as adults, thus totalling nine adults with relevant data. For further details on the number of spoonbills fitted with tags per year and which individuals provide information at different age classes, see Appendix Table A5.1 and Fig. A5.1.

To consider seasonal variation in protected area use due to different ecological requirements by the spoonbills (e.g., breeding, fuelling for migration) and the changes in local conditions throughout the year (specifically in management, climate, and hunting season – 21 August to 31 January), we divided the year into four periods of four months: (i) breeding – from 15th of February till the 14th of May. During this period, breeding adults are mainly present at the colonies and a few juveniles may have fledge in some years; (ii) early dispersal – from 15th of May till 14th of August. During this period, many juveniles have fledged and begin to disperse, while late breeding adults (or those with a second clutch), remain in the colonies; (iii) late dispersal – from 15th of August to 14th of November. The colonies are generally empty with all juveniles fledged, and during this period, migratory birds of all age classes gradually leave Camargue to winter at other locations (Chapter 6); and (iv) wintering – from 15th of November to 14th of February. In this period only resident birds are present in the Camargue. Although spoonbills usually remain on the wintering grounds (until reaching breeding maturity), some immature birds do return to the breeding area, where they likely have exploratory behaviour and do not engage in breeding (Boulinier et al., 2008, 1996; Johnstone et al., 2002; Lok et al., 2015; Tenan et al., 2017).

GPS data treatment

Areas highly revisited by animals are often considered to be of ecological significance and their identification can provide important insights into the life history of populations (Bracis et al., 2018). To identify fixes registered by the spoonbills when they are potentially breeding, resting, and foraging, causing multiple revisits of the same area, we conducted a revisitation analysis using the *recurse* package (Bracis et al., 2018). This analysis allowed us to calculate the number of times (revisits) an individual trajectory entered a circular area centred on each position of the trajectory. To perform this calculation, we defined a circular radius of 100 m, obtained by following and adapted procedure of the exploratory analysis performed by Rodrigues et al. (2022) (for details, see Appendix Table A5.3; Fig. A5.2; and Fig. A5.3). This analysis resulted in the same radius (100 m) as the one obtained by Rodrigues et al. (2023), being a good compromise between avoiding spurious results, without neglecting changes in habitat use due to overlap of GPS fixes if using a larger radius. To ensure that revisits were independent not only in space but also in time, a threshold of 30 minutes between two consecutive GPS fixes was defined. This means that if after a given GPS fix, the following one was recorded within a radius of 100 meters during a 30-minute period, it was not considered to be a new revisit. Due to computational limitations and to avoid pseudoreplication issues, only GPS fixes of the same aggregated group (age class; land protection level; period; and year) were considered as potential revisits. Hereafter, only the GPS fixes with the most revisited circles (> 5% quantile of each individual) were kept ($n_{\text{GPS fixes}}$= 1,628,448; n_{Ind}= 92). Finally, to avoid revisit misclassifications we kept only fixes which were revisited at least three times ($n_{\text{GPS fixes}}$= 1,565,015; n_{Ind}= 92; Appendix, Table A5.4). When inspecting the data, one individual (AZZT) had only one valid GPS fix revisited several times and thus was removed from the analysis. Furthermore, two juveniles only had valid fixes registered during the breeding period and thus, they were removed due to their small number (n_{A22C} = 3; n_{ATTL} = 1). Thus, our data totalised $n_{\text{GPS fixes}}$= 1,565,015 and n_{Ind}= 91 (Appendix, Table A5.4).

Data visualization – heat maps & day plots

To evaluate the importance of specific areas with varying levels of protection across the annual and life cycles, we produced spatially explicit heat maps of spoonbills GPS fixes for each combination of age class and period. We successfully identified the most relevant areas for each type of land protection level and proceed to discuss how their management could be connected to their use by the spoonbills. Furthermore, the percentage of GPS fixes for each age class and period of the year was calculated. To identify temporal peaks in the use of areas with strong protection, a plot was created for each age class, showing the average proportion of GPS fixes located in areas of strong protection per Julian day.

Statistical analysis

To test the relationship between the number of GPS fixes (i.e. those revisited ≥ three times, henceforward revisitation fixes) and the variables of interest, we used generalized linear mixed models in an information-theoretic model selection framework (Burnham and Anderson, 2003). To account for overdispersion we considered a negative binomial distribution (*Ml* and *nlminb* optimizer; *glmmTMB* package – Brooks et al., 2017) and manually developed models for competition. We considered the total number of revisitation fixes as a response variable and considered land protection level (*Protection*, categorical with two levels), period of the year (*Period*, categorical with four levels), and age class (*Age*, categorical with three levels) as fixed effects. To incorporate the dependency among revisitation fixes from the same individual (*Ind*) and colony of birth (*Colony*, categorical with seven levels), we used *Ind* nested within *Colony* as a random intercept. Additionally, to incorporate the dependency among observations of the same year, year was also considered as a random intercept (*Year*, categorical with eight levels). No interaction between *Age* and *Period* was considered due convergence issues likely caused by the absence of data from juveniles during the breeding period. Using the *DHARMa* package, we performed a Dharma nonparametric dispersion test which confirmed a lack of overdispersion (overdispersion = *0.47*; $p = 0.248$). Consequently, we obtained the following equation as the initial complex model:

$$\log_{(\mu ijkl)} = \beta_0 + \beta_1 X_{ij} \times \beta_2 X_{ij} + \beta_1 X_{ij} \times \beta_3 X_{ij} + \gamma_{0i} + \gamma_{1i} \times X_{ij} + \delta_{0i} + \delta_{1i} + \epsilon_{ijkl}$$

$$\log\left(Fixes_{\mu ijkl}\right) = Protection_{ij} \times Period_{ij} + Age_{ij} \times Protection_{ij} + Colony_i \times Ind_{ij} + Year_i$$

$$Colony_i \sim N\left(0, \sigma_{Colony}{}^2\right)$$

$$Ind_{ij} \sim N\left(0, \sigma_{Ind}{}^2\right)$$

$$Year_i \sim N\left(0, \sigma_{Year}{}^2\right)$$

(equation 1)

The different models were ranked and selected according to their Akaike´s Information Criterion adjusted for small sample size (*AICc*) (Anderson and Burnham, 2002). In order to explore the differences among the marginal means of each group, subsequent pairwise Tukey HSD post-hoc test comparisons were conducted to the most parsimonious model using the *emmeans* package (Lenth et al., 2024). A Sidak correction was applied, which adjusts for the family-wise error rate across all tests and provides a more conservative control over Type I errors (Sidak, 1967).

All analyses were carried out in the software R version 4.2.1 (R Core Team, 2022) and plots were created using the package *ggplot2* (Wickham, 2016) and *sjPlot* (Lüdecke et al., 2023). To perform additional spatial data analysis and the visualization of the geographical data, the software QGIS, version 3.34, was used.

Results

From the 91 tagged spoonbills used in the analysis (Fig. 2), 82 registered revisitation fixes in strongly protected areas in Camargue. These fixes represented on average 40% (±5 SE) of the total amount of revisitation fixes of the 82 individuals. The proportion of fixes located in strongly protected areas strongly varied between individuals, ranging from no presence to 100%, with four individuals having more than 90% (±2 SE) and nine with less than 10% (±4 SE) inside strongly protected areas.

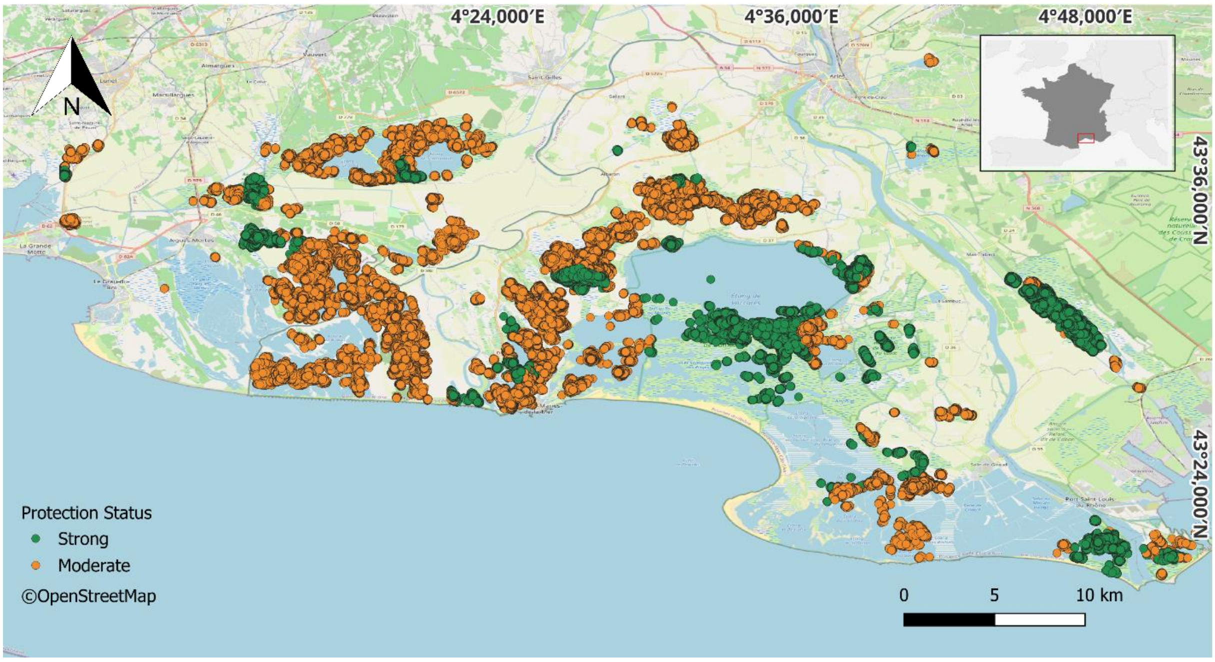

Fig. 2 – Distribution of revisitation fixes ($n_{\textit{Revisitation fixes}}$= 1,565,010; $n_{\textit{Ind}}$= 91) across the study area classified according to protection levels: moderate (orange) and strong (green).

When considering the variation in the amount of revisitation fixes per individual (equation $_1$), the most complex model was also the most-supported model (Model 13; Table 2).

Table 2. Generalized linear mixed models' selection for amount of revisitation fixes ($n_{Revisitation\ fixes}$= 1,565,010; n_{Ind}= 91). *Ind* was considered as a random variable nested in *Colony*. Additionally, *Year* was also considered as a random variable. Models were ranked according to the Akaike value, and the most parsimonious model is indicated in bold.

Number	Model	*df*	AIC$_c$	ΔAIC$_c$	Akaike weight
13	***Age* × *Protection* + *Period* × *Protection***	16	10309.7	0.0	0.8
12	*Age* + *Period* × *Protection*	14	10312.6	2.9	0.2
9	*Age* × *Protection*	10	10323.0	13.2	0.0
11	*Period* × *Protection*	12	10328.9	19.2	0.0
10	*Age* × *Protection* + *Period*	13	10336.5	26.8	0.0
8	*Period* + *Protection*	9	10345.8	36.1	0.0
6	*Age* + *Period*	10	10350.8	41.0	0.0
7	*Age* + *Period* + *Protection*	11	10354.5	44.8	0.0
5	*Age* + *Protection*	8	10360.5	50.8	0.0
4	*Period*	8	10362.8	53.1	0.0
3	*Age*	7	10363.2	53.5	0.0
1	*Constant*	5	10386.0	76.3	0.0
2	*Protection*	6	10386.3	76.6	0.0

This model retained both interactions (*Age* × *Protection*; *Period* × *Protection*), hence, confirming that there are significant differences in how protected areas are used according to the age of the individual and the period of the year (Fig. 3).

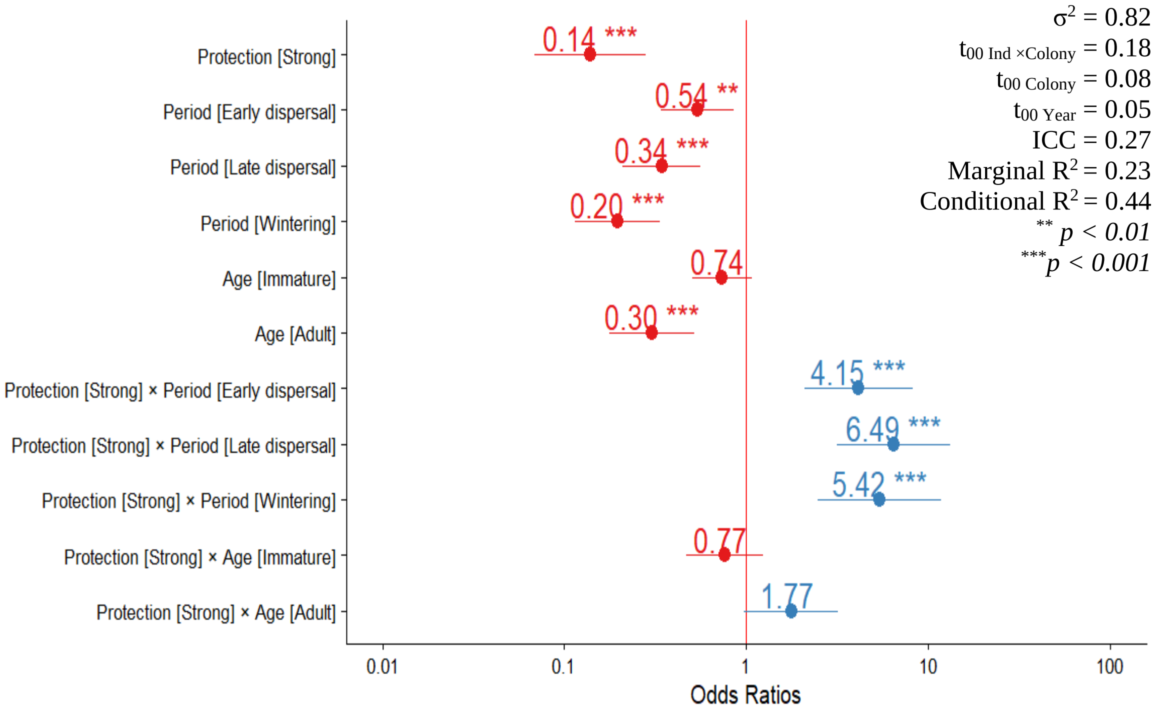

Fig. 3 – Odds ratios of a revisitation fix occurring according to: protection level (Moderate – Reference); Period (Breeding – Reference); Age (Juvenile – Reference); Protection × Period (Strong × Breeding – Reference); Protection × Age (Strong × Juvenile – Reference). Red colour represents lower odds of GPS fix occurring when compared to the reference level, while blue colour represents higher odds. The “neutral” line (red vertical line) indicates no effect when intercepted. Horizontal lines indicate 95% confidence intervals. For details check Supplementary Information, Table A5.5.

When comparing the combined groups of annual period and protection level, our results indicated that there are significantly fewer revisitation fixes located within areas of strong protection during the breeding period (Fig. 4). No differences in the number of fixes between protection levels were detected in the remaining periods. Furthermore, the number of revisitation fixes located in areas of moderate protection appears to be lowest during the wintering period, despite no difference was detected with the late dispersal period.

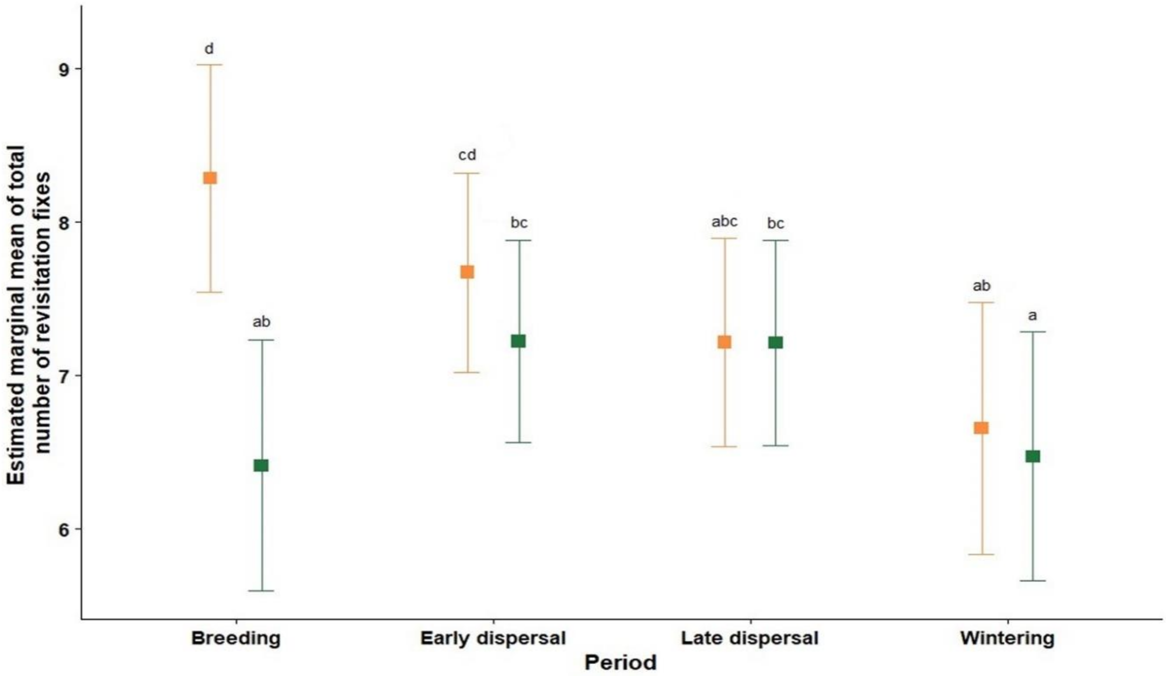

Fig. 4 – Post-hoc comparisons of estimated marginal mean of total amount of revisitation fixes between two levels of protection (Moderate – orange; Strong – green), across the annual cycle. Vertical lines indicate 95% confidence intervals after Sidak correction. Different letters indicate statistical differences between groups.

Juveniles and immatures have significantly more revisitation fixes within areas of moderate protection than in areas of strong protection (Fig. 5). Whereas no differences were detected for adults (Fig. 5).

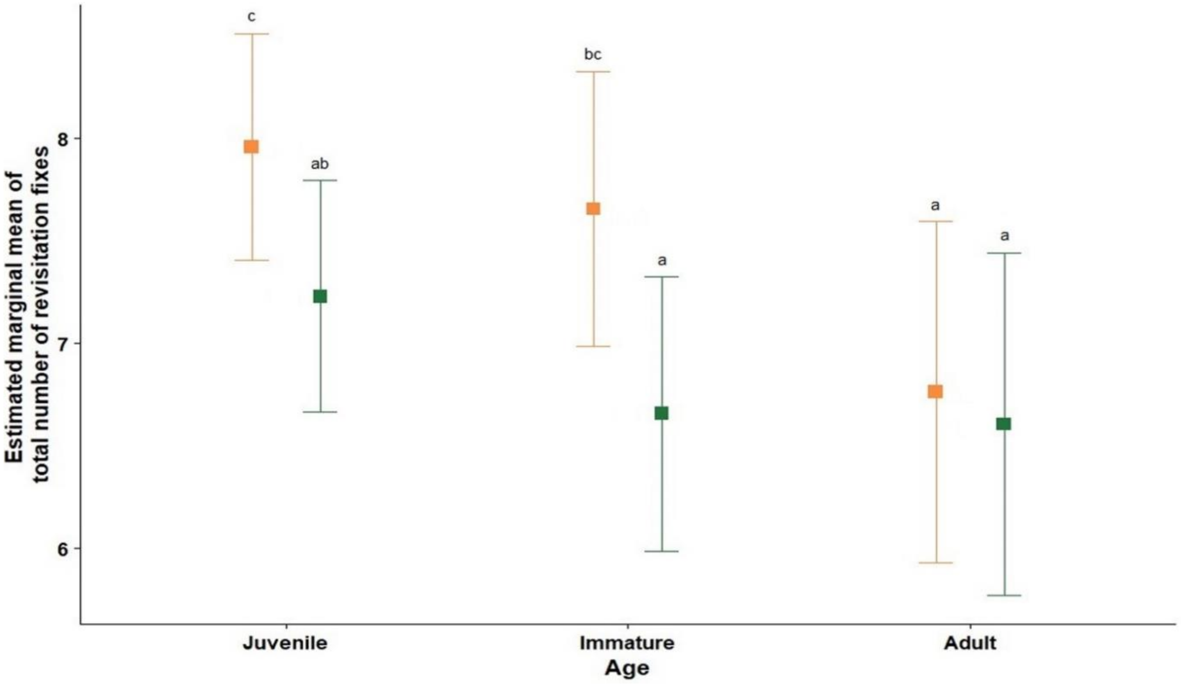

Fig. 5 – Post-hoc comparisons of estimated marginal mean of total revisitation fixes two protection levels (moderate – orange; strong – green) across the different age class. Vertical lines indicate 95% confidence after Sidak correction. Different letters indicate statistical differences between groups.

When plotting the average proportion of revisitation fixes located inside areas of strong protection (Fig. 6), we identified an increasing use of these areas during early dispersal, which is common to all age classes. Juveniles appear to decrease their use of strongly protected areas during the early wintering period, while the decrease for adults is more pronounced in the later part of this period.

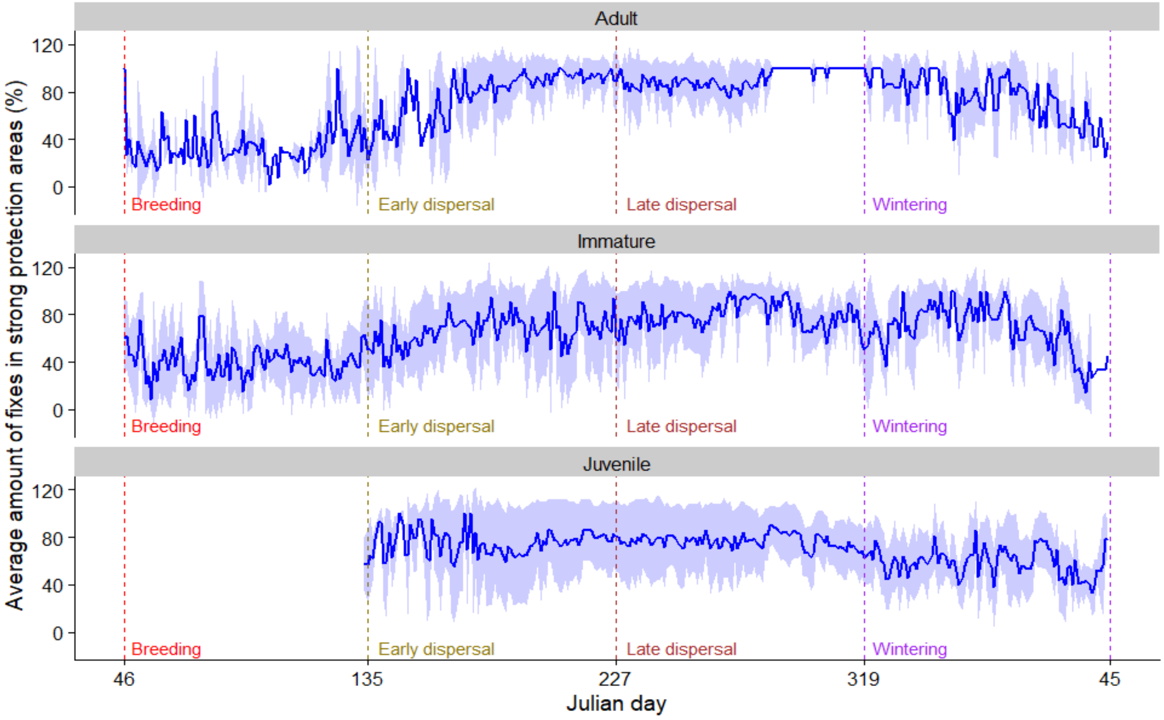

Fig. 6 – Variation in the average frequency of revisitation fixes ($n_{Revisitation\ fixes}$= 1565010; n_{Ind}= 91), throughout the annual cycle according to each period, for each age class (juvenile, immature, and adult). Dashed vertical lines delimitate the different periods: Breeding; Early dispersal; Late dispersal; and Wintering. No fixes during Breeding were considered for juveniles. Shaded-blue area represents standard deviation.

When plotting each combination of age class and period of the year, we successfully identified the most relevant areas (with highest concentration of revisitation fixes) within areas of moderate (orange) and strong protection (green) (Fig. 7). In the case of the areas of moderate protection, the data highlights the following sites: 1 – Sensitive Natural Area of the *Étang des Impériaux* managed by Department council; private estates managed for duck hunting (2 – *Basse Méjanes*; 3 – *Tamaris*; 4 – *Lairan*); and communal 5 – *Etang du Crey*. As for the areas of strong protection, they were identified to be all within the *"Conservatoire du Littoral"* dependencies (1 – *Vigueirat* National Nature Reserve; 2 – Camargue National Nature Reserve; 3 – *Domaine de la Palissade* protected area; and 4 – *Domaine des Grandes Cabanes du Vaccarès)*, except for 5 – *Scamandre* Regional Nature Reserve (see top-left panel in Fig. 7 for the location of these sites).

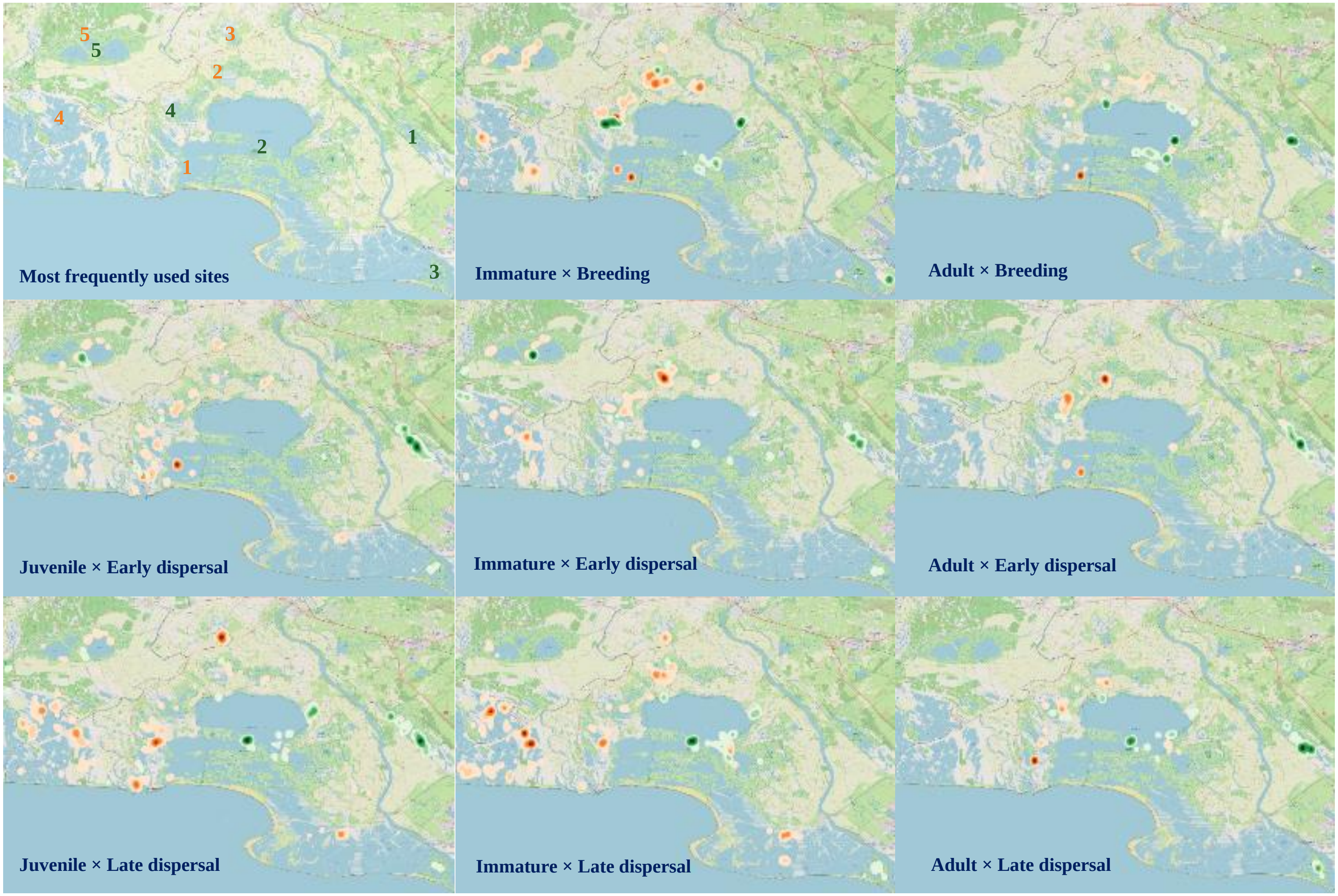
5
5
3
2
4
4
1
2
1
3
Most frequently used sites
Immature × Breeding
Adult × Breeding
Juvenile × Early dispersal
Immature × Early dispersal
Adult × Early dispersal
Juvenile × Late dispersal
Immature × Late dispersal
Adult × Late dispersal

Fig. 7 – Heat maps of revisitation fixes according to protection levels (moderate – orange; strong – green), in each period of the annual cycle (rows: breeding, early dispersal, late dispersal, and wintering) across age classes (columns: juvenile, immature, and adult). The top left map, identifies the five most frequently areas across all age classes of moderate (orange) and strong (green) protected areas (see text for details)

Discussion

Our results indicate that spoonbills in Camargue are selective in the areas they use, with both moderately and strongly protected areas contributing to overall wetland connectivity in a fragmented and highly anthropogenic landscape. This is suggested by the lack of differences in use by spoonbills between areas of moderate and strong protection throughout their annual cycle, except during the breeding period when spoonbill presence is highly concentrated in the colonies. Indeed, tracking data showed that spoonbills were mainly present in areas managed to promote the presence of waterbirds for recreational (e.g., ecotourism and hunting activities) or conservation purposes (highlighted in top-left panel in Fig.7). Overall, juveniles and immatures were significantly less likely to use areas of strong protection (Fig. 5) and appear to be more dispersive using several different areas over the annual cycle (Fig 6, with lower percentages than adults across the annual cycle; Fig. 7). Finally, adults did not differ in their use of different types of protected areas and appeared to be more consistent and selective in the areas they use. This suggests that less experienced individuals might be more dispersive and use a higher number of different areas to avoid competition, or simply because they are exploring more sites and/or may have yet failed to realize potential advantage of using such sites.

Overall relevance of strongly protected areas

Despite evidence showing that the level of protection of protected areas is essential to determine their effectiveness (Di Lorenzo et al., 2020; Wauchope et al., 2022; Zupan et al., 2018), populations usually use a variety of habitats with different levels of protection (Soriano-Redondo et al., 2023). Thus, given that all Camargue is protected to some extent throughout its geographical area (Lefebvre and Moncorps, 2010; Vallecillo et al., 2023), that several areas of moderate protection are managed to attract or protect waterbirds (Galewski and Devictor, 2016), and that the spoonbill is an opportunistic forager with some flexibility in its diet (El-Hacen et al., 2014; Enners et al., 2020; Rodrigues et al., 2023), it is not surprising that we did not find a significant selection of strongly protected areas overall. Moderately protected areas being significantly more selected during the breeding period is explained by the fact that only adult and immature revisitation fixes were considered. At this point of the annual cycle, adults spend about half of their day in the breeding colonies to incubate their eggs or attend their chicks, while immatures can also be observed in a lower extent at colonies, although to a lower extent, gathering social cues, or even attempting to breed (Boulinier et al., 1996, 2008; Johnstone et al., 2002; Lok et al., 2013; Tenan et al., 2017). In Camargue, spoonbills nest in small islets to avoid terrestrial predation by Eurasian wild boar (*Sus scrofa*) and Red fox (*Vulpes vulpes*) (Champagnon et al., 2021). These islets are mainly located in the *Étang des Impériaux* (orange site 1 in Fig. 7), an area of moderate protection (according to our classification), but as it is part of Natura 2000 and a sensitive natural area (ENS, Table 1), it has an additional layer of protection. This area is therefore actively managed by the Bouches-du-Rhône Departmental Council to avoid disturbance caused by anthropogenic activities. Considering that the other major spoonbill colonies in France (Marion, 2019) are all located in areas of strong protection (according to our classification), this underlines that spoonbills, at least in Europe, require active management and strong protection measurements to avoid anthropogenic disturbance of their colonies in order to improve productivity (Kazantzidis et al., 2024; Mikuska et al., 2023; Spanoghe, 2023).

Camargue is one of the major waterfowl (primarily ducks) hunting areas in Europe (Mathevet, 2004; Mondain-Monval et al., 2009). Waterfowl hunting is therefore one of the main management objectives of several private wetlands in Camargue (Galewski and Devictor, 2016; Guillemain et al., 2010; Mondain-Monval et al., 2009). Private areas are often actively managed to provide space and food resources for the influx of migrating and wintering waterfowl, such as artificial flooding, creation of artificial ponds, manipulation of water levels, and scattering of seeds as bait (Brochet et al., 2009; Davis et al., 2014; Mathevet and Guillemain, 2016; Vallecillo et al., 2019), whereas areas under strong protection are less likely to be managed to provide abundant food resources, but rather to allow for the ecosystem to persist in its natural rhythm (Central Valley Joint Venture, 2006). Spoonbills in Camargue are often observed feeding in private areas managed for duck hunting, such as *Basse Méjanes* (orange site 2 in Fig. 7), *Lairan* (orange site 4 in Fig. 7), and *Tamaris* (orange site 3 in Fig. 7). As high food availability for waterfowl is the main priority for hunting managers during the hunting season (i.e., during most of the late dispersal and wintering period), the marshes in these areas can be attractive to spoonbills throughout the year. During the breeding period and before the onset of the hunting season (21 August) these may stay permanently flooded and relatively undisturbed, providing good conditions for spoonbills.

In addition, every four or five years, managers may practice the "*assec*", i.e., drying out their estates to manage exotic vegetation (e.g., Floating primrose-willow – *Ludwigia peploides*) and prevent siltation. Some managers may even carry out this practice annually or in rotating sections when managing large estates. During *assec*, the receding water, when not actively drained, promotes the gathering of prey (particularly fish) in the remaining "pools" making them easily accessible to waterbirds (e.g., Beerens et al., 2011; Lorenz, 2014). Subsequently, in June and July (early dispersal), private wetlands are flooded (including temporary ponds that would otherwise be dry), to maximise food availability (aquatic plant production) in preparation for the arrival of waterfowl from late summer (late dispersal) (Davis et al., 2014; Tamisier and Grillas, 1994). Even if management practices vary among the 200 hunting estates in Camargue (Mondain-Monval et al., 2009), there will frequently be some that provide good conditions to spoonbills which may explain the high number of different moderately protected sites used by them (Fig. 7).

Seasonal change in the use of strongly protected areas

In a variety of species, strongly protected areas have been shown to by particularly important during the breeding and wintering season, when resources might be lacking and disturbance due to waterfowl hunting might be higher in moderately or non-protected areas (Gaget et al., 2021; Soriano-Redondo et al., 2023). Soriano-Redondo et al. (2023) revealed that Whooper swans wintering in Nature Reserves have higher survival rates than the ones wintering in non-protected areas. This is thought to be connected to management actions such as protection measurements against natural predators, hunting and the supply of food. Surprisingly, despite coinciding with the waterfowl hunting season, there was no significant increase in the use of strongly protected areas in Camargue during the late dispersal and wintering periods. This could be explained by the hunting practices in Camargue and the size of the hunting estates used by spoonbills. For instance, *Lairan* is a 697 ha estate where hunting takes place at varying intensities, with some parts of this estate only being hunted once a month. Similarly, *Basse Méjanes* (489 ha) and *Tamaris* (16 ha) are relatively large estates, which only allow hunting once a week. Furthermore, several private hunting areas in Camargue (ca. 57% of the hunting estates – Mondain-Monval et al., 2009) prohibit hunting in certain parts of their estates, that serve as waterfowl refuges (Vallecillo et al., 2023). Thus, waterfowl hunting activities in some private areas are unlikely to be sufficiently high in frequency and area to significantly deter spoonbills from being present, even if only outside the hunting day of the week or month or the actively hunted locations.

The overall average percentage of adult revisitation fixes in strongly protected areas does increase during the hunting season (c.a. 25 % to > 60% on average, Appendix Fig. A5.4). Although, this increase was not significant in terms revisited fixes in strongly protected areas in our models (Appendix, Table A5.5), strongly protected areas such as the Camargue National Nature Reserve (> 14,000 ha), have a high density of revisitation fixes during the wintering period (green site 2 in Fig. 7). Despite based on a single individual, this is supported by aerial surveys carried out monthly during the wintering period (Tamisier and Dehorter, 1999; Vallecillo et al., 2023) which consistently identify this reserve as the main wintering area of spoonbills in Camargue. In contrast to adults, this overall increase in the use of strongly protected areas is not observed in less experienced individuals. During wintering, the number of revisitation fixes in strongly protected areas appears to decrease for these individuals, as indicated by the daily use of strongly protected areas by juveniles (Fig. 6), and a three-way Post-hoc comparison between immatures and adults (Appendix, Fig. A5.5). These results, despite statistically not significant, may suggest a density-dependent process, consistent with the dominance-competitive hypothesis (Verhulst et al., 2014; Weimerskirch et al., 2014) in which more experienced (adults) individuals, push less experienced individuals into less suitable areas. Alternatively, immatures may not yet have realised the potential benefits of using this area during periods of higher disturbance or potentially lower food availability. The fact that disturbance may affect spoonbills (and other waterbirds) more during the wintering period than during late dispersal may be related to the increased hunting pressure that occurs later in the hunting season. While hunting pressure is strong at the onset of the season, some privately large managed areas may wait for the arrival of more migratory birds (around October and November) to carry out their activities. However, this could also be connected to fish availability in strongly protected areas which may increase during the winter (Bouchard et al., 2022). This increase in fish availability is illustrated by the observation of fish-eating species such as the Great cormorant (*Phalacrocorax carbo*) and Grebes (*Podicipedidae*) that congregate in such sites.

Variation in use of strongly protected areas between age classes

Apart from using moderately protected areas more frequently than adults, juveniles and immatures also appear to be more dispersive and to use a higher number of different areas in Camargue, as indicated by the heat maps (Fig. 7). These results could be related to exploratory behaviour typical of these age classes (Hertel et al., 2023), their difficulty or simply the process of finding suitable areas, or even competition (Bosè and Sarrazin, 2007) for the use of strongly protected areas (Aguilera et al., 1996; El-Hacen et al., 2014; Enners et al., 2020; Kralj et al., 2012; Rodrigues et al., 2023; Volponi et al., 2008). Juveniles and immatures are often still developing their foraging skills and knowledge of the environment, and are known to be less competitive when large number of individuals congregate in the same area (Kokko, 1999; Rotics et al., 2016; Votier et al., 2017). Indeed, tracked juvenile spoonbills in Ria Formosa (southern Portugal), were also found to use a considerable number of different areas (although with no formal comparison to adults), which was hypothesised to be due to opportunistic foraging behaviour and competition avoidance.

Relationship between management and waterbird presence

To better understand which management measures might be associated with the presence of spoonbills in certain areas and at certain periods, we identified five clusters of heavily used areas for each type of protection (Fig. 7). One of them is the Vigueirat National Nature Reserve (green site 1 in Fig. 7), a strongly protected area of 1,200 ha, with actively managed water levels to provide optimal conditions for waterbird species, considering climatic conditions, the annual cycle, and the biology of the targeted species (e.g., ducks in winter, *Ardeidae,* terns, waders and spoonbills in summer), which exemplifies many other strongly protected areas in terms of management. Here, managers maintain high-water levels until July to create favourable breeding conditions for various waterbird species (e.g., *Ardeidae* and Glossy ibis). Then, to simulate a typical Mediterranean hydro-system, they allow the site to slowly dry out, promoting a concentration of prey (e.g., fish and crustaceans), which in turn attracts waterbirds such as spoonbills. This site is also relatively protected from anthropogenic disturbance, with only expert guides and small groups of visitors being allowed into some sections of the area. This provides suitable conditions for newly fledged juveniles to forage safely with their parents, thus potentially explaining the high presence of spoonbills in the area during the early and late dispersal periods. Surprisingly, although immatures were present during early dispersal, they were absent during the late dispersal period, suggesting that there may be some competition for the area when resources are declining, displaced by the high number of adults and respective juveniles. By the end of September, the marshes used by spoonbills for foraging have largely dried up and spoonbills are completely absent from the area during wintering period. During fall, managers fill the marshes again with water, however the persisting absence of spoonbills might be due to the relatively low abundance of fishes and crustaceans.

Recent studies suggest that the relation between protected and surrounding landscapes are complex, especially when considering highly mobile species that can move between these areas throughout the annual and life cycles (Nightingale et al., 2023; Soriano-Redondo et al., 2023). Our results suggest that privately managed areas play a complementary role in Camargue, where they are likely to provide suitable foraging habitat for spoonbills and other waterbirds, through their management targeting waterfowl, which is absent in strongly protected areas at certain periods of the year. However, considerably reliance on privately managed areas can have serious consequences for species highly dependent on them, with high chances of becoming ecological traps (Central Valley Joint Venture, 2006; Champagnon et al., 2023; Fasola et al., 2022; Pernollet et al., 2015). Indeed, changing land management practices may convert sites with suitable foraging resources into areas of low resource quality (e.g., Central Valley Joint Venture, 2006), or unusable areas (e.g., abandonment of fish production; Mikuska et al., 2023). Furthermore, the continued use of highly managed habitat may compromise the resilience of these species (Champagnon et al., 2023). On the other hand, management such as that of the Vigueirat National Nature Reserve (see above), which provides high quality habitat while emulating local environmental conditions, may now be essential to maintain species resilience in a considerably modified and fragmented landscape. Thus, as is often recommended for bird species (Stephens et al., 2004), landscape-level approaches to habitat management are needed when considering the conservation of waterbirds (Qiu et al., 2024). By ensuring the presence of well-distributed foraging and roosting habitats across a highly heterogeneous landscape, it is possible to successfully mitigate the negative effects of disturbance and produce a more robust and resilient ecosystem (McDuie et al., 2021). Indeed, wetland ecosystems with heterogeneous landscape promote waterbird diversity (Qiu et al., 2024). Nevertheless, it essential to understand how specific management actions may affect waterbird presence and habitat use, not only to enhance the effectiveness of conservation efforts, but also to promote wetland connectivity and species resilience in these fragmented landscapes.

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Ethics approval

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Appendices 5

Table A5.1. Summary of tagged spoonbill details: when each tag was fitted; the type of device; attachment techniques; weight; and age class (i.e., if individual had usable data in Camargue when classified as immature or adult).

PVC	Date of GPS/GSM attachment	Mass before equipped (g)	GPS type	Attachment type	Age class when equipped	Immature/Adult data in Camargue
APVA	25/05/2016	2120	Skua-H 20g (Ecotone)	backpack harness	adult	No / Yes
ATTL	10/06/2016	1925	Skua-H 20g (Ecotone)	backpack harness	juvenile	Yes / Yes
ATZF	03/05/2017	1550	OrniTrack-25 3G (Ornitela)	backpack harness	adult	No / Yes
AXXX	07/05/2018	1700	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / Yes
AZZA	26/06/2018	1690	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
AZDC	17/04/2019	1640	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
AXVJ	13/06/2019	1840	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
AXVN	13/06/2019	1490	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
AXVP	13/06/2019	1350	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
AXVT	13/06/2019	1700	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
AXVV	13/06/2019	1520	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile (1)	No / No
AXVZ	13/06/2019	1600	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
AZHS	13/06/2019	1450	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
AZZT	13/06/2019	1200	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile (1)	No / No
AZZZ	13/06/2019	1550	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FAFA	13/06/2019	1310	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FANN	15/06/2020	1400	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FBZA	09/07/2020	1425	Balise Lego-LEG 25g	Tarsus Ring	juvenile	Yes / Yes
FBZB	09/07/2020	1525	Balise Lego-LEG 25g	Tarsus Ring	juvenile	No / No
FBTZ	29/07/2020	1540	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FBXA	29/07/2020	1560	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / No
FBXB	29/07/2020	1490	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / No
FBXC	29/07/2020	1625	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FBXN	29/07/2020	1590	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FBXX	29/07/2020	1650	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No

A111	01/06/2021	1720	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A112	01/06/2021	1410	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A11A	01/06/2021	1500	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A12A	29/07/2020	1700	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A16T	01/06/2021	1300	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FCAB	01/06/2021	1800	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FCAF	01/06/2021	1750	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FCAH	01/06/2021	1720	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FCAT	01/06/2021	1700	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / Yes
A16J	08/06/2021	1520	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A1NH	08/06/2021	1250	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2LA	16/06/2021	1700	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2LL	08/06/2021	1320	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2XC	08/06/2021	1400	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2XF	16/06/2021	1520	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FCAN	08/06/2021	1690	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FCCT	08/06/2021	1630	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A116	01/06/2021	1580	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / No
A16C	01/06/2021	1440	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A16L	01/06/2021	1670	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A16P	01/06/2021	1500	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A1NJ	08/06/2021	1600	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A1NP	16/06/2021	1450	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / Yes
A1TH	01/06/2021	1500	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / Yes
A2A1	16/06/2021	1590	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2X2	16/06/2021	1550	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2XZ	16/06/2021	1820	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FCAD	01/06/2021	1250	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / No
FCAJ	01/06/2021	1340	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FCCS	01/06/2021	NA	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2NL	08/06/2021	1440	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No

A2X3	08/06/2021	1400	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2DB	16/06/2021	1620	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2DD	16/06/2021	1600	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / Yes
A2L1	16/06/2021	1570	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2L6	16/06/2021	1700	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2L9	16/06/2021	1480	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2NS	16/06/2021	1500	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A1J6	26/04/2022	1580	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / No
A1J9	26/04/2022	1540	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A1AZ	02/06/2022	1610	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile (1)	No / No
A23A	02/06/2022	1780	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A23B	02/06/2022	1760	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / No
A212	08/06/2022	1780	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A25D	08/06/2022	1640	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A251	20/06/2022	1780	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A252	20/06/2022	1600	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / No
A255	20/06/2022	1380	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A22B	26/04/2023	2000	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / No
A22C	26/04/2023	1800	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A22J	26/04/2023	1900	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A22N	26/04/2023	1700	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A22D	23/05/2023	1850	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A22F	23/05/2023	1900	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A22H	23/05/2023	2000	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A22P	23/05/2023	1900	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / No
A22S	23/05/2023	1850	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A3AC	23/05/2023	1980	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A3AF	23/05/2023	1550	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A3AT	23/05/2023	1950	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A2ZP	25/05/2023	1810	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A235	25/05/2023	1820	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile (1)	No / No

A3CN	25/05/2023	1790	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A3C1	25/05/2023	1820	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile (1)	No / No
A3C2	25/05/2023	1580	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / No
A3C6	25/05/2023	1810	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
A3AH	15/06/2023	1620	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / No
A3AJ	15/06/2023	1560	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	Yes / No
A5AX	15/06/2023	1680	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FCNZ	15/06/2023	1720	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No
FDDT	15/06/2023	1650	OrniTrack-25 3G (Ornitela)	backpack harness	juvenile	No / No

note (1): No valid fixes in Camargue even as juveniles, individuals completely excluded from the analysis.

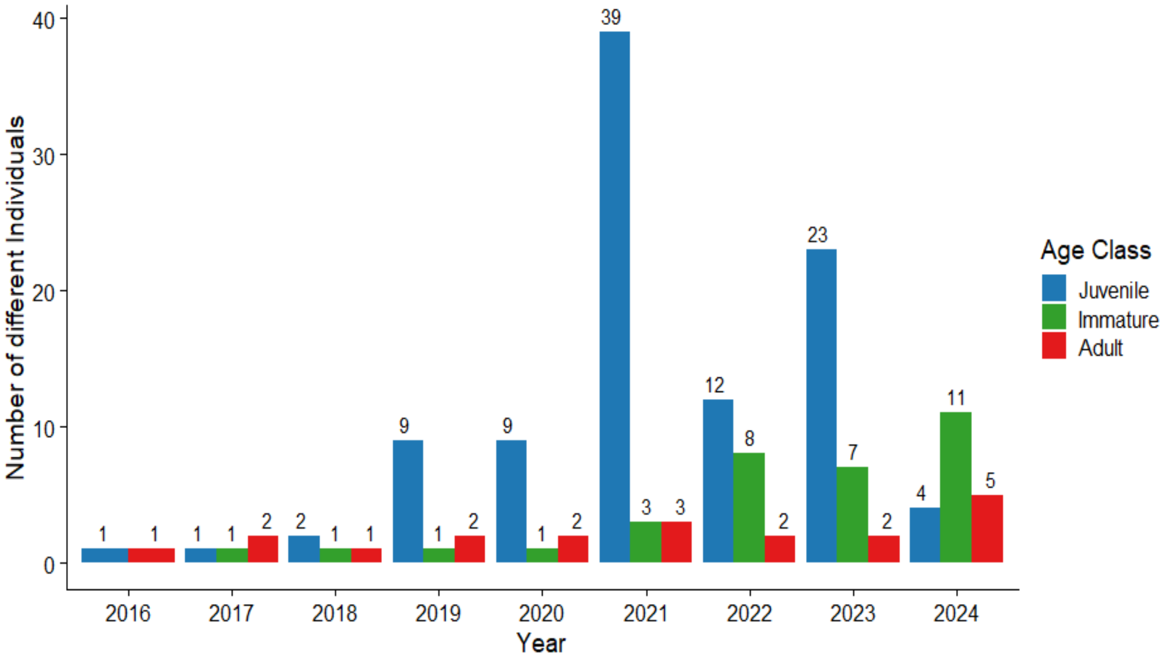

Fig. A5.1 – Summary of number of different spoonbills with valid revisitation fixes (for this study) in Camargue per year and per age class.

In the years of 2019 and 2021, an egg exchange with the Netherlands occurred, meaning that some individuals in our study have different genetics from the rest of the population (Dutch origins: $n_{2019} = 6$ | $n_{2021} = 15$). However, there is no *a priori* reason to believe that the genetics of these birds could influence their presence or not in strongly protected areas. Indeed, when comparing birds with Dutch origin against French birds, we did not detect any significant difference in the number of fixes within strongly protected areas, and thus, all individuals were kept in the analysis (Table A5.2).

Table A5.2. Summary of a general linear mixed model analysis of individual genetic origin (Dutch and French) and land protection levels (moderate and strong), amount of revisitation fixes. Interaction between genetic origin and land protection levels, was also considered.

Coefficient	**Estimates**	**Standard error**	**z-value**	**Pr(>|z|)**	***p*-value**	***2.5%***	***97.5%***
(Intercept)	7.9	0.2	40.9	0.0	***	7.6	8.3
Dutch	0.3	0.3	0.7	0.5		-0.3	0.7
Strong	-0.5	0.1	-4.6	0.0	***	-0.7	0.0
Dutch × Strong	0.0	0.3	-0.1	0.9		-0.6	0.5

*Note: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

For the sensitivity analysis we adapted the methodology described by Rodrigues et al. (2023). Due to the amount and complexity of the data (i.e. multiple individuals, across multiple years, age classes, and different ecological periods), as well as a lack of computing power, we only performed this analysis on a subset of 20 random individuals (ca. 23% of the individuals). First, we calculated the average number of revisits to all areas per radius value and observed that, on average, there is a minimal increase in the mean number of revisits after a radius of 100m despite a higher chance of overlapping radii. Additionally, we plotted the variance of the log of revisits across the same radii and at 100m it appears to contain a considerable amount of the population variance (Fig. A5.2). Finally, we performed a sensitivity analysis to confirm that changing the selected radius by -50 to +150 metres would not impact the percentage of fixes in strongly protected areas (Fig. A5.3 and Table A5.3). In conclusion, these plots suggest that a 100-meter radius is a suitable radius choice as it captures a significant number of revisits while also providing a high degree of variance (Fig. A5.2) and not significantly changing the percentage of strongly protected areas compared to other radii (Fig. A5.3 and Table A5.2).

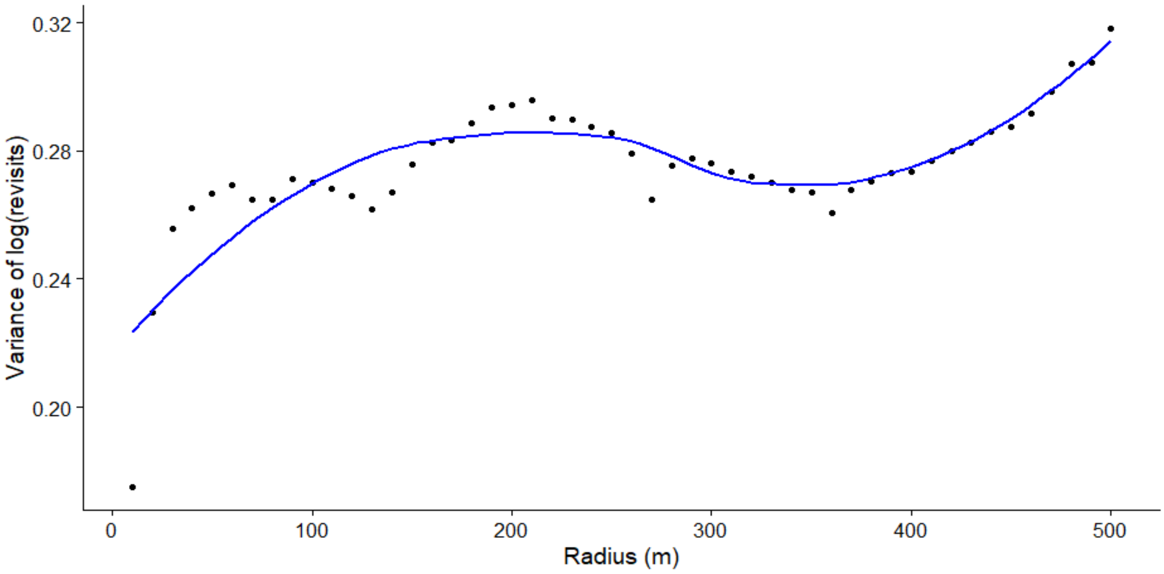

Fig. A5.2 – Variation on the log of revisits made by the Camargue population per radius tested. Blue line represents the LOESS curve that smooths the scatter plot points to reveal the trend in variance as the radius increases.

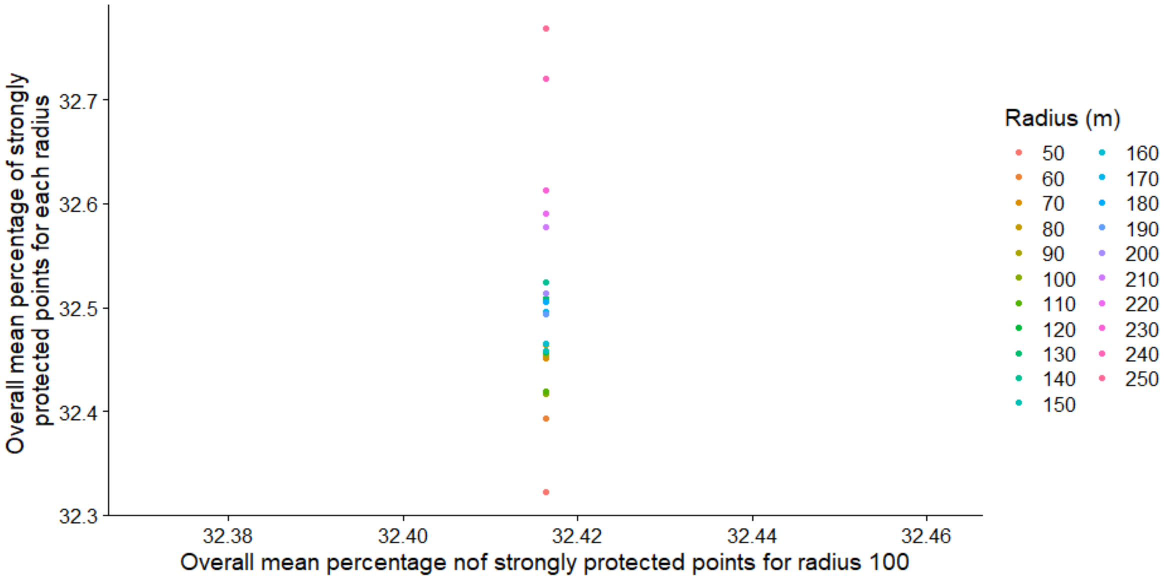

Fig. A5.3 – Variation in the mean percentage of fixes within strongly protected areas while varying the values of the radius in the revisitation analysis. See Table A5.3 to see the lack of statistical significance between radius results.

Table A5.3 – The R- and p-values show the level of association between the percentage of fixes within strongly protected areas using a radius of 100 m and several other proposed radii (from -50 to +150m), in the revisitation analysis.

Radius	**R**	***p*-value**	**Radius**	**R**	***p*-value**
50	32.32	0.988	160	32.46	0.994
60	32.39	0.997	170	32.50	0.990
70	32.45	0.995	180	32.51	0.988
80	32.46	0.994	190	32.49	0.990
90	32.45	0.995	200	32.51	0.987
110	32.42	1.000	210	32.58	0.979
120	32.46	0.995	220	32.59	0.977
130	32.51	0.988	230	32.61	0.975
140	32.52	0.986	240	32.72	0.961
150	32.46	0.995	250	32.77	0.954

Table A5.4. Total number of revisitation fixes considered per combination of age class and period of the annual cycle ($n_{Revisitation\ fixes}$= 1565010; n_{Ind}= 91).

Age class × Period	*Total number of revisitation fixes*
Juvenile × Breeding	-
Juvenile × Early dispersal	*473898*
Juvenile × Late dispersal	*441721*
Juvenile × Wintering	*69399*
Immature × Breeding	*187183*
Immature × Early dispersal	*181171*
Immature × Late dispersal	*90102*
Immature × Wintering	*36402*
Adult × Breeding	*50186*
Adult × Early dispersal	*27227*
Adult × Late dispersal	*6607*
Adult × Wintering	*1114*

Table A5.5. Summary of a general linear mixed model analysis of age class (juvenile, immature, and adult), land protection levels (moderate and strong), and period (breeding, early dispersal, late dispersal, and wintering) in amount of revisitation fixes. The interaction between age class and land protection levels, as well as the one between land protection levels and period, were also included.

Coefficient	**Estimates**	**Standard error**	***z*-value**	**Pr(>|z|)**	***p*-value**	***2.5%***	***97.5%***
(Intercept)	8.8	0.3	29.7	0.0	***	8.2	9.4
Strong	-2.0	0.4	-5.5	0.0	***	-2.7	-1.3
Early dispersal	-0.6	0.2	-2.6	0.0	**	-1.1	-0.2
Late dispersal	-1.1	0.3	-4.2	0.0	***	-1.6	-0.6
Wintering	-1.6	0.3	-5.9	0.0	***	-2.2	-1.1
Immature	-0.3	0.2	-1.6	0.1		-0.7	0.1
Adult	-1.2	0.3	-4.4	0.0	***	-1.7	-0.7
Strong × Early dispersal	1.4	0.3	4.1	0.0	***	0.7	2.1
Strong × Late dispersal	1.9	0.4	5.1	0.0	***	1.2	2.6
Strong × Wintering	1.7	0.4	4.2	0.0	***	0.9	2.5
Strong × Immature	-0.3	0.2	-1.1	0.3		-0.8	0.2
Strong × Adult	0.6	0.3	1.9	0.1	.	0.0	1.2

*Note: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

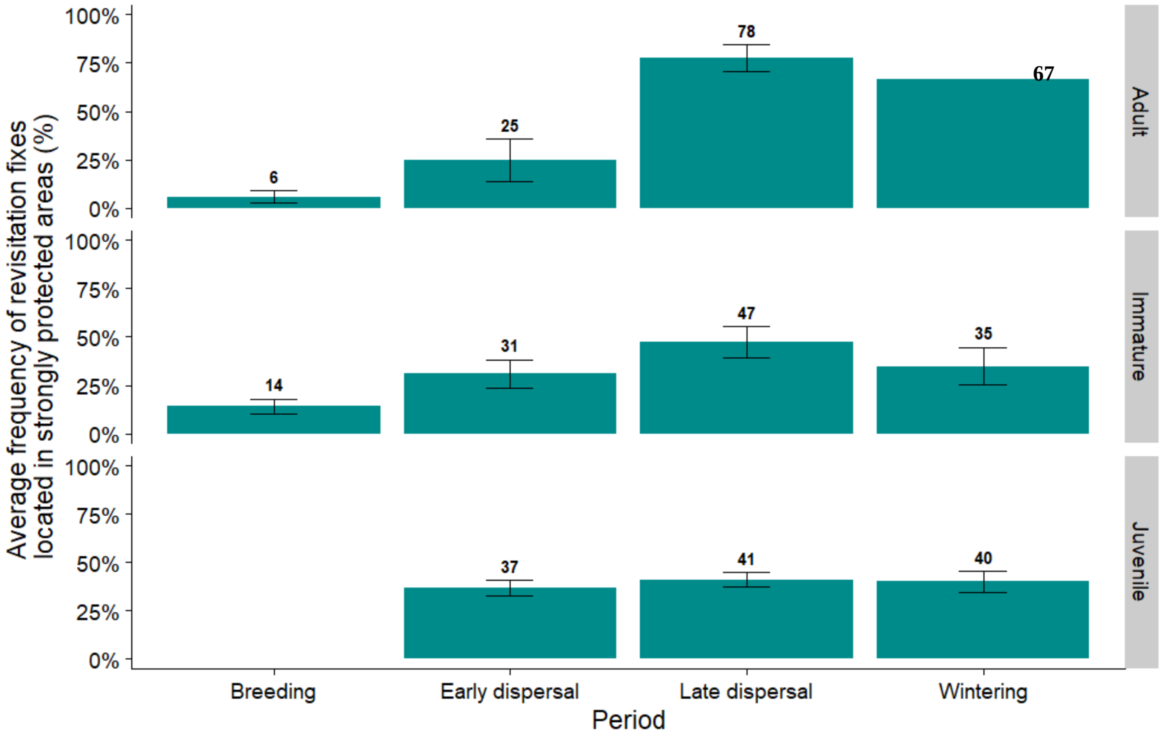

Fig. A5.4 – Variation in the average frequency of revisitation fixes ($n_{Revisitation\ fixes}$= 1565010; n_{Ind}= 91), throughout the annual cycle (breeding, early dispersal, late dispersal, and wintering) according to age class (juvenile, immature, and adult). Whiskers indicate the standard error around the average proportion of each group with averaged frequency of revisitation fixes provided above them.

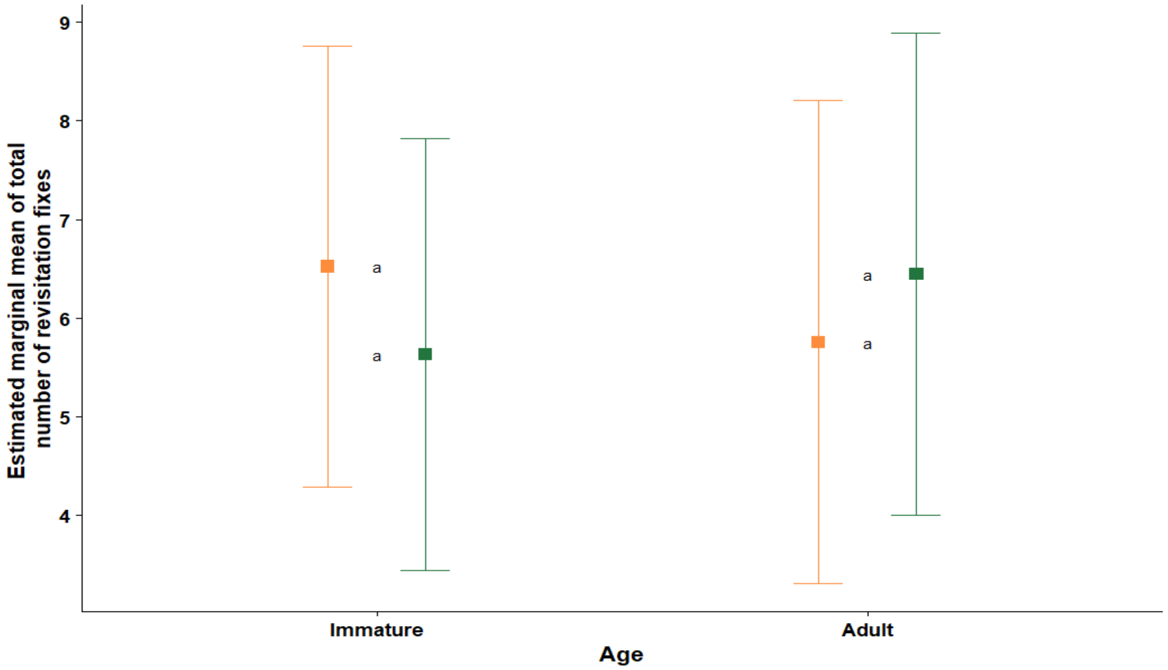

Fig. A5.5 – Post-hoc comparisons of estimated marginal mean of total revisitation fixes between protection levels (moderate – orange; strong – green) across two different age class (immature; and adult) during the wintering period. Vertical lines indicate 95% confidence interval after Sidak correction. Different letters indicate statistical differences between groups.

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CHAPTER 6

Relationship between wintering site and survival in a migratory waterbird using different migration routes

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Spoonbills flying with a guest, Camargue, 2023

Spoonbill migration pattern is described as “hopping”, rather than “jumping”, which is characterised by long-distance flights. These birds can fly both during the day and at night, and make regular stops along their migration route.

Relationship between wintering site and survival in a migratory waterbird using different migration routes

Abstract

When wintering at different sites, individuals from the same breeding population can experience different conditions, with costs and benefits that may have implications throughout their lifetime. Using a dataset from a longitudinal study on Eurasian spoonbills from southern France, we explored whether survival rate varied among individuals using different wintering sites. In the last 13 years, more than 3000 spoonbills have been ringed as chick in Camargue. These birds winter in five main regions that vary in both migratory flyway (East Atlantic vs. Central European) and migration distance (long-distance vs. short-distance vs. resident). We applied Cormack–Jolly–Seber models and found evidence for apparent survival to correlate with migration distance, but not with flyway. During the interval between the first winter sighting and the next breeding period, long-distance migrants had the lowest survival, independently of the flyway taken. Additionally, as they age, spoonbills seem to better cope with migratory challenges and wintering conditions as no differences in apparent survival among wintering strategies were detected during subsequent years. As dispersal to other breeding colonies was rarely observed, the lower apparent survival during this period is likely partly driven by lower true survival. This supports the potential role of crossing of natural barriers and degradation of wintering sites in causing high mortality rates as recorded for a variety of long-distance migrants. Our work confirms variation in demographic parameters across winter distribution ranges and reinforces the importance of longitudinal studies to better understand the complex demographics of migratory species.

Keywords/phrases: apparent survival; capture-recapture; Cormack–Jolly–Seber models; life history; *Platalea leucorodia*; pre-breeding migration; resighting probability; seasonal migration; wintering strategies.

Introduction

Seasonal migration is a fascinating phenomenon in which animals travel between sites to take advantage of seasonal peaks in resources (Alerstam and Lindström, 1990; Dingle, 1980; Lok et al., 2015; Newton, 2008). However, migration is a challenging process (Alerstam et al., 2003), and different migratory decisions (e.g., migratory route and the selection of wintering site) may be associated with different fitness outcomes.

The considerable variation within and between species in wintering site use (Alerstam et al., 2003; Newton, 2008) has been suggested to affect demographic parameters, including survival and productivity (via carry-over effects) (Acker et al., 2021; Alves et al., 2013; Carneiro et al., 2021; Grist et al., 2017; Lok et al., 2015; Reid et al., 2020). Such associations could be due to a mixture of geographically and ecologically distinct environments, experienced by individuals at their wintering site or during migration (Boyle, 2008; Chapman et al., 2011; Gillis et al., 2008; Harrison et al., 2011; Hötker, 2003; Loonstra et al., 2019; Sergio et al., 2014; Swift et al., 2020). For instance, individuals of Pied avocets (*Recurvirostra avosetta*) wintering closer to the breeding site arrived earlier and fledged more chicks than those wintering further away (Hötker, 2003). Conversely, in Icelandic black-tailed godwits (*Limosa limosa islandica*), those wintering furthest arrived earlier at the breeding area (Alves et al., 2012), suggesting that distance by itself cannot explain variation on arrival dates, which in seasonal environments tends to be positively related to productivity (Alves et al., 2019; Morrison et al., 2019). Partial migration is an extreme case of within species variation (Chapman et al., 2011; Newton, 2008), where some individuals do not migrate at all (residents), while others do, which potentially leads to variation in key fitness components like survival (Gillis et al., 2008; Kokko, 2011). For example, resident American dippers (*Cinclus mexicanus*) were recorded to have higher annual productivity than migratory individuals, and slightly lower survival, indicating a possible trade-off between productivity and survival (Gillis et al., 2008).

Nevertheless, the underlying mechanisms linking survival and wintering site remain poorly understood, owing to the difficulty in following individual birds throughout their annual cycles (Lok et al., 2015). In fact, despite some studies showing the benefits of a shorter migration, in other systems, migrating further can be advantageous in terms of survival (Alves et al., 2013; Reneerkens et al., 2020) and/or productivity through carry-over effects

(Carneiro et al., 2021; Lourenço et al., 2008). Additionally, certain costs and benefits of wintering location can also vary depending on the age of the individual and the environmental conditions experienced at the wintering sites. This is the case for the Greater flamingo (*Phoenicopterus roseus*), where long-distance migration appears to be costly for young and inexperienced individuals, but beneficial for adults (Sanz-Aguilar et al., 2012). Furthermore, the survival of resident flamingos in Southern France seems to be severely impacted by cold spells estimated to occur every 25 years (Sanz-Aguilar et al., 2012).

The Eurasian spoonbill (*Platalea leucorodia leucorodia*, hereafter spoonbill) is a migratory waterbird species, distributed from the East-Atlantic Coast to Southeast Asia (Triplet et al., 2008). This species has been extensively monitored due to being easily detected (Pigniczki and Végvári, 2015; Triplet et al., 2008) and its potential as an umbrella species for ecosystem-level conservation of wetland areas (Jin et al., 2008; Lorenz et al., 2009; Schneider-Jacoby, 2008; Sergio et al., 2006, 2008).

In Europe, breeding spoonbills are currently divided in three distinct meta-populations (Champagnon et al., 2019c), each using different wintering sites located along different flyways: the East Atlantic Flyway meta-population (hereafter EAF population), which is steadily increasing at several breeding sites; the Central European Flyway meta-population, which is undergoing a moderate decline (hereafter CEF population; (Champagnon et al., 2019b); and the South-eastern European Flyway, that was recently separated from the CEF (Champagnon et al., 2019c) and which knowledge of migration, wintering and genetic differentiation are lacking (Kralj et al., 2023). During the past decade, the population dynamics and wintering site use of the Dutch breeding population have been studied, thereby providing detailed insight into the demography of the EAF population (Lok et al., 2011, 2013a, 2017). In this population, long-distance migrants had lower survival and reproductive output compared to short-distance migrants (Lok et al., 2011, 2017). In contrast, much less is known regarding the CEF population, despite several efforts to better understand the migration and dispersal patterns of individuals from several breeding colonies in Croatia, Hungary, and Italy (Azafzaf et al., 2006; Kralj et al., 2012; Mikuska et al., 2006; Pigniczki et al., 2016, 2020; Pigniczki, 2022). In this flyway, apparent survival was estimated for an expanding breeding colony in Italy (Tenan et al., 2017), however, no comparison between survival rates of individuals with different wintering sites was made.

The EAF and CEF populations were initially assumed to breed allopathically (i.e. not to overlap in the breeding area) (Brouwer, 1964; Müller, 1984), but by the end of the 20th century, breeding adults from both populations (EAF from Netherlands and CEF from Italy) settled in Camargue, Southern France (Blanchon et al., 2010). Individuals from this recent colony currently migrate along two distinct flyways: one within the EAF, following a south-western route to Spain and West Africa, and another within the CEF, following a south-eastern route to Italy and Tunisia. Additionally, and not previously described for the EAF and CEF populations, some individuals from this colony remain in Camargue all year around (i.e. residents) (Blanchon et al., 2019). Due to their wide array of migratory routes and distances, including residency, spoonbills from Camargue present a unique opportunity to not only further investigate the relationship between survival rates and migratory distance across wintering sites, but also to compare survival rates within and between different flyways, shedding light on the potential effects of crossing ecological barriers on survival, such as the Mediterranean Sea and the Sahara Desert.

Here, using resighting data collected at the main breeding area in Camargue and throughout the wintering range, we applied capture-mark-recapture models (Lebreton et al., 1992; Pradel, 2005) to explore the relationships between survival rate, migratory flyway and distance. (i) We compared the survival rates of individuals using different flyways (resident, EAF migrant and CEF migrant), predicting that, as suggested by the contrasting populations trends (Champagnon et al., 2019b), CEF migrants have lower survival rates than EAF migrants, potentially associated with habitat degradation in wintering sites such as Tunisia (OTEDD, 2016). (ii) We also explored the relationship between survival and migration distance, distinguishing long-distance vs short-distance migrants vs resident individuals, predicting that survival declines with increasing migration distance. In both flyways, only long-distance migrants encounter natural barriers (Sahara Desert – EAF / Mediterranean Sea – CEF), whose crossing involves high energy demands and few (or no) possibilities for emergency stopovers if needed, possibly leading to lower survival compared to short-distance migrants or resident individuals. The potential impact of crossing such barriers was also suggested by the lower survival rates of the long-distance migrants from Dutch colonies, likely influenced by the Sahara crossing during pre-breeding migration (Lok et al., 2015). (iii) Finally, we assess the interactive effect of flyway and distance by comparing differences in survival between birds with different wintering strategies (i.e., short-distance EAF migrants, long-distance EAF migrants, short-distance CEF migrants and long-distance CEF migrants, residents).

Material and Methods

Study population and data collection

This study is based on a long-term colour-ringing program on the breeding population of spoonbills in the Camargue, which settled in 1998 and reached more than 300 breeding pairs in 2018 (Blanchon et al., 2019; Marion, 2019). The Camargue is a semi-natural region of 180,000 ha making it the largest wetland in France (Galewski and Devictor, 2016; Roche et al., 2009). Here, spoonbills breed mainly on two small islands in a protected coastal lagoon (*Étang des Impériaux* – N43°28, E4°28).

Each year (from 2008 to 2020), between April and July, approximately 200-300 chicks around 20-25 days of age (prior to fledging) were fitted with a metal ring (with a unique alphanumeric code; FRP scheme) on one leg and an engraved PVC ring (white ring with a unique set of four black characters) on the other leg, to allow individual visual identification from a distance using a telescope or a camera (i.e., resighting). To minimize the risk of chick mortality, ringing operations occurred in the early morning (avoiding heat stress) and only under favourable weather conditions (i.e., no precipitation and/or strong winds).

From 2008 onwards, observations of previously marked individuals were performed during the incubation and early chick-rearing phase using a telescope at the breeding colony. Since 2016, these efforts were complemented with automated camera traps placed in the colony and moved regularly to survey different nests in different sections of the colony. For winter resightings, we relied on a large network of amateur and professional ornithologists and nature photographers, supplemented by dedicated expeditions to major wintering sites where resighting effort was low (i.e., Banc d’Arguin and Tunisia).

Data selection

A total of 3540 chicks were considered for this analysis (Appendix, Table A6.1 for further details), which resulted in ca. 16,000 resightings, of which ca. 10,000 during the breeding season (March to July) and ca. 3,000 during the winter (October to February). We excluded from our analysis: (i) individuals ringed as adults (n = 2), due to their low number; (ii) recoveries (n = 155) that mainly encompassed chicks that died before fledging and ring recoveries of which we did not know the time since death or if it corresponds to ring loss; (iii) individuals fitted with GPS tags, as these could have a potential effect in survival (n = 21) (Bodey et al., 2018; Pennycuick et al., 2012; Weiser et al., 2016); and (iv) duplicated rings that originated from a fieldwork error in one year (n = 22). During the breeding season only resightings from the *Étang des Impériaux* were considered and limited to one observation per individual per year, considering only records with no reading uncertainty, thus resulting in n_{Obs} = 1527 resightings.

We defined five wintering regions, considering both the migratory flyway (East Atlantic Flyway – EAF; Central European Flyway – CEF) and the distance travelled (long-distance – LD; short-distance – SD; and residents – RES; Figure 1 & Appendix, Table A6.1).

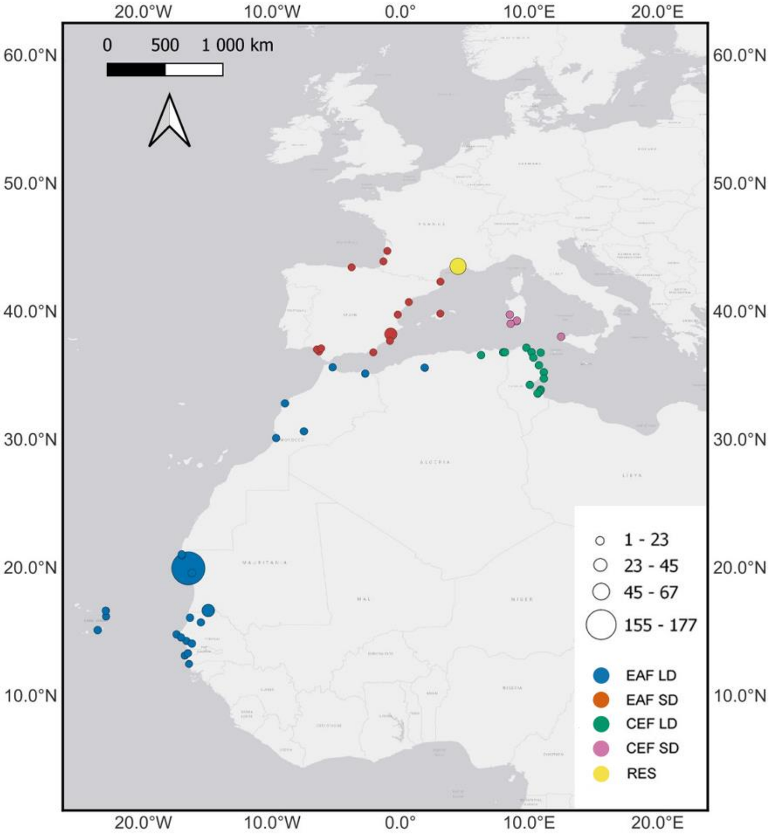

Fig. 1 – Distribution of the 484 individuals (size of circle indicates quantiles of individuals) according to their southernmost wintering site and flyway: EAF LD – long-distance migrants East-Atlantic Flyway: Cape Verde, Gambia, Morocco, Mauritania, Senegal, and West Algeria; EAF SD – short-distance migrants East-Atlantic Flyway: Portugal, Spain and Southwest France; CEF LD – long-distance migrants Central European Flyway: East Algeria and Tunisia; CEF SD – short-distance migrants Central European Flyway: Italy and Malta; RES – Residents in Camargue, France.

Note: Two individuals resighted in West Algeria were considered as EAF LD and not CEF LD, as recent GPS data of tagged individuals shows that some of the birds migrate through West Algeria while following the EAF (Lok, 2021).

Individuals were assigned to a wintering region according to the site where they were resighted during winter, which was defined as the period between October and February for long-distance migrants. To avoid the possible misclassification for the short-distance migrating (and resident) individuals due to a late-autumn or early-spring stopover resighting, we only considered winter resightings during the months of November to January (Lok et al., 2011; Navedo et al., 2010). In our analysis, we assumed that individuals do not change wintering site (Lok et al., 2013a). This was done to avoid overparameterization of the models with state uncertainty due to the small number of such records (n = 24) (Pradel, 2005). If an individual was observed at different sites within the same flyway, either within the same winter or in different winters, we selected the southernmost site as its winter site (n = 10). We excluded birds that changed their migratory flyway or switched from being migratory to resident or vice versa (n = 14). Three individuals resighted in South Sudan were excluded as these did not match any of the main wintering areas and their number was very limited. Since the main objective of this study is to understand how wintering strategies affect the survival of the Camargue spoonbills, we only considered individuals for which their wintering sites were known. Therefore, we excluded birds that were not seen in winter. Hence, the first winter resighting marked the start of an individual's encounter history, thus resulting in 484 individuals distributed among the various wintering strategies (Appendix, Table A6.1).

Mark-Recapture modelling and statistical analysis

To estimate the survival rates of spoonbills, we developed Cormack–Jolly–Seber models (CJS) (Cormack, 1964; Jolly, 1965; Seber, 1965) in E-surge v. 2.2.3 (Choquet et al., 2009b), which provided a flexible modelling framework to develop, constrain and rank complex mark-recapture models (Pradel, 2005, 2009).

In our study, all individuals have an initial state of alive at the wintering site, hence the initial state probability was fixed to "1". As for the transition probabilities, we assumed that our individuals did not change wintering and breeding sites, and therefore the only transition probability considered was in fact survival probability (Lok et al., 2013). As we only used resightings in the Camargue to estimate survival, permanent emigration from this breeding site cannot be distinguished from mortality (Lebreton et al., 1992). As such, the resulting estimates reflected "apparent" or "local" survival (Lebreton et al., 1992). Finally, the models also estimated the probability of being resighted at the *Étang des Impériaux* (p) during the breeding season. Since the initial state is alive at the wintering site and only resightings at the breeding site were considered in subsequent occasions, survival during the first interval (hereafter Φ^1) corresponds to the probability that an individual survived from the winter when it was first observed until the next breeding period (for details regarding the age at first sighting, see Appendix, Table A6.2). Therefore, the first interval is shorter (half a year) than the subsequent intervals that correspond to a full year, from one breeding season to the next (hereafter Φ^{2+}). Due to lack of data, subsequent resightings obtained at wintering sites were not used. As a result, Φ^{2+} reflects the apparent survival of birds that survived and returned to the breeding grounds after their first winter observation, while Φ^{1} includes any residual mortality occurring prior to return to the breeding grounds, or permanent emigration from the breeding grounds, that cannot be explained by the Φ^{2+} estimates.

In capture-mark-recapture models, the goodness-of-fit test allows to assess if the data does not infringe any assumption of parameter homogeneity (Burnham et al., 1987; Lebreton et al., 1992; Pradel et al., 1997). We used program U-Care V2.3.4 (Choquet et al., 2005, 2009a) to test the goodness-of-fit of the CJS model $\Phi_{g*t}\ p_{g*t}$ to the data with the five previously defined wintering regions (Fig. 1) as groups (*g*). This model does not account for time-since-marking (or in this case, time since the first winter sighting) or age effects. TEST3sr estimated a lack of fit possibly caused by transients and/or the shorter first time interval (6 months) compared to later intervals (12 months; $\chi^2 = 126.07$, $df = 26$, $P \leq 0.001$) which was accounted for by separately estimating Φ^{1} and Φ^{2+} (Pradel et al., 1997). The remaining lack of fit (as estimated by TEST2 and TEST3sm) was accounted for by adjusting for overdispersion ($\hat{c} = \chi^2/df = 93.56/68 = 1.38$) (Choquet et al., 2005).

As reported by Lok et al. in previous studies (2009, 2017) and substantiated by observations at the study colony (Champagnon et al., 2019a), spoonbills have delayed maturity and usually start breeding in their fourth calendar year (*cy*) (Cramp and Simmons, 1977). Until reaching maturity, spoonbills usually stay at the wintering grounds. Combined with the fact that the first interval after the first winter sighting is only half a year, the goodness-of-fit model (Model 1, Appendix, Table A6.3) does not correspond to our general biologically meaningful model. In our general model, survival was constrained as a function of the following explanatory variables: (i) time since first winter observation (categorical with two levels: Φ^{1}, half year interval from first winter observation to next breeding season vs Φ^{2+}, subsequent one-year intervals); (ii) age class (*2age*, categorical with two levels: immatures (0.5-3.5 cy) and adults (4^{+} cy)). Individuals were categorized in groups according to their age at first winter resighting, which allowed us to estimated age-specific survival and resighting probabilities. For example, if an individual was observed for the first time in winter in its 1st winter, it starts its encounter history as 0.5 cy, but will be considered an adult (4^+ cy) as soon as it reaches its fourth breeding season; (iii) wintering region (a categorical interaction of distance and migratory flyway (*Dis*Fly*), resulting in five levels: EAF LD, EAF SD, CEF LD, CEF SD and RES); and (iv) year (*t*, categorical with 12 levels). Resighting probability was modelled as a function of: (i) three age classes (*3age*, categorical with three levels: 2 cy, 3 cy and 4^+ cy - adult). Although spoonbills usually remain at the wintering grounds through their third winter (until reaching maturity), some immature birds do return to the colony and can thus be resighted (Lok et al., 2013b; Tenan et al., 2017); (ii) annual variation (*t*, categorical with 13 levels); and (iii) migration distance (*Dis:* LD; SD; RES), as long-distance migrants may have a shorter stay at the breeding sites, owing to delayed arrival in spring and/or earlier departure in autumn. This could translate into a shorter probability of being resighted compared to short-distance migrating or resident birds (Lok et al., 2013a). Although annual variation was included, between 2008-2013, the estimates were fixed to zero due to the absolute lack of resightings despite field efforts. As an alternative to modelling annual variation in *p*, we considered models in which *p* differed between three periods according to whether camera traps were used (*Ct*): (i) 2008-2013 fixed to zero; (ii) 2014-2015, efforts without camera traps; and (iii) 2016-2020, efforts with camera traps. Our final full complex model is $\Phi^{1}_{2age*Dis*Fly*t}\ \Phi^{2+}_{2age*Dis*Fly*t}\ p_{3age*Dis*Fly*t}$. However, only the interactions between *dis* and *Fly* (EAF; CEF; RES) were considered afterwards, as testing interactions with year and age led to problems of parameter identifiability due to the data being scarce for some wintering strategies, years, and age classes. Based on previous findings (Lok et al., 2013b), we accounted for a potential effect of age on survival and resighting probabilities in all models. Subsequently, different models were developed and variables of interest compared following a *stepwise* approach with a two-step process (Anderson and Burnham, 2002; Grosbois and Tavecchia, 2003; Lebreton et al., 1992). First, we kept survival fully parameterized while we constrained the parameterization of resighting probability (*p*). Using the best-supported parameterization of *p,* we then constrained the parameterization of survival probabilities (Doherty et al., 2012; Grosbois and Tavecchia, 2003) during the first and/or subsequent intervals (Φ^{1} versus Φ^{2+}). To confirm the robustness of our selection procedure, as the survival and resighting probability parameters are not entirely independent in these models, we repeated this process, while reversing the order of the two steps by first constraining the parameterization of survival probability and then of resighting probability (Doherty et al., 2012). Parameter estimates and profile likelihood confidence intervals from the best-supported model are reported. Model selection was based on the Akaike Information Criterion, adjusted for small sample sizes and overdispersion (QAIC$_c$), considering a better model fit when $\Delta QAIC_c < 2$ (Anderson and Burnham, 2002). When there were multiple models within two QAIC$_\mathbf{c}$ points of the best-supported model, the model with the fewest parameters was selected (i.e., the most parsimonious model, Anderson and Burnham 2002).

Permanent emigration cases

To approximate true survival, we calculated the possible cases of permanent emigration in our dataset. For individuals that were not resighted again after their first winter sighting, we checked whether they were subsequently seen during spring or summer (March to July) en route to/from or at breeding sites outside the Camargue in the EAF and CEF. If so, we considered them as 'possible permanent emigration case'. From these cases, we calculated the 'minimal' permanent emigration probabilities per wintering region and divided it by the total number of individuals never seen again per wintering region. We then approximated true survival by correcting the estimated apparent survival per wintering region during the first half-year interval with these 'minimal' permanent emigration probabilities, where true survival = Φ^1 / (1- permanent emigration).

Results

When applying the *stepwise* approach by first constraining the resighting probability, the best-supported parameterization for resighting probability included camera trap use (*Ct*), three age classes (*3age*) and migration distance (*Dis*) effects (Model 4, Appendix, Table A6.3). Resighting probability was higher in years when camera traps were used, lower for long-distance migrants and increased with age (Fig. 2).

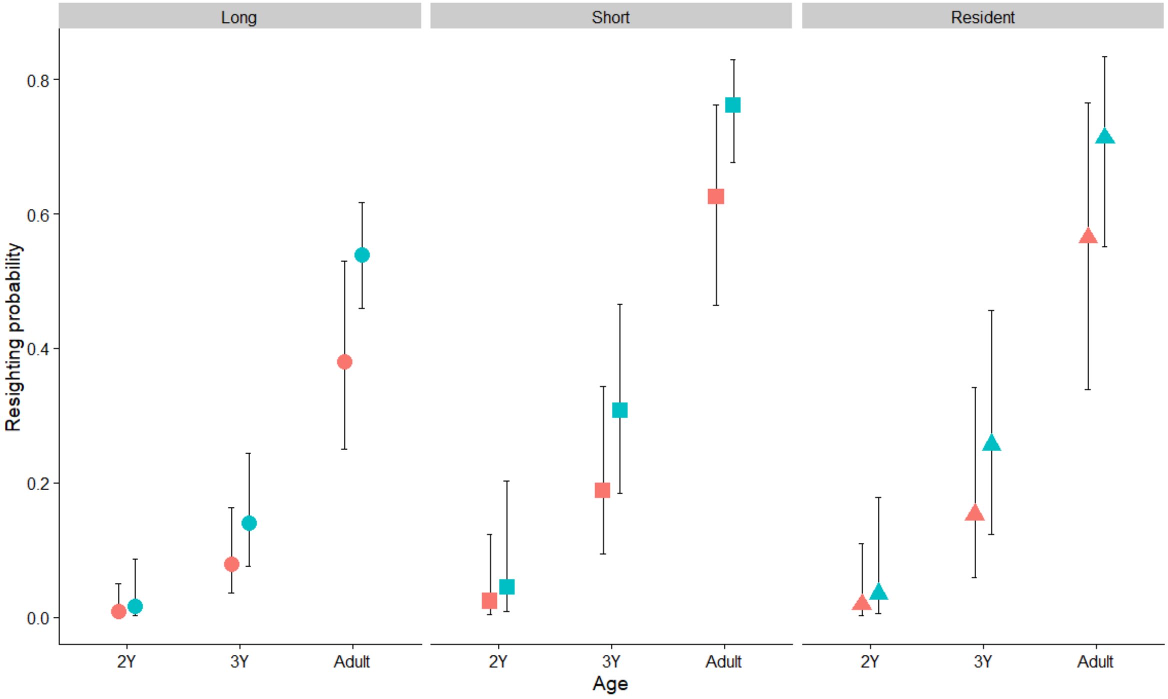

Fig. 2 – Resighting probability of spoonbills according to age class (*2Y* = 2 calendar-years; *3Y* = 3 calendar-years; AD = adult), use of camera traps (red – no camera trap used; green – camera trap used) and migration distance (Long; Short; Resident). Estimates are based on the best-supported model from Table 1 (Model 100). Vertical lines indicate 95% confidence intervals.

Using the best-supported parameterization of resighting probability, three competitive parameterizations for survival with $QAIC_c < 2$ were identified, which included either an effect of migratory flyway and/or distance on survival during the first half-year interval (Φ^1, Table 1). The best-supported and most parsimonious model contained an effect of age and migration distance on Φ^1 and of age on Φ^{2+}, with $\Delta QAIC_c = -13$ compared to the model without an effect of migration distance (Model 110, Appendix, Table A6.3). The same most parsimonious model was selected when applying the reverse *stepwise* approach (Model 104, Appendix, Table A6.4).

Table 1. Model results of survival probability from the *stepwise* approach.

Model	ϕ^1	ϕ^{2+}	*K*	Deviance	ΔQAIC$_c$	Akaike weight
100	***2age + Dis***	***2age***	**12**	**1397.9**	**0.0***	**0.37**
70	*2age + Dis*Fly*	*2age*	14	1392.7	0.3	0.34
80	*2age + Dis + Fly*	*2age*	13	1397.3	1.7	0.19
98	*2age + Dis*	*2age + Fly*	14	1396.8	3.3	0.04
99	*2age + Dis*	*2age + Dis*	14	1397.4	3.8	0.02
68	*2age + Dis*Fly*	*2age + Fly*	16	1392.2	4.1	0.01
69	*2age + Dis*Fly*	*2age + Dis*	16	1392.2	4.1	0.01

Abbreviations: Φ^1= apparent survival first half year Φ^{2+} = apparent survival subsequent full years; *K* = number of parameters; *2age* = 2 age classes: immatures (0.5-3.5 cy) and adults (4^+ cy); *Dis* = migration distance; *Dis*Fly* = wintering region; *Fly* = migratory flyway.

Notes: *QAIC$_c$ = 1040.35. Models were ranked according to the Akaike weight and only models with an Akaike weight of ≥ 0.01 are shown (the complete model results are shown in Appendix, Table A6.3). The best-supported model is indicated in bold.

Apparent survival of spoonbills during the first half-year interval (Φ^1) was lower for long-distance migrants compared to residents and short-distance migrants, who had similar survival (Figure 3a). During the second interval survival ($\Phi 2^{2+}$) was of 0.86 (0.64 – 0.92, 95%CI) for immatures and 0.94 (0.88 – 0.97, 95%CI) for adults. When considering the second-best model (Table 1, Model 70), which included the interaction between migration distance and flyway, survival of short-distance migrants appeared to differ between flyways, with CEF SD having lower survival than EAF SD (Figure 3b). There was no support for an effect of migratory flyway or distance on survival after the first half year period (Φ^{2+}).

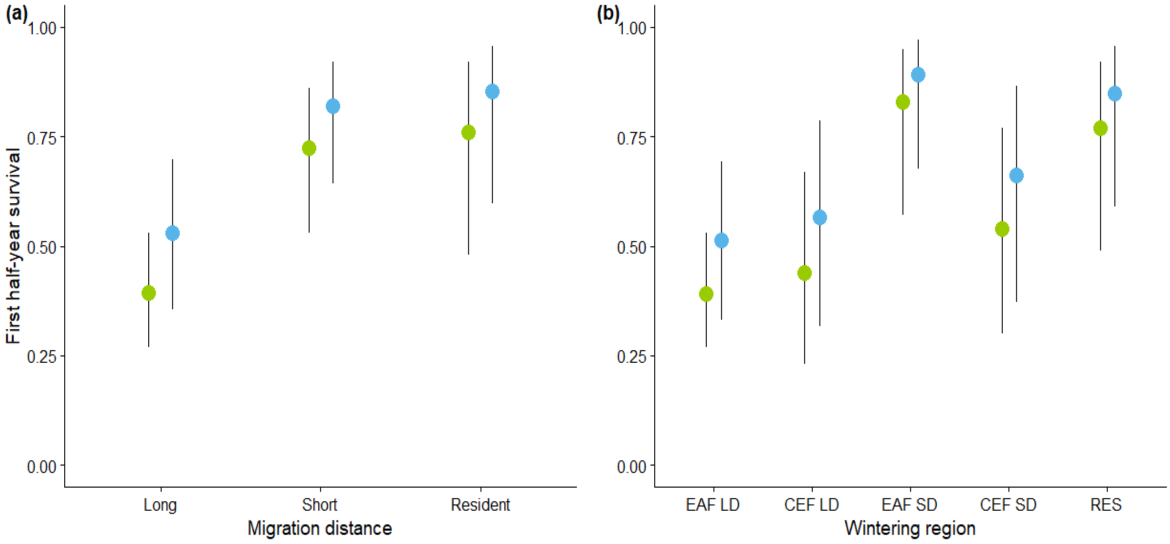

Fig. 3 – Apparent survival estimates of immature (green) and adult (blue) spoonbills during the first half-year interval (Φ^1) (a) according to migration distance (Long; Short; Resident) as estimated by the best supported model of the Table 1 (Model 100, Φ^1: *2age+Dis*) and (b) according to the wintering region (East Atlantic Flyway long-distance – EAF LD; Central European Flyway long-distance – CEF LD; East Atlantic Flyway short-distance – EAF SD; Central European Flyway short-distance – CEF SD; Resident – RES) as estimated by the second-best model in Table 1 (Model 70, Φ^1: *2age+Dis*Fly*). The *2age* variable corresponds to two age classes: immatures (0.5-3.5 cy) and adults (4^+ cy). Vertical lines indicate 95% confidence intervals.

When considering the possible permanent emigration cases of Table 2, permanent emigration was estimated to be highest in EAF LD (11%), intermediate for EAF SD and CEF SD (7% and 6%) and very low for CEF LD (1%) and RES (2%). This would imply a "true survival" rate of 0.37 and 0.58 for immatures and adults performing long-distance migration, which is still considerably lower than the estimates of 0.77 and 0.88 for immature and adult short-distance migrants and 0.79 and 0.87 for resident birds.

Table 2. Number of individual spoonbills wintering in each region, number of individuals never recorded again after their first winter resighting at the breeding site in Camargue and number of individuals observed on their way from/to or at breeding sites other than Camargue.

Wintering region	Total	Not recorded again	Possible permanent emigration cases	
			Number of individuals	%[1]
EAF LD	257	195	29	11%
EAF SD	71	26	5	7%
CEF LD	75	57	1	1%
CEF SD	33	19	2	6%
RES	48	19	1	2%

Abbreviations: East Atlantic Flyway long-distance – EAF LD; East Atlantic Flyway short-distance – EAF SD; Central European Flyway long-distance – CEF LD; Central European Flyway short-distance – CEF SD; resident – RES.

Note[1]: Percentage was calculated by dividing the number of potentially permanently emigrated individuals by the total number of individuals in each winter region.

Discussion

Our results do not support differences in survival rates of Camargue spoonbills following different migratory flyways, as flyway was not included in the best-supported model. This contradicts our initial prediction that individuals using the Central European Flyway would have lower survival than the individuals with other migratory routes or behaviours, given the apparent decreasing trend of this population and the degradation of wintering sites in Tunisia (Champagnon et al., 2019b; OTEDD, 2016). Yet, confirming our initial prediction, we did find a correlation between migration distance and apparent survival, but only in the first half year, not in subsequent years.

As we only use resightings performed in Camargue, our estimates of Φ^1 and Φ^{2+} reflect apparent survival, which is the product of true survival and permanent emigration. Although usually highly philopatric, breeding dispersal (i.e., permanent emigration) from the Camargue to other European breeding sites may sometimes occur (Cilimburg et al., 2002; Lebreton et al., 1992; Lindberg et al., 2007). Like White storks (*Ciconia ciconia*) (Chernetsov et al., 2004), spoonbills are social birds, also during their migration (de Goeij et al., 2012; Lok et al., 2019; Navedo and Garaita, 2012), where social interactions likely influence the decisions of immatures regarding when and where to migrate (Aikens et al., 2022). When wintering along the Atlantic coast of Africa (EAF LD region – Cape Verde, Gambia, Mauritania, Morocco, Senegal, and West Algeria), individuals from Camargue mix with spoonbills from other EAF breeding populations (e.g., Dutch & Iberian). Likewise, individuals wintering in Northeast Africa (CEF LD region – East Algeria & Tunisia) mix with spoonbills from breeding populations like Hungary and Italy. Thus, immatures from Camargue could possibly follow adults from other breeding populations to their breeding sites in South- and North-Western Europe (EAF) or Italy and Central Europe (CEF).

The lower apparent survival in the first half-year interval after the first winter sighting (Φ^1) of long-distance migrants may therefore be partially driven by a higher probability of permanent emigration of Camargue spoonbills to other breeding sites (Cilimburg et al., 2002; Lebreton et al., 1992; Lindberg et al., 2007). Nevertheless, despite considerable observation efforts along the migratory flyways and in other European breeding sites (Lok et al., 2013a; Pigniczki, 2017), only few individuals from our dataset were resighted along migratory routes to or in other breeding sites. Furthermore, differences in survival rates between wintering regions persisted even after correcting for winter-region specific 'minimal' permanent emigration probabilities (Table 2).

To estimate Φ^{2+}, only resightings in Camargue during the breeding season were considered. Thus, Φ^{2+} reflects survival of individuals that survived and returned to the breeding site at least once after their first winter observation. Most birds were still relatively young (≤5 years old, Appendix, Table A6.2) when seen for the first time at their wintering sites. As spoonbills usually only start breeding when they are 4 years old, and usually stay at the wintering site until that age, most of these individuals are yet to make their first return migration. Therefore, our finding that the effect of migration distance was only supported for Φ^1 and not Φ^{2+} could imply that the increased mortality of long-distance migrants primarily occurred before their first return to the breeding grounds, i.e., either at the wintering grounds or during the first return migration. Mortality may also have been higher for juveniles attempting to migrate long distances during their first southward migration compared to resident or short-distance migrating juveniles, but since our analysis started at the first winter sighting, this potential effect on juvenile survival could not be estimated. After their first return migration, spoonbills appeared experienced enough to be equally likely to survive the next annual cycle independently of where they winter. In fact, the apparent survival of adult Camargue long-distance migrants after the first half-year ($\Phi_{ad}^{2+}=$ 0.94, 94% CI [0.88–0.96]) is higher than that of long-distance migrants in the Dutch population (Lok et al., 2015). This partly supports our hypothesis that despite the lower apparent survival of long-distance migrants being mainly driven by higher mortality, with experience, spoonbills seem to successfully respond to migration challenges independently of the wintering region used.

As shown in other studies (Alves et al., 2013; Lok et al., 2015), the variation in survival detected in our study is not fully explained by migration distance. In fact, there are likely additional factors contributing to the observed variation in mortality, such as the crossing of natural barriers and habitat degradation. Reaching the wintering sites south of the Sahara clearly involves travelling a longer distance than reaching Tunisia, yet no difference in survival between these two wintering regions was detected in the top-ranking models. In both cases, however, individuals must cross a natural barrier, namely the Sahara Desert in the East Atlantic Flyway and the Mediterranean Sea (between France, Sardinia, and Tunisia) in the Central European Flyway. Similarly, the majority of CEF SD individuals are wintering on the island of Sardinia and therefore also must cross part of the Mediterranean Sea. This could be part of the reason why they have lower survival compared to individuals wintering in the EAF SD region and those resident to the Camargue, who do not have to cross any natural barriers.

Habitat degradation has also been reported to cause population declines in migratory species (Morrison et al., 2001; Piersma et al., 2016; Studds et al., 2017). Hence, the deterioration of wintering and stop-over sites in Africa could amplify the difficulties of undertaking a long-distance migration (Brochet et al., 2016) that involves the crossing of natural barriers. In contrast, in some European wintering sites, changes in water management as well as enforced wetland protection (e.g., European Union's Birds and Habitats Directives; Water Framework Directive – 2000/60/EC) are likely to have improved stopover and wintering conditions in Europe (Donald et al., 2007; Novo and Cabrera, 2006). Additionally, winter temperatures in France and Iberia have increased over the last decades, which reduced the thermoregulation costs of spoonbills wintering in Europe and may also have increased food availability (Klein et al., 2002; Lok et al., 2013a; Shukla et al., 2019).

Although the migratory flyway effect was not included in the best-supported model, the second-best model included an interaction between migration distance and flyway, implying that the distance effect on survival differed depending on the flyway taken. This model (Model 70, Table 1) estimated similar survival for EAF LD, CEF LD and CEF SD migrants that was lower than the survival of EAF SD and RES birds (Figure 3b). That this was not the best-supported model may be due to the relatively low sample sizes of birds with known wintering site in the Central European Flyway (Appendix, Table A6.1), causing large confidence intervals around the survival estimates of CEF migrants (Figure 3b). Assuming that spoonbills from other CEF breeding sites experience similarly low survival as we estimated for the CEF SD and CEF LD migrants from the Camargue, while a high and increasing proportion of the EAF spoonbills use high survival regions in France and Spain (Lok et al., 2013a), this could explain the contrasting population trends of the CEF (slightly declining) versus the EAF (increasing) meta-population (Champagnon et al., 2019b). The decline of the CEF meta-population is mainly driven by the Hungarian population (Champagnon et al., 2019b), from which spoonbills are mainly seen wintering in Gulf of Gabes (Tunisia, Pigniczki, 2022). Nevertheless, spoonbills from the Italian population have high adult survival rates (0.91, 95%CI [0.85–0.96]) and this population is currently increasing (Tenan et al., 2017), contrasting to the overall slight decline of the entire CEF meta-population. To better understand the causes of the different trends, we strongly advocate for an analysis combining the several interconnected spoonbill populations throughout Europe, not only to get more precise survival estimates for the different wintering regions, but also to estimate the proportion of birds from the CEF and EAF populations wintering in regions associated with relatively low or high survival.

Despite considerable variation within and among species in wintering site use being previously shown to affect demographic parameters, few longitudinal studies have been able to compare the survival rates of a population using different flyways or migratory ranges (specifically contrasting residency vs short-distance vs long-distance). While confirming previous studies by Lok and collaborators that indicated lower survival of long-distance migrating spoonbills (Lok et al., 2011, 2013a, 2015), this study is the first to indicate that such survival cost becomes apparent during the first return migration. Additionally, our results highlighted that spoonbills seem to better cope with migratory challenges and wintering conditions as they age. Our study therefore highlights the heterogeneity in demographic parameters across wintering ranges, but also the relevance of long-term studies to better understand the complex demography of a migratory species and thus help prioritise conservation priorities according to population dynamics and connectivity.

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Ethics approval

All fieldwork procedures were compliant with applicable animal welfare regulations by the Centre de Recherches sur la Biologie des Populations d'Oiseaux (Museum National d'Histoire Naturelle, [https://crbpo.mnhn.fr]), programme personnel 580.

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Appendices 6

Table A6.1. Number of spoonbills ringed and resighted in winter, in total and per wintering region, specified per year of birth, and the number of different spoonbills resighted per wintering region during summer in *Etang des Impériaux, Camargue,* specified per year.

			Resighted per wintering region							No. of different birds resighted in *Etang des Impériaux* per wintering region				
Year of birth	Ringed	Seen in winter	EAF LD	EAF SD	CEF LD	CEF SD	RES	Summer Year	Seen in summer	EAF LD	EAF SD	CEF LD	CEF SD	RES
2008	30	4	4	0	0	0	0	2009	0	0	0	0	0	0
2009	55	24	10	11	1	2	0	2010	0	0	0	0	0	0
2010	140	35	19	12	3	1	0	2011	0	0	0	0	0	0
2011	240	57	31	10	12	1	3	2012	0	0	0	0	0	0
2012	224	67	40	6	12	3	6	2013	0	0	0	0	0	0
2013	262	101	80	14	1	4	2	2014	23	11	9	1	1	1
2014	542	114	45	12	23	14	20	2015	36	14	13	3	3	3
2015	401	133	78	18	16	7	14	2016	74	24	25	4	6	15
2016	454	53	30	8	7	3	5	2017	86	29	27	6	7	17
2017	370	44	24	5	10	3	2	2018	119	38	35	17	8	21
2018	73	32	12	4	9	4	3	2019	111	35	34	10	10	22
2019	421	54	30	5	12	4	3	2020	105	30	34	11	8	22
2020	228	24	19	0	2	0	3							

Abbreviations: East Atlantic Flyway long-distance – EAF LD; East Atlantic Flyway short-distance – EAF SD; Central European Flyway long-distance – CEF LD; Central European Flyway short-distance – CEF SD; resident – RES.

Table A6.2. Number of individual spoonbills seen for the first time at the wintering site by age.

Age	Number of different individuals seen for the first time
1st winter (= 0.5 cy)	227
2nd winter (= 1.5 cy)	90
3rd winter (= 2.5 cy)	57
4th winter (= 3.5 cy)	39
5th winter (= 4.5 cy)	33
>5th winter (> 4+ cy)	38

Table A6.3. *Stepwise* approach, model selection results by step.

	Model	ϕ^1	ϕ^{2+}	*p*	*K*	Deviance	$\Delta QAIC_c$
Step 1 - Selection on p	**1****	*Dis*Fly * t*		*Dis*Fly * t*	87	2116.4	690.9
	2	*2age * Dis*Fly * t*	*2age * Dis*Fly * t*	*Dis * 3age * t*	167	1197.2	241.5
	3	*2age * Dis*Fly * t*	*2age * Dis*Fly * t*	*Dis + 3age + t*	136	1235.0	178.8
	4	***2age * Dis*Fly * t***	***2age * Dis*Fly * t***	***Dis + 3age + Ct***	**131**	**1255.4**	**179.7**
	5	*2age * Dis*Fly * t*	*2age * Dis*Fly * t*	*Dis + 2age + Ct*	130	1267.9	186.0
	6	*2age * Dis*Fly * t*	*2age * Dis*Fly * t*	*Dis + Ct*	129	1370.8	258.0
	7	*2age * Dis*Fly * t*	*2age * Dis*Fly * t*	*Ct + 3age*	129	1276.9	189.8
	8	*2age * Dis*Fly * t*	*2age * Dis*Fly * t*	*Ct*	127	1384.3	262.4
	9	*2age * Dis*Fly * t*	*2age * Dis*Fly * t*	*3age*	133	1319.3	231.7
	10	*2age * Dis*Fly * t*	*2age * Dis*Fly * t*	*c*	131	1474.6	338.8
Step 2 - Selection on S	**11**	*2age + Dis*Fly + t*	*2age + Dis*Fly + t*	*Dis + 3age + Ct*	37	1357.5	23.6
	12	*2age + Dis*Fly + t*	*2age + Dis + Fly + t*	*Dis + 3age + Ct*	36	1357.8	21.7
	13	*2age + Dis*Fly + t*	*2age + Fly + t*	*Dis + 3age + Ct*	35	1358.8	20.2
	14	*2age + Dis*Fly + t*	*2age + Dis + t*	*Dis + 3age + Ct*	35	1358.2	19.8
	15	*2age + Dis*Fly + t*	*2age + t*	*Dis + 3age + Ct*	33	1359.6	16.5
	16	*2age + Dis*Fly + t*	*2age + Dis*Fly*	*Dis + 3age + Ct*	29	1365.1	11.9
	17	*2age + Dis*Fly + t*	*2age + Fly + Dis*	*Dis + 3age + Ct*	28	1365.5	10.0
	18	*2age + Dis*Fly + t*	*2age + Fly*	*Dis + 3age + Ct*	27	1366.6	8.7
	19	*2age + Dis*Fly + t*	*2age + Dis*	*Dis + 3age + Ct*	27	1366.0	8.2
	20	*2age + Dis*Fly + t*	*2age*	*Dis + 3age + Ct*	25	1367.3	4.9
	21	*2age + Dis + Fly + t*	*2age + Dis*Fly + t*	*Dis + 3age + Ct*	36	1362.7	25.2
	22	*2age + Dis + Fly + t*	*2age + Dis + Fly + t*	*Dis + 3age + Ct*	35	1362.9	23.1

23	_2age + Dis + Fly + t_	_2age + Fly + t_	_Dis + 3age + Ct_	34	1363.9	21.7
24	_2age + Dis + Fly + t_	_2age + Dis + t_	_Dis + 3age + Ct_	34	1363.1	21.1
25	_2age + Dis + Fly + t_	_2age + t_	_Dis + 3age + Ct_	32	1364.5	17.8
26	_2age + Dis + Fly + t_	_2age + Dis*Fly_	_Dis + 3age + Ct_	28	1369.7	13.0
27	_2age + Dis + Fly + t_	_2age + Fly + Dis_	_Dis + 3age + Ct_	27	1369.9	11.1
28	_2age + Dis + Fly + t_	_2age + Fly_	_Dis + 3age + Ct_	26	1371.1	9.8
29	_2age + Dis + Fly + t_	_2age + Dis_	_Dis + 3age + Ct_	26	1370.2	9.2
30	_2age + Dis + Fly + t_	_2age_	_Dis + 3age + Ct_	24	1371.8	6.1
31	_2age + Fly + t_	_2age + Dis*Fly + t_	_Dis + 3age + Ct_	35	1376.1	32.8
32	_2age + Fly + t_	_2age + Dis + Fly + t_	_Dis + 3age + Ct_	34	1376.9	31.2
33	_2age + Fly + t_	_2age + Fly + t_	_Dis + 3age + Ct_	33	1386.8	36.2
34	_2age + Fly + t_	_2age + Dis + t_	_Dis + 3age + Ct_	33	1378.6	30.2
35	_2age + Fly + t_	_2age + t_	_Dis + 3age + Ct_	31	1388.4	33.0
36	_2age + Fly + t_	_2age + Dis*Fly_	_Dis + 3age + Ct_	27	1382.1	19.9
37	_2age + Fly + t_	_2age + Fly + Dis_	_Dis + 3age + Ct_	26	1382.5	18.0
38	_2age + Fly + t_	_2age + Fly_	_Dis + 3age + Ct_	25	1393.9	24.2
39	_2age + Fly + t_	_2age + Dis_	_Dis + 3age + Ct_	25	1382.6	16.0
40	_2age + Fly + t_	_2age_	_Dis + 3age + Ct_	23	1394.7	20.6
41	_2age + Dis + t_	_2age + Dis*Fly + t_	_Dis + 3age + Ct_	35	1363.3	23.5
42	_2age + Dis + t_	_2age + Dis + Fly + t_	_Dis + 3age + Ct_	34	1363.5	21.4
43	_2age + Dis + t_	_2age + Fly + t_	_Dis + 3age + Ct_	33	1364.4	19.9
44	_2age + Dis + t_	_2age + Dis + t_	_Dis + 3age + Ct_	33	1364.5	20.0
45	_2age + Dis + t_	_2age + t_	_Dis + 3age + Ct_	31	1365.8	16.6
46	_2age + Dis + t_	_2age + Dis*Fly_	_Dis + 3age + Ct_	27	1370.0	11.1
47	_2age + Dis + t_	_2age + Fly + Dis_	_Dis + 3age + Ct_	26	1370.2	9.1
48	_2age + Dis + t_	_2age + Fly_	_Dis + 3age + Ct_	25	1371.3	7.8
49	_2age + Dis + t_	_2age + Dis_	_Dis + 3age + Ct_	25	1371.2	7.8
50	_2age + Dis + t_	_2age_	_Dis + 3age + Ct_	23	1372.8	4.7
51	_2age + t_	_2age + Dis*Fly + t_	_Dis + 3age + Ct_	33	1383.0	33.5
52	_2age + t_	_2age + Dis + Fly + t_	_Dis + 3age + Ct_	32	1383.9	31.9
53	_2age + t_	_2age + Fly + t_	_Dis + 3age + Ct_	31	1394.8	37.7
54	_2age + t_	_2age + Dis + t_	_Dis + 3age + Ct_	31	1385.1	30.7
55	_2age + t_	_2age + t_	_Dis + 3age + Ct_	29	1397.1	35.1
56	_2age + t_	_2age + Dis*Fly_	_Dis + 3age + Ct_	25	1389.5	21.0
57	_2age + t_	_2age + Fly + Dis_	_Dis + 3age + Ct_	24	1390.0	19.3
58	_2age + t_	_2age + Fly_	_Dis + 3age + Ct_	23	1402.9	26.6
59	_2age + t_	_2age + Dis_	_Dis + 3age + Ct_	23	1390.4	17.5
60	_2age + t_	_2age_	_Dis + 3age + Ct_	21	1404.4	23.5
61	_2age + Dis*Fly_	_2age + Dis*Fly + t_	_Dis + 3age + Ct_	28	1378.5	19.4
62	_2age + Dis*Fly_	_2age + Dis + Fly + t_	_Dis + 3age + Ct_	27	1378.6	17.3
63	_2age + Dis*Fly_	_2age + Fly + t_	_Dis + 3age + Ct_	26	1379.7	16.1
64	_2age + Dis*Fly_	_2age + Dis + t_	_Dis + 3age + Ct_	26	1378.6	15.2
65	_2age + Dis*Fly_	_2age + t_	_Dis + 3age + Ct_	24	1380.7	12.5
66	_2age + Dis*Fly_	_2age + Dis*Fly_	_Dis + 3age + Ct_	18	1391.5	7.8

67	*2age + Dis*Fly*	*2age + Fly + Dis*	*Dis + 3age + Ct*	17	1391.8	5.9
68	*2age + Dis*Fly*	*2age + Fly*	*Dis + 3age + Ct*	16	1392.2	4.1
69	*2age + Dis*Fly*	*2age + Dis*	*Dis + 3age + Ct*	16	1392.2	4.1
70	*2age + Dis*Fly*	*2age*	*Dis + 3age + Ct*	14	1392.7	0.3
71	*2age + Fly + Dis*	*2age + Dis*Fly + t*	*Dis + 3age + Ct*	27	1382.5	20.2
72	*2age + Fly + Dis*	*2age + Dis + Fly + t*	*Dis + 3age + Ct*	26	1383.0	18.4
73	*2age + Fly + Dis*	*2age + Fly + t*	*Dis + 3age + Ct*	25	1384.3	17.3
74	*2age + Fly + Dis*	*2age + Dis + t*	*Dis + 3age + Ct*	25	1383.0	16.3
75	*2age + Fly + Dis*	*2age + t*	*Dis + 3age + Ct*	23	1385.3	13.7
76	*2age + Fly + Dis*	*2age + Dis*Fly*	*Dis + 3age + Ct*	17	1396.2	9.1
77	*2age + Fly + Dis*	*2age + Fly + Dis*	*Dis + 3age + Ct*	16	1396.4	7.2
78	*2age + Fly + Dis*	*2age + Fly*	*Dis + 3age + Ct*	15	1396.7	5.3
79	*2age + Fly + Dis*	*2age + Dis*	*Dis + 3age + Ct*	15	1396.8	5.4
80	*2age + Fly + Dis*	*2age*	*Dis + 3age + Ct*	13	1397.4	1.7
81	*2age + Fly*	*2age + Dis*Fly + t*	*Dis + 3age + Ct*	26	1394.4	26.7
82	*2age + Fly*	*2age + Dis + Fly + t*	*Dis + 3age + Ct*	25	1394.7	24.9
83	*2age + Fly*	*2age + Fly + t*	*Dis + 3age + Ct*	24	1403.5	29.1
84	*2age + Fly*	*2age + Dis + t*	*Dis + 3age + Ct*	24	1394.8	22.7
85	*2age + Fly*	*2age + t*	*Dis + 3age + Ct*	22	1404.9	25.9
86	*2age + Fly*	*2age + Dis*Fly*	*Dis + 3age + Ct*	16	1407.1	14.9
87	*2age + Fly*	*2age + Fly + Dis*	*Dis + 3age + Ct*	15	1407.5	13.2
88	*2age + Fly*	*2age + Fly*	*Dis + 3age + Ct*	14	1415.9	17.2
89	*2age + Fly*	*2age + Dis*	*Dis + 3age + Ct*	14	1407.5	11.1
90	*2age + Fly*	*2age*	*Dis + 3age + Ct*	12	1416.1	13.2
91	*2age + Dis*	*2age + Dis*Fly + t*	*Dis + 3age + Ct*	26	1383.3	18.7
92	*2age + Dis*	*2age + Dis + Fly + t*	*Dis + 3age + Ct*	25	1383.6	16.7
93	*2age + Dis*	*2age + Fly + t*	*Dis + 3age + Ct*	24	1384.8	15.5
94	*2age + Dis*	*2age + Dis + t*	*Dis + 3age + Ct*	24	1384.0	14.9
95	*2age + Dis*	*2age + t*	*Dis + 3age + Ct*	22	1386.0	12.2
96	*2age + Dis*	*2age + Dis*Fly*	*Dis + 3age + Ct*	16	1396.4	7.1
97	*2age + Dis*	*2age + Fly + Dis*	*Dis + 3age + Ct*	15	1396.5	5.2
98	*2age + Dis*	*2age + Fly*	*Dis + 3age + Ct*	14	1396.8	3.3
99	*2age + Dis*	*2age + Dis*	*Dis + 3age + Ct*	14	1397.4	3.8
100	***2age + Dis***	***2age***	***Dis + 3age + Ct***	**12**	**1397.9**	**0***
101	*2age*	*2age + Dis*Fly + t*	*Dis + 3age + Ct*	24	1398.1	25.2
102	*2age*	*2age + Dis + Fly + t*	*Dis + 3age + Ct*	23	1398.5	23.3
103	*2age*	*2age + Fly + t*	*Dis + 3age + Ct*	22	1408.3	28.4
104	*2age*	*2age + Dis + t*	*Dis + 3age + Ct*	22	1398.6	21.3
105	*2age*	*2age + t*	*Dis + 3age + Ct*	20	1410.7	25.9
106	*2age*	*2age + Dis*Fly*	*Dis + 3age + Ct*	14	1410.5	13.3
107	*2age*	*2age + Fly + Dis*	*Dis + 3age + Ct*	13	1411.0	11.6
108	*2age*	*2age + Fly*	*Dis + 3age + Ct*	12	1420.5	16.4
109	*2age*	*2age + Dis*	*Dis + 3age + Ct*	12	1411.1	9.6
110	*2age*	*2age*	*Dis + 3age + Ct*	10	1421.2	12.8

Abbreviations: Φ^1= apparent survival first half year Φ^{2+} = apparent survival subsequent full years; p = resighting; K = number of parameters; *dis*fly* = wintering region; *t* = annual variation; *dis* = distance; *2age* = 2 age classes; *3age* = 3 age classes; *ct* = camera trap; *c* = constant; *fly* = migratory flyway.

Notes: The selected model in step one and step two is highlighted in bold and corresponds to the most parsimonious model with a $\Delta QAIC_c < 2$.; *QAIC$_c$ = 1040.35; **Model 1 corresponds to the GOF model which did not distinguish Φ^1 and Φ^{2+}, nor included age effects.

Table A6.4. *Reverse stepwise* approach, model selection results by step.

	Model	ϕ^1	ϕ^{2+}	p	K	**Deviance**	**ΔQAIC$_c$**
Step 1 - Selection on S	**1****	*Dis*Fly * t*		*Dis*Fly * t*	87	2116.4	690.9
	2	*2age * Dis*Fly * t*	*2age * Dis*Fly * t*	*Dis * 3age * t*	167	1197.2	241.5
	3	*2age + Dis*Fly + t*	*2age + Dis*Fly + t*	*Dis * 3age * t*	86	1297.4	93.2
	4	*2age + Dis*Fly + t*	*2age + Dis + Fly + t*	*Dis * 3age * t*	85	1297.4	90.8
	5	*2age + Dis*Fly + t*	*2age + Fly + t*	*Dis * 3age * t*	84	1298.2	88.9
	6	*2age + Dis*Fly + t*	*2age + Dis + t*	*Dis * 3age * t*	84	1297.6	88.5
	7	*2age + Dis*Fly + t*	*2age + t*	*Dis * 3age * t*	82	1299.3	84.9
	8	*2age + Dis*Fly + t*	*2age + Dis*Fly*	*Dis * 3age * t*	78	1307.0	80.8
	9	*2age + Dis*Fly + t*	*2age + Fly + Dis*	*Dis * 3age * t*	77	1307.1	78.5
	10	*2age + Dis*Fly + t*	*2age + Fly*	*Dis * 3age * t*	76	1308.7	77.2
	11	*2age + Dis*Fly + t*	*2age + Dis*	*Dis * 3age * t*	76	1307.4	76.3
	12	*2age + Dis*Fly + t*	*2age*	*Dis * 3age * t*	74	1309.2	72.8
	13	*2age + Dis + Fly + t*	*2age + Dis*Fly + t*	*Dis * 3age * t*	73	1314.2	74.1
	14	*2age + Dis + Fly + t*	*2age + Dis + Fly + t*	*Dis * 3age * t*	84	1302.8	92.3
	15	*2age + Dis + Fly + t*	*2age + Fly + t*	*Dis * 3age * t*	83	1303.6	90.4
	16	*2age + Dis + Fly + t*	*2age + Dis + t*	*Dis * 3age * t*	83	1303.0	90.0
	17	*2age + Dis + Fly + t*	*2age + t*	*Dis * 3age * t*	81	1304.6	86.3
	18	*2age + Dis + Fly + t*	*2age + Dis*Fly*	*Dis * 3age * t*	77	1317.9	86.3
	19	*2age + Dis + Fly + t*	*2age + Fly + Dis*	*Dis * 3age * t*	76	1311.9	79.6
	20	*2age + Dis + Fly + t*	*2age + Fly*	*Dis * 3age * t*	75	1313.7	78.5
	21	*2age + Dis + Fly + t*	*2age + Dis*	*Dis * 3age * t*	75	1312.0	77.2
	22	*2age + Dis + Fly + t*	*2age*	*Dis * 3age * t*	73	1314.2	74.1
	23	*2age + Fly + t*	*2age + Dis*Fly + t*	*Dis * 3age * t*	84	1315.8	101.7
	24	*2age + Fly + t*	*2age + Dis + Fly + t*	*Dis * 3age * t*	83	1316.6	99.8
	25	*2age + Fly + t*	*2age + Fly + t*	*Dis * 3age * t*	82	1325.1	103.6
	26	*2age + Fly + t*	*2age + Dis + t*	*Dis * 3age * t*	82	1317.3	97.9
	27	*2age + Fly + t*	*2age + t*	*Dis * 3age * t*	80	1326.5	99.8
	28	*2age + Fly + t*	*2age + Dis*Fly*	*Dis * 3age * t*	76	1321.3	86.4
	29	*2age + Fly + t*	*2age + Fly + Dis*	*Dis * 3age * t*	75	1321.8	84.3
	30	*2age + Fly + t*	*2age + Fly*	*Dis * 3age * t*	74	1332.9	90.1
	31	*2age + Fly + t*	*2age + Dis*	*Dis * 3age * t*	74	1321.8	82.0

32	*2age + Fly + t*	*2age*	*Dis * 3age * t*	72	1333.6	85.8
33	*2age + Dis + t*	*2age + Dis*Fly + t*	*Dis * 3age * t*	84	1303.7	92.9
34	*2age + Dis + t*	*2age + Dis + Fly + t*	*Dis * 3age * t*	83	1303.9	90.6
35	*2age + Dis + t*	*2age + Fly + t*	*Dis * 3age * t*	82	1304.5	88.6
36	*2age + Dis + t*	*2age + Dis + t*	*Dis * 3age * t*	82	1304.8	88.8
37	*2age + Dis + t*	*2age + t*	*Dis * 3age * t*	80	1306.0	84.9
38	*2age + Dis + t*	*2age + Dis*Fly*	*Dis * 3age * t*	76	1312.1	79.7
39	*2age + Dis + t*	*2age + Fly + Dis*	*Dis * 3age * t*	75	1312.5	77.6
40	*2age + Dis + t*	*2age + Fly*	*Dis * 3age * t*	74	1326.4	85.3
41	*2age + Dis + t*	*2age + Dis*	*Dis * 3age * t*	74	1313.2	75.7
42	*2age + Dis + t*	*2age*	*Dis * 3age * t*	72	1315.3	72.5
43	*2age + t*	*2age + Dis*Fly + t*	*Dis * 3age * t*	82	1321.3	100.9
44	*2age + t*	*2age + Dis + Fly + t*	*Dis * 3age * t*	81	1322.2	99.1
45	*2age + t*	*2age + Fly + t*	*Dis * 3age * t*	80	1331.5	103.4
46	*2age + t*	*2age + Dis + t*	*Dis * 3age * t*	80	1323.4	97.6
47	*2age + t*	*2age + t*	*Dis * 3age * t*	78	1334.4	100.7
48	*2age + t*	*2age + Dis*Fly*	*Dis * 3age * t*	74	1328.8	87.1
49	*2age + t*	*2age + Fly + Dis*	*Dis * 3age * t*	73	1329.5	85.2
50	*2age + t*	*2age + Fly*	*Dis * 3age * t*	72	1341.3	91.4
51	*2age + t*	*2age + Dis*	*Dis * 3age * t*	72	1329.8	83.0
52	*2age + t*	*2age*	*Dis * 3age * t*	70	1342.7	87.6
53	*2age + Dis*Fly*	*2age + Dis*Fly + t*	*Dis * 3age * t*	77	1317.9	86.3
54	*2age + Dis*Fly*	*2age + Dis + Fly + t*	*Dis * 3age * t*	76	1317.9	83.9
55	*2age + Dis*Fly*	*2age + Fly + t*	*Dis * 3age * t*	75	1318.6	82.0
56	*2age + Dis*Fly*	*2age + Dis + t*	*Dis * 3age * t*	75	1317.9	81.5
57	*2age + Dis*Fly*	*2age + t*	*Dis * 3age * t*	73	1333.3	88.0
58	*2age + Dis*Fly*	*2age + Dis*Fly*	*Dis * 3age * t*	67	1332.1	72.9
59	*2age + Dis*Fly*	*2age + Fly + Dis*	*Dis * 3age * t*	66	1332.3	70.7
60	*2age + Dis*Fly*	*2age + Fly*	*Dis * 3age * t*	65	1332.7	68.7
61	*2age + Dis*Fly*	*2age + Dis*	*Dis * 3age * t*	65	1332.5	68.6
62	*2age + Dis*Fly*	*2age*	*Dis * 3age * t*	63	1333.0	64.3
63	*2age + Fly + Dis*	*2age + Dis*Fly + t*	*Dis * 3age * t*	76	1321.6	86.6
64	*2age + Fly + Dis*	*2age + Dis + Fly + t*	*Dis * 3age * t*	75	1322.2	84.6
65	*2age + Fly + Dis*	*2age + Fly + t*	*Dis * 3age * t*	74	1323.1	82.9
66	*2age + Fly + Dis*	*2age + Dis + t*	*Dis * 3age * t*	74	1322.2	82.3
67	*2age + Fly + Dis*	*2age + t*	*Dis * 3age * t*	72	1324.1	78.9
68	*2age + Fly + Dis*	*2age + Dis*Fly*	*Dis * 3age * t*	66	1337.1	74.2
69	*2age + Fly + Dis*	*2age + Fly + Dis*	*Dis * 3age * t*	65	1337.4	72.1
70	*2age + Fly + Dis*	*2age + Fly*	*Dis * 3age * t*	64	1337.8	70.0
71	*2age + Fly + Dis*	*2age + Dis*	*Dis * 3age * t*	64	1337.6	69.9
72	*2age + Fly + Dis*	*2age*	*Dis * 3age * t*	62	1338.1	65.7
73	*2age + Fly*	*2age + Dis*Fly + t*	*Dis * 3age * t*	75	1332.5	92.1
74	*2age + Fly*	*2age + Dis + Fly + t*	*Dis * 3age * t*	74	1332.8	90.0
75	*2age + Fly*	*2age + Fly + t*	*Dis * 3age * t*	73	1340.2	92.9

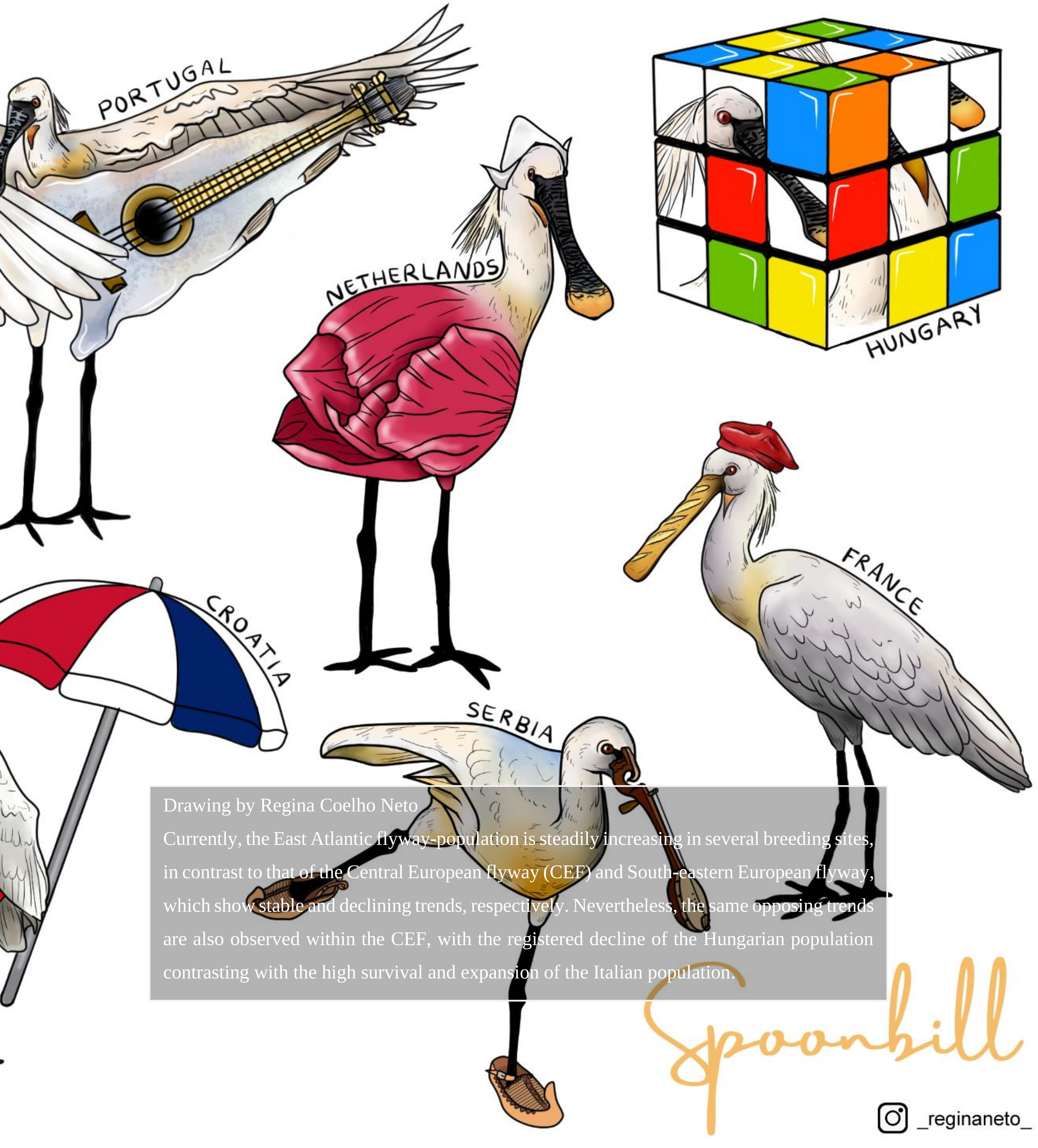
	76	*2age + Fly*	*2age + Dis + t*	*Dis * 3age * t*	73	1333.0	87.7
	77	*2age + Fly*	*2age + t*	*Dis * 3age * t*	71	1340.4	89.1
	78	*2age + Fly*	*2age + Dis*Fly*	*Dis * 3age * t*	65	1345.6	78.0
	79	*2age + Fly*	*2age + Fly + Dis*	*Dis * 3age * t*	64	1346.0	76.0
	80	*2age + Fly*	*2age + Fly*	*Dis * 3age * t*	63	1353.3	79.0
	81	*2age + Fly*	*2age + Dis*	*Dis * 3age * t*	63	1346.0	73.7
	82	*2age + Fly*	*2age*	*Dis * 3age * t*	61	1353.4	74.5
	83	*2age + Dis*	*2age + Dis*Fly + t*	*Dis * 3age * t*	75	1322.8	85.1
	84	*2age + Dis*	*2age + Dis + Fly + t*	*Dis * 3age * t*	74	1323.3	83.0
	85	*2age + Dis*	*2age + Fly + t*	*Dis * 3age * t*	73	1323.9	81.1
	86	*2age + Dis*	*2age + Dis + t*	*Dis * 3age * t*	73	1323.5	80.8
	87	*2age + Dis*	*2age + t*	*Dis * 3age * t*	71	1325.0	77.2
	88	*2age + Dis*	*2age + Dis*Fly*	*Dis * 3age * t*	65	1337.4	72.1
	89	*2age + Dis*	*2age + Fly + Dis*	*Dis * 3age * t*	64	1337.7	70.0
	90	*2age + Dis*	*2age + Fly*	*Dis * 3age * t*	63	1337.9	67.8
	91	*2age + Dis*	*2age + Dis*	*Dis * 3age * t*	63	1338.3	68.1
	92	***2age + Dis***	***2age***	*Dis * 3age * t*	**61**	**1338.8**	**63.8**
	93	*2age*	*2age + Dis*Fly + t*	*Dis * 3age * t*	73	1336.6	90.4
	94	*2age*	*2age + Dis + Fly + t*	*Dis * 3age * t*	72	1337.0	88.2
	95	*2age*	*2age + Fly + t*	*Dis * 3age * t*	71	1344.7	91.5
	96	*2age*	*2age + Dis + t*	*Dis * 3age * t*	71	1337.0	85.9
	97	*2age*	*2age + t*	*Dis * 3age * t*	69	1346.9	88.4
	98	*2age*	*2age + Dis*Fly*	*Dis * 3age * t*	63	1348.9	75.8
	99	*2age*	*2age + Fly + Dis*	*Dis * 3age * t*	62	1349.1	73.9
	100	*2age*	*2age + Fly*	*Dis * 3age * t*	61	1357.3	77.3
	101	*2age*	*2age + Dis*	*Dis * 3age * t*	61	1349.4	71.6
	102	*2age*	*2age*	*Dis * 3age * t*	59	1357.8	73.0
Step 2 - Selection on P	**103**	*2age + Dis*	*2age*	*Dis + 3age + t*	18	1390.5	7.1
	104	***2age + Dis***	***2age***	***Dis + 3age + Ct***	**12**	**1397.9**	**0.0***
	105	*2age + Dis*	*2age*	*Dis + 2age + Ct*	11	1411.4	7.8
	106	*2age + Dis*	*2age*	*Dis + Ct*	10	1510.0	77.4
	107	*2age + Dis*	*2age*	*Ct + 3age*	10	1420.7	12.5
	108	*2age + Dis*	*2age*	*Ct*	8	1523.4	83.0
	109	*2age + Dis*	*2age*	*3age*	9	1457.7	37.3
	110	*2age + Dis*	*2age*	*c*	7	1597.1	134.6

Abbreviations: Φ^1= apparent survival first half year Φ^{2+} = apparent survival subsequent full years; *p* = resighting; *K* = number of parameters; *dis*fly* = wintering region; *t* = annual variation; *dis* = distance; *2age* = 2 age classes; *3age* = 3 age classes; *ct* = camera trap; *c* = constant; *fly* = migratory flyway.

Notes: The selected model in step one and step two is highlighted in bold and corresponds to the most parsimonious model with a $\Delta QAIC_c < 2$. *QAIC$_c$ = 1040.35; **Model 1 corresponds to the GOF model which did not distinguish Φ^1 and Φ^{2+}, nor included age effects.

CHAPTER 7

Integrating continental scale multisite capture-recapture analysis to estimate survival and natal dispersal of a partially migratory bird across the Western Palearctic



Drawing by Regina Coelho Neto

Currently, the East Atlantic flyway-population is steadily increasing in several breeding sites, in contrast to that of the Central European flyway (CEF) and South-eastern European flyway, which show stable and declining trends, respectively. Nevertheless, the same opposing trends are also observed within the CEF, with the registered decline of the Hungarian population contrasting with the high survival and expansion of the Italian population.

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Abstract

Effective conservation at the flyway scale requires not only the identification of local and range-wide threats, but also an understanding of the demographic rates in different locations, and of the frequency of exchange between different breeding populations that underline population trends. Although information on productivity is often available for several waterbird species, estimating other demographic rates is seldom possible as these analyses are data-hungry, and range wide approaches are logistically challenging. Here, we combine mark-capture-recapture data from eight interconnected Eurasian spoonbill populations across continental Europe ($n_{Ind.}$ = 26 056; $n_{Resighting}$ = 199 589) and assess survival at distinct breeding and non-breeding regions, as well as natal dispersal. By combining multiple datasets, we were able to overcome several limitations of traditional capture-recapture analyses (e.g., limited to comparisons of single populations and few sites) and obtain survival estimates closer to true survival. Using multistate Arnason-Schwarz model, we were able to identify a higher mortality of juveniles and immatures from the Carpathian Basin compared to South and West European populations, consistent with the decreasing trend displayed by this population. Additionally, adult survival during the period between the non-breeding and breeding seasons was not affected by origin (i.e., natal site) nor by non-breeding region location. This suggests that as they age, spoonbills are likely to become experienced and better able to overcome the challenges associated with migration and environmental conditions during the non-breeding season. Nevertheless, breeding region does influence survival during the period between the breeding and non-breeding seasons, despite no clear specific pattern being detected. Finally, immatures and adults travelling across breeding locations when returning to their natal breeding region, showed high levels of natal and breeding region dispersal into those regions, than would be expected for philopatric species as the spoonbill. Information on the survival rates and the exchange of individuals among breeding populations can improve our understanding of population trends and thus guide conservation actions, as well as serve as a template for similar analysis for other migratory species of conservation concern.

Keywords/phrases: Central European Flyway East Atlantic Flyway; Long-term monitoring; Partial migration; *Platalea leucorodia*; Residency.

Introduction

Bird migration is a challenging process (Alerstam et al., 2003), typically involving two main seasonal journeys, with several stopover sites often visited during the non-breeding season (Chapman et al., 2014; Salewski and Bruderer, 2007). Migratory species distribution range can extend over large geographical areas (often expanding across several continental landmasses) and different migratory decisions (e.g., migration route and location of the breeding or non-breeding sites) may lead to different fitness outcomes (Newton, 2008). Local weather conditions (Castro et al., 1992; Hötker, 2003), in addition to variation in resource quality and availability (Mathot et al., 2007; van Gils et al., 2005), have been suggested to affect demographic parameters, including, survival and productivity (via carry-over effects) (Alerstam et al., 2003; Alves et al., 2013; Boyle, 2008; Chapman et al., 2011; Gillis et al., 2008; Harrison et al., 2011; Lok et al., 2015; Newton, 2008; Norris, 2005; Swift et al., 2020). Thus, assessing the effects of different migratory routes and site selection (during breeding or non-breeding seasons) in parameters such as survival, is invaluable not only for understanding contrasting population trends (e.g., across migratory flyways or between non-breeding sites), but also for identifying regions of critical conservation importance. However, quantifying demographic parameters across such vast spatial scales (continent wide) is extremely challenging and limits our capacity to better understand the underlying demographic processes underpinning population growth rates.

In cases of extreme within species variation, such as in partial migrants, where some individuals do not migrate at all (residents), while others do (Chapman et al., 2011; Newton, 2008), variation in key fitness components like survival is likely to be more apparent (Gillis et al., 2008; Kokko, 2011). This is the case of American dippers (*Cinclus mexicanus*), for which resident individuals are known to have slightly lower survival rates and higher annual productivity than migratory ones (Gillis et al., 2008). Furthermore, even among migratory individuals, migration can vary considerably, with metrics as migration distance possibly varying by thousands of kilometres between migrants (Alves et al., 2012; Carneiro et al., 2019). For instances, the Sanderling (*Calidris alba*), which breeds in Greenland, is found from the coasts of the North Sea to Southern Africa during the non-breeding season (Reneerkens et al., 2009). Due to carry-over effects, such variation in the location of non-breeding sites may also affect demographic factors such as survival (Acker et al., 2021; Alves et al., 2013; Carneiro et al., 2021; Grist et al., 2017; Lok et al., 2015; Reid et al., 2020). In the case of the Icelandic black-tailed godwits (*Limosa limosa islandica*), where individuals experiencing favourable winter conditions had higher survival rates, even when migration costs were substantially higher (due to longer migration distances), than individuals from locations where the energetic balance on the non-breeding season was less favourable (Alves et al., 2013). Consequently, understanding the underlying mechanisms linking migratory wide distributions with survival in order to better understand population trends remains a very challenging task. Furthermore, owing to the wide geographical variation and the difficulty of individually tracking a substantial number of birds throughout their annual cycle (Lok et al., 2015), survival studies based on capture-recapture analysis are usually limited to one or a few study sites. It is therefore often impossible to distinguish between permanent emigration from the study site and mortality (Lebreton et al., 1992). As a result, survival estimates typically reflect “apparent” or “local” survival (Lebreton et al., 1992; Nichols and Kendall, 1995) and differences in local survival rates among populations may simply reflect variation in dispersal probability (Doligez et al., 2002).

Breeding dispersal is often associated with avoidance of competition at natal sites (Clobert et al., 2001), a process that may lead to the establishment of new colonies (Black et al., 2007; Kerbes, 1983). The Ideal Free Distribution theory suggests that if individuals can move freely between resource patches and have perfect knowledge of the quality of all patches, allowing them to choose the ‘ideal’ patch, then the distribution of animals across resource patches should result from individual strategies to maximise fitness by minimising resource competition (Fretwell and Lucas, 1969; Sutherland, 1998). This theory however fails to predict breeding site selection, as most bird species display a high degree of fidelity to their natal sites, i.e. philopatry, the tendency to return to the site of birth (Gunnarsson et al., 2011; Trochet et al., 2016; Winger et al., 2019). Additionally, in social migratory species, recruitment could occur by following conspecifics and/or being attracted to areas with conspecific presence (Gill, 2019). Which questions to what extent philopatry or social cues from conspecifics may determine breeding site selection in those species.

Current conservation and management programmes of migratory waterbirds use flyway populations as the basic unit (Boere et al., 2006; Madsen et al., 2014). Thus, in order to produce effective conservation and better interpret population trends, it is essential not only to identify flyway and local threats to the survival of these populations, but also to attain knowledge of the rate of exchange among flyway populations (Madsen et al., 2014). However, the information available on this last aspect is usually patchy and insufficient for population management, except for rare long-term study systems such as the Barnacle goose (*Branta leucopsis*; e.g., Owen and Black, 1991). Furthermore, even when there are multiple marking schemes for the same species, they are usually set up by individual researchers or teams and there is a widespread lack of coordination and/or resources to combine these mostly individual efforts in an overall species level framework analysis (Madsen et al., 2014).

The Eurasian spoonbill (*Platalea leucorodia leucorodia*, hereafter spoonbill) is a migratory waterbird with breeding populations spanning from the East-Atlantic Coast to Southeast Asia (Triplet et al., 2008), which has been extensively monitored thanks to its rather easy detection (Pigniczki and Végvári, 2015; Triplet et al., 2008), and its conservation relevance (Jin et al., 2008; Lorenz et al., 2009; Schneider-Jacoby, 2008; Sergio et al., 2006, 2008; Triplet et al., 2008). Metapopulations are a network of spatially separated subpopulations of the same species that are linked by migration, dispersal and gene flow (Hanski and Gilpin, 1977; Matthiopoulos et al., 2005). Each subpopulation can experience independent demographic rates such as reproduction and survival, but the overall persistence of the species across its distribution range, as well as the creation and extinction of breeding colonies depends on the exchange of individuals between subpopulations (Hanski and Gilpin, 1977; Matthiopoulos et al., 2005). In Europe, breeding spoonbills are divided into three distinct meta-populations, (Champagnon et al., 2019b): (i) the Central European Flyway (hereafter CEF meta-population), where several colonies, such as those in Italy, and the Carpathian Basin have been monitored (Azafzaf et al., 2006; Kralj et al., 2012; Pigniczki et al., 2016; Pigniczki, 2022; Tenan et al., 2017); (ii) the South-eastern European Flyway (hereafter SEF meta-population), that was recently separated from CEF (Champagnon et al., 2019b) and for which knowledge of migration, non-breeding distribution, and genetic differentiation is lacking (Kralj et al., 2023); and (iii) the East Atlantic Flyway (hereafter EAF meta-population), for which, due to previous studies, the survival and fidelity rates of the Dutch breeding population are already known (Lok et al., 2011, 2013a, 2015). However, such detailed information is currently absent for any other population across the three flyways, with the recent exception of the mediterranean French population (Chapter 6). Currently, the EAF meta-population is steadily increasing in several breeding sites, in contrast to the CEF and SEF meta-populations, which are currently experiencing stable and declining trends, respectively (Champagnon and Kralj, 2023). Opposing trends are also observed within the CEF, with the registered decline of the Hungarian population currently contrasting with the high survival and expansion of the Italian population (Tenan et al., 2017). Thus, this system provides a great opportunity to better understand the underlying causes of such disparate population trends, while also obtaining much needed survival estimates for the understudied populations. Furthermore, as is often the case with survival analysis, previous studies are likely to have encountered a number of common challenges that often limit the estimation and interpretation of survival rates: (i) inability to consider connectivity (i.e. exchange of individuals) between different breeding and non-breeding sites; (ii) the relatively small sample size of individuals with known non-breeding site; and (iii) the difficulty in accounting for permanent emigration, as mortality and emigration are confounded. Some of these limitations are likely overcome when information on several metapopulations is analysed together.

Here, thanks to the collective effort of eight different long-term colour-ringing programmes, we applied multistate capture-mark-recapture models (Lebreton et al., 1992; Pradel, 2005) to a unique dataset composed of resighting data collected at the main breeding regions in Europe, and throughout the main non-breeding range of spoonbills, thus encompassing its distribution across the Western Palearctic. Owing to the exceptional spatial and temporal coverage of our combined dataset, we aimed to: (i) assess whether detectability at different breeding and non-breeding sites depends on the natal origin of the individual; (ii) investigate the probability of natal dispersal. We predict that there is a low probability of birds breeding away from their natal region, due to the small number of known cases of permanent emigration (Lok et al., 2013a; Pigniczki, 2017); (iii) investigate the probability of survival in relation to breeding and non-breeding regions. We predict that survival will be particularly low for birds in African non-breeding sites, due to the decreasing quality of these sites (combined effects of density dependence and site degradation; (Lok et al., 2013b; OTEDD, 2016), a higher probability of encountering major ecological barriers on migration to/from those sites (Chapter 6; Lok et al., 2015), and an increasing quality of South-European sites (owing to more efficient wetland protection & higher food availability; Donald et al., 2007; Klein et al., 2002; Lok et al., 2013a; Novo and Cabrera, 2006; Shukla et al., 2019). Nevertheless, we also predict that survival will also be lower for birds breeding in the Carpathian Basin due to the known habitat loss and recorded decreasing trend of these populations (Champagnon et al., 2019a; Triplet et al., 2008).

Material and Methods

Study populations and data collection

This study was possible due to the collective effort of long-term colour-ringing programmes implemented in the spoonbill breeding colonies of: Croatia, France, Hungary, Italy, Netherlands, Portugal, Serbia, and Spain. Despite some of these programmes being already in existence in earlier years, only chicks colour-ringed between 2003 and 2021 were considered for this analysis (Appendix, Table A7.1). This was done to avoid skewing the results towards the oldest programmes and largest datasets (i.e., Dutch – 1992, Italian –1991, & Spanish – 1982). During the breeding season (March to July), pre-fledged chicks in each breeding colony (sites where individuals were ringed) were fitted with a national country specific metal ring (with a unique alphanumeric code), and an unique combination of coloured and/or engraved coded rings from specific marking schemes (Appendix, Table A7.2), which allowed individual visual identification from a distance using a telescope or camera (resighting). To minimize disturbance, ringing operations usually occurred in the early morning (to avoid heat stress) and only under favourable weather conditions (no precipitation and/or strong winds) (Chapter 6; Kralj et al., 2012; Lok et al., 2011; Navedo et al., 2010; Pigniczki et al., 2016; Pigniczki, 2022; Rodrigues et al., 2023; Tenan et al., 2017). All ringing sessions were conducted in accordance with national legislation, animal welfare, and by experienced ringers.

Resighting data of marked individuals were collected opportunistically by a volunteer network of dedicated observers, such as ornithologists and nature photographers, scattered throughout the distribution range of the species in the Western Palearctic. It should be noted that, as no data from SEF programmes was possible to include in this analysis, resightings from this flyway were not considered. Furthermore, at breeding colonies, an additional effort was performed by several programmes to collect data during the breeding season, for example with the deployment of camera traps near the nests and specific resightings session from strategically placed hides near the colonies. During the non-breeding season, resightings from observers were supplemented by expeditions to major non-breeding sites where spoonbills are known to be abundant and resighting data is known to be scarce (specifically to the Banc d’Arguin in Mauritania, the Senegal river delta in Senegal, and the Gabes gulf in Tunisia). Here, we considered resighting data collected between March 2003 and February 2022 by the different ringing programmes.

Data gathering, cleaning and selection

A total of 26 056 individuals ringed by the eight programmes and their ca. 200 000 resightings were initially considered for analysis. For most of the death recoveries present in the databases, it was not possible to determine the date of death, so these were excluded. Records associated with uncertainty (e.g. due to ring loss), were also excluded. Data selection was carried out as described for the survival analysis of the Camargue spoonbill population (Chapter 6) and thus, only individuals ringed as chicks, without having GPS trackers and with no duplicates (cases when the same combination was deployed in two different individuals due to field error) were considered, resulting on 25 337 individuals suitable for analysis for further ringing details see, Appendix, Table A7.1).

Resightings were split into two periods: the breeding season (1st March to 31st July) and the non-breeding season (1st October to 29th February). All resightings made during August and September were therefore excluded. Moreover, during the breeding season, only resightings from, or close to the main breeding regions (i.e. within a defined buffer of 60 km around the main ringing sites in Europe) were considered. These buffer areas were defined due to the difficulties encountered in accessing and monitoring several of the spoonbill colonies while keeping disturbance low during the sensitive breeding phase (e.g., Croatian colonies are located in reed beds and Portuguese colonies in salt-marsh islands). Spoonbills are rather mobile birds and may cover up to 50 km from breeding to feeding sites during the breeding season (Pigniczki et al., 2016). Additionally, in Italy, active breeders were detected in surrounding wetlands at a maximum distance of about 60 km from the colony (Tenan et al. 2017). Five main breeding regions were therefore determined, encompassing breeding colonies in close proximity and considering the aforementioned buffer: Carpathian Basin; Southwest-Iberia; Northern Italy; Mediterranean France; and Northwest (mainland) Europe (Fig. 1).

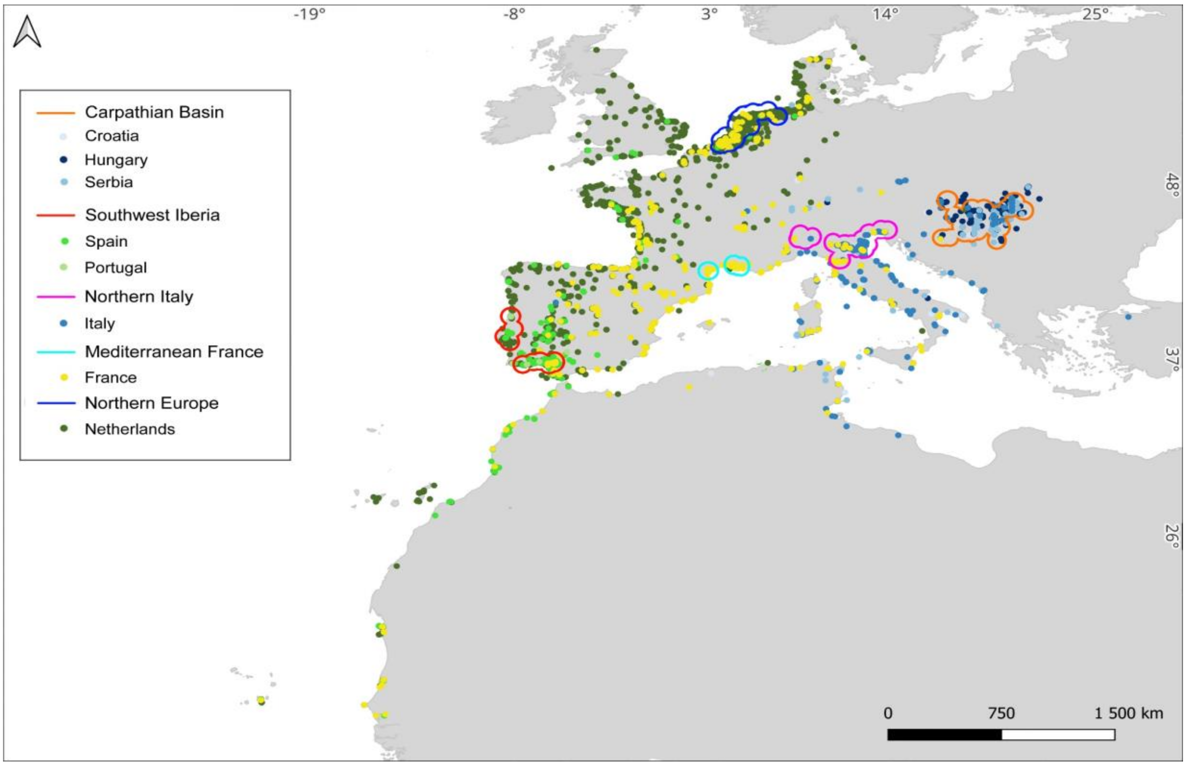

Fig. 1 – Range wide locations of spoonbill resightings during the breeding season (March to July) according to the country of natal origin. Breeding regions include the following countries: Carpathian Basin (Croatia, Austria, Hungary, Servia, Slovakia, and Romania; orange); Southwest-Iberia (Portugal & Spain; red); Northern Italy (Italy; violet); Mediterranean France (France; light blue); and Northwest Europe (the Netherlands, Belgium and Germany; dark blue).

Only resightings within the defined breeding regions were considered breeding season resightings, with the exception of resightings within the Carpathian Basin, where all resightings during this period were considered as breeding within the Carpathians, due to the ecological barrier provided by the Carpathian Mountains. Interpretation of the map in Figure 1 must be done with care, as locations with several resightings may appear underrepresented, and resightings from the same individual in the same year can lead to overrepresentation of some nearby locations. If an individual was resighted at different breeding regions within the same breeding season, the northernmost site was set as its breeding region, as it likely stopped on a southern breeding region on its way to its actual breeding region ($n_{Ind.}$ = 144). Since the EAF and CEF meta-populations are assumed to breed allopatrically (i.e. not to overlap in the breeding area), with few known exceptions (Pigniczki, 2022), individuals resighted breeding in a different flyway from the one where they were originally ringed were excluded from the analysis ($n_{Ind.}$ = 37). Nevertheless, spoonbills from Mediterranean France are known to use both flyways during migration (Blanchon et al., 2019), hence individuals from this breeding region that met the above exclusion condition were in fact retained. Resightings outside the described main breeding areas were excluded from the analysis, as most were made either during spoonbill's migration to the main breeding areas (as migration timing is unlikely to be similar across all breeding regions; Chapter 2), in the non-breeding areas (as some individuals do not return to the breeding colonies each year, particularly immatures) or in smaller colonies not monitored regularly ($n_{Resighting}$ = 8 182).

During the non-breeding season, defined as the period between 1st October to 29th February, six different regions were considered (Fig. 2). Individuals were assigned to a non-breeding region according to the southernmost site where they were resighted during this period. To avoid the possible misclassification due to a late-autumn or early-spring stopover resighting, observations in Europe, were only considered from 1st November to 31st January (Lok et al. 2011; Navedo et al. 2010). When an individual was resighted at different sites within the same non-breeding season, the southernmost site was considered its non-breeding region ($n_{Ind.}$ = 44). Individuals resighted in a flyway other than the one in which they were ringed (e.g. a bird with an EAF natal origin being resighted in the CEF and vice-versa; except for individuals from Mediterranean France) were excluded ($n_{Ind.}$ = 9; birds already excluded during the breeding season data treatment above were not considered here). To avoid overparameterization, individuals resighted in non-breeding sites outside the main regions considered here were excluded ($n_{Ind.}$ = 125; birds already excluded during previous data treatment above were not considered here). A single individual ringed in Mediterranean France was excluded from the analysis due to being resighted in multiple flyways (EAF and CEF) in the same year, likely due to a misclassification in one of the non-breeding regions.

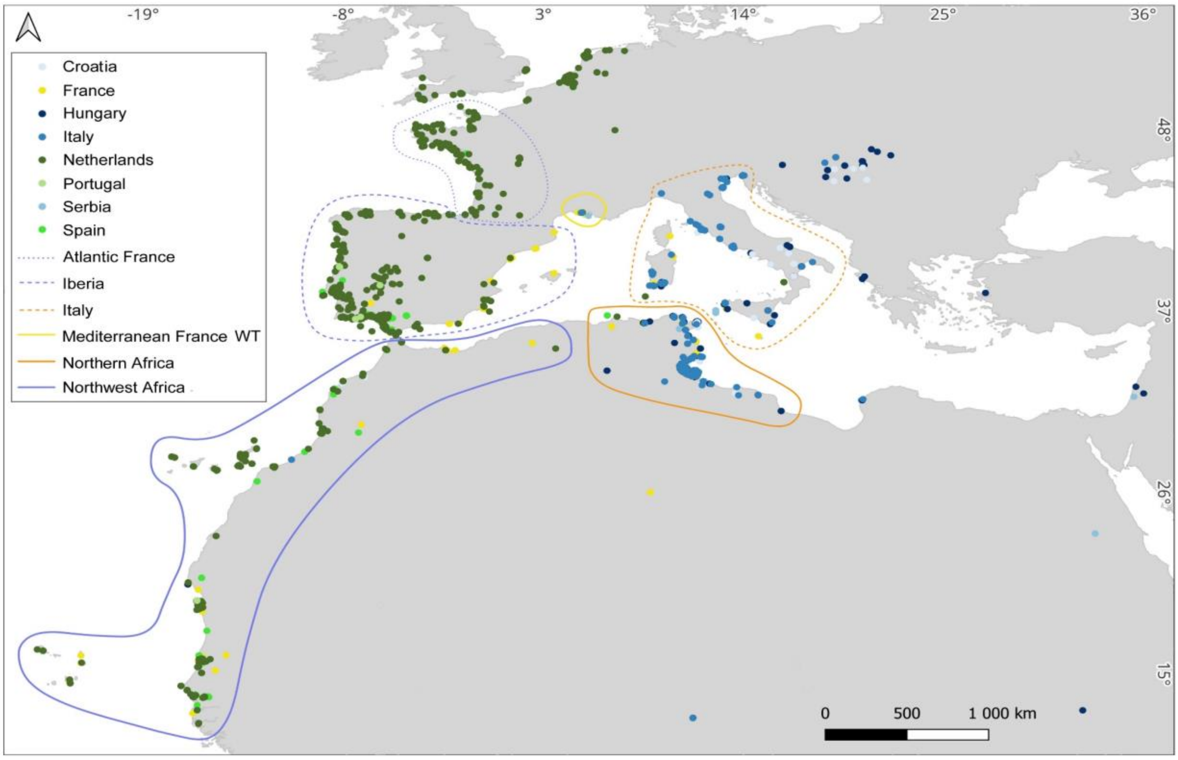

Fig. 2 – Range wide locations of spoonbill resightings during the non-breeding season (October to February for resightings in Africa; November to January for resightings in Europe) according to their country of natal origin (colour of each circle). Non-breeding regions were based on previous works (Chapter 6; Lok et al., 2011) and include the following countries: Atlantic France (France; blue dotted line); Iberia (Portugal and Spain; blue dashed line); Corsica and Italy (Corsica and Italy; orange dashed line; and hereafter called Italy); Mediterranean France (France; yellow line); Northern Africa (East Algeria, Libya, & Tunisia; orange line); and Northwest Africa (Cape Vert, Gambia, Mauritania, Morocco, Senegal, & West Algeria; blue line).

Breeding and non-breeding resightings were limited to one resighting per individual in each season, considering only records with no reading uncertainty, thus resulting in a final dataset containing 25 293 individuals, 15 675 breeding resightings (Appendix, Table A7.3), and 6 673 non-breeding resightings (Appendix, Table A7.4).

Mark-Recapture modelling and statistical analysis

To estimate the survival rates of spoonbills, we developed multistate models in the E-surge software (v. 2.2.3; Choquet et al., 2009), which provided a flexible framework to develop and rank complex constrained models (Pradel, 2005, 2009).

All individuals were given the initial state of being alive in their natal region. The subsequent states of any individual was related to the season of the year and the region where the individual was last resighted: (BCB) breeding in Carpathian Basin; (BSI) breeding in Southwest-Iberia; (BNI) breeding in Northern Italy; (BMF) breeding in Mediterranean France; (BNE) breeding in Northwest Europe; (WAF) non-breeding Atlantic France; (WIB) non-breeding in Iberia; (WCI) non-breeding in Italy; (WMF) non-breeding in Mediterranean France; (WNA) non-breeding in Northern Africa; and (WWA) non-breeding in Northwest Africa.

Table 1. Transition matrix discriminating all the possible state transitions (‘*Ψ*’ transition probability) between breeding and non-breeding regions. Transitions considered impossible were not allowed and marked with a hyphen.

Transition matrix		Carpathian Basin	Southwest-Iberia	Northern Italy	Mediterranean	North Europe	Atlantic France	Italy	Iberia	Mediterranean	North Africa	Northwest Africa
		BR	BR	BR	BR	BR	NBr	NBr	NBr	NBr	NBr	NBr
Carpathian Basin	BR	-	-	-	-	-	-	*Ψ*	-	-	*Ψ*	-
Southwest-Iberia	BR	-	-	-	-	-	-	-	*Ψ*	-	-	*Ψ*
Northern Italy	BR	-	-	-	-	-	-	*Ψ*	-	-	*Ψ*	-
Mediterranean France	BR	-	-	-	-	-	-	*Ψ*	*Ψ*	*Ψ*	*Ψ*	*Ψ*
Northwest Europe	BR	-	-	-	-	-	*Ψ*	-	*Ψ*	-	-	*Ψ*
Atlantic France	NBr	-	-	-	-	*Ψ*	-	-	-	-	-	-
Iberia	NBr	-	*Ψ*	-	*Ψ*	*Ψ*	-	-	-	-	-	-
Italy	NBr	*Ψ*	-	*Ψ*	*Ψ*	-	-	-	-	-	-	-
Mediterranean France	NBr	-	-	-	*Ψ*	-	-	-	-	-	-	-
Northern Africa	NBr	*Ψ*	-	*Ψ*	*Ψ*	-	-	-	-	-	-	-
Northwest Africa	NBr	-	*Ψ*	-	*Ψ*	*Ψ*	-	-	-	-	-	-

For each breeding occasion we considered six possible resighting classes (‘events’ hereafter) during the breeding season. Each individual was thus resighted: (1) in Carpathian Basin; (2) in Southwest-Iberia; (3) in Northern Italy; (4) in Mediterranean France; (5) in Northwest Europe or (6) not resighted. For each non-breeding occasion, we considered seven possible events during the non-breeding season. Each individual was thus resighted: (1) in Atlantic France; (2) in Iberia; (3) in Italy; (4) in Mediterranean France; (5) in Northern Africa; (6) in Northwest Africa or (7) not resighted.

The goodness-of-fit (GOF) test for multistate Arnason-Schwarz model (Gimenez et al., 2018) was used to assess whether the data infringed any assumption of parameter homogeneity (Burnham et al., 1987; Lebreton et al., 1992; Pradel et al., 1997a). The dataset was first split in two, considering breeding and non-breeding events. Although the ringing region of the individual (group) was not considered, we did consider multiple states in the model according to the region where the individuals were resighted. This GOF model does not account for age, and the only states considered were thus “resighted in the breeding regions” or “resighted in the non-breeding regions”. However, to account for transience and trap dependence effects, age classes were considered for all competing models (0.5 cy, 1-3.5 cy, >3.5 cy) when estimating survival and detectability (Kentie et al., 2023; Pradel et al., 1997a). Any remaining lack of fit (as estimated by WBWA;TEST 3G.sm; Test M.LTec) was accounted for by adjusting for overdispersion ($\hat{c} = \chi^2/df$ = 1043.35/594 = 1.76) (Choquet et al., 2005; Gimenez et al., 2018; Kentie et al., 2023). For further details on the GOF see Appendix B.

Since the split of years into breeding and non-breeding seasons was not considered in the GOF procedure, we first tested a general biologically meaningful model that considered both seasons together (*Season*, categorical with two levels: breeding and non-breeding seasons as defined above). Thus, the survival estimates obtained correspond to the period between breeding and non-breeding seasons and vice-versa. In addition, this general model considered age classes (*Age*, categorical with three levels: juvenile (0.5 cy), immatures (1^+ to 3.5 cy) and adults (4^+ cy)); region where individuals were resighted (*Region*, categorical with two subgroups: *Br_Region* with five levels – Carpathian Basin; Southwest-Iberia; Northern Italy; Mediterranean France; Northwest Europe; *NBr_Region* with six levels – Atlantic France; Iberia; Italy; Mediterranean France NBr; Northern Africa, and Northwest

Africa); and natal region (*Natal origin*, categorical with five levels: Carpathian Basin, Southwest-Iberia, Northern Italy, Mediterranean France and Northwest Europe). The final general model then considered full interaction among these variables: $\Phi_{Season*Age*Region*Natal\_origin}\ \Psi_{Season*Age*Region*Natal\_origin}\ p_{Season*Age*Region*Natal\_Origin}$.

Several reduced models were then developed to investigate the support for variables of interest. Specifically, if birds with the different *Natal origin* had the same detectability in different breeding and non-breeding regions by competing the General Model against Models 1 and 2; if birds from different *Age* classes had the same detectability in different breeding and non-breeding regions by competing the General Model against Models 3 and 4; birds with the different *Natal origin* had the same chance of transition to the same non-breeding region from the same breeding region by competing the General Model against Model 5; if survival in the period between the non-breeding and breeding seasons depend on *Region* or *Natal origin* by competing the General Model against Models 6 to 9. Once model 9 was preliminary selected as the most-supported model, this model was competed against the same variations of detectability and transition as the general model (Models 10 to 13 and Model 14 respectively). For further details of tested models, see Table 2.

Model selection was based on the Akaike Information Criterion, adjusted for small sample sizes and overdispersion ($QAIC_c$), considering a better model fit when $\Delta QAIC_c < 2$ (Anderson and Burnham, 2002). When there were multiple models within two QAIC points from the most-supported model, the model with the fewest parameters was selected (i.e., the most parsimonious model, Anderson and Burnham 2002). Parameter estimates and profile likelihood confidence intervals from the most-supported model are reported. The general model was unable to successfully converge and provide estimates, likely due to overparameterization of the complex transition matrix and associated possibilities. This was resolved by removing individuals resighted during the non-breeding season in the Atlantic France non-breeding region, which was the non-breeding region with fewest individuals (n = 281) and was therefore likely to limit the model's capacity to estimate the requested parameters. This resulted in a simplified model with 11 states instead of 12, for which survival, transition and detectability matrixes were therefore modified accordingly.

Results

When considering different competing models, Models 6, 7, and 9 had similar AIC support ($\Delta QAIC_c$ <2; Table 2), however Model 9 was the most parsimonious. This model included a *Season*, *Age*, *Region*, and *Natal origin* effect in almost all parameters (survival, transition, and detection), with the exception of survival rate during the period between non-breeding season and breeding season, which was neither thus influenced by *NBr_Region* nor individual *Natal origin*.

Table 2. Details of the 14 competing multistate models, and their resulting statistics. The most parsimonious model is highlighted in bold and corresponds to the most parsimonious model with a $\Delta QAIC_c < 2$.; *QAIC =137672.3. Abbreviations: Φ = apparent survival; *p* = resighting; *K* = number of parameters; *Season* = *Breeding* and *Non-breeding* seasons; *Age* = *Juvenile*, *Immature*, and *Adult*; *Region* = *Breeding* or *Non-breeding* region; *Natal origin* = natal site of the of marked individual.

Model	ϕ		Ψ		***p***		***K***	**Deviance**	**ΔQAIC**	***Weight***
	Br->NBr	***NBr->Br***	***Br->NBr***	***NBr->Br***	***Br***	***NBr***				
General	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region* + *Ad*Natal origin*Region*	*Age*Natal origin*Region*		*Age*Natal origin*Region*		146	241809.8	12.5	0.00
1	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region* + *Ad*Natal origin*Region*	*Age*Natal origin*Region*		*Age*Natal origin*Region*	*Age*Region*	130	242304.4	261.5	0.00
2	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region* + *Ad*Natal origin*Region*	*Age*Natal origin*Region*		*Age* Region*		118	243616.1	982.8	0.00
3	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region* + *Ad*Natal origin*Region*	*Age*Natal origin*Region*		*Age*Natal origin*Region*	*Region*Natal origin*	133	241920.5	49.4	0.00
4	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region* + *Ad*Natal origin*Region*	*Age*Natal origin*Region*		*Natal origin*Region*		122	242427.1	315.2	0.00
5	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region* + *Ad*Natal origin*Region*	*Age *Region*	*Age *Natal origin *Region*	*Age*Natal origin*Region*		134	242053.8	127.2	0.00

6	*Age*Region*		*Age*Natal origin*Region*		*Age*Natal origin*Region*		138	241818.6	1.5	0.22
7	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region + Ad*Natal origin*	*Age*Natal origin*Region*		*Age*Natal origin*Region*		138	241816.0	0.0	0.46
8	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region + Ad *Region*	*Age*Natal origin*Region*		*Age*Natal origin*Region*		130	241949.1	59.7	0.08
9	***Juv*Natal origin*Region*** ***Imt*Region*Ad*Region***	***Imt*Region + Ad***	***Age*Natal origin*Region***		***Age*Natal origin*Region***		**134**	**241831.4**	**0.8**	**0.32**
10	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region + Ad*	*Age*Natal origin*Region*		*Age*Natal origin*Region*	*Age*Region*	118	242368.1	273.7	0.00
11	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region + Ad*	*Age*Natal origin*Region*		*Age* Region*		106	243644.2	974.8	0.00
12	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region + Ad*	*Age*Natal origin*Region*		*Age*Natal origin*Region*	*Region*Natal origin*	121	241936.1	34.2	0.00
13	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region + Ad*	*Age*Natal origin*Region*		*Natal origin*Region*		110	242451.7	305.2	0.00
14	*Juv*Natal origin*Region* *Imt*Region* Ad*Region*	*Imt*Region + Ad*	*Age *Region*	*Age *Natal origin *Region*	*Age*Natal origin*Region*		122	241987.0	65.2	0.00

In general, detectability was low during the non-breeding season (≤ 25%) and similar for immatures and adults (Appendix, Fig. A7.1). In the case of breeding regions, detectability of adults, when present in their respective natal regions, was quite high (> 60%), especially in Mediterranean France, while lower in Southwest-Iberia (15%). Individuals in breeding regions other than their natal region had an overall very low probability of being detected (≤ 5%). Furthermore, in the breeding regions, adults resighted in their natal region have a higher chance of being detected than immatures, from the Northwest Europe region, where detectability was similar between the two age classes. The detection probabilities for Iberian natal immature and adult birds in the Iberian non-breeding region were hardly possible to estimate, having large confidence intervals at the limit of realistic variables (30 or 100%). This same parameter was impossible to estimate for adult spoonbills from Mediterranean France (*Natal origin*) in the Northwest Europe breeding region.

Overall juveniles were more likely to go to African regions than to European regions for the non-breeding season (Fig. 4).

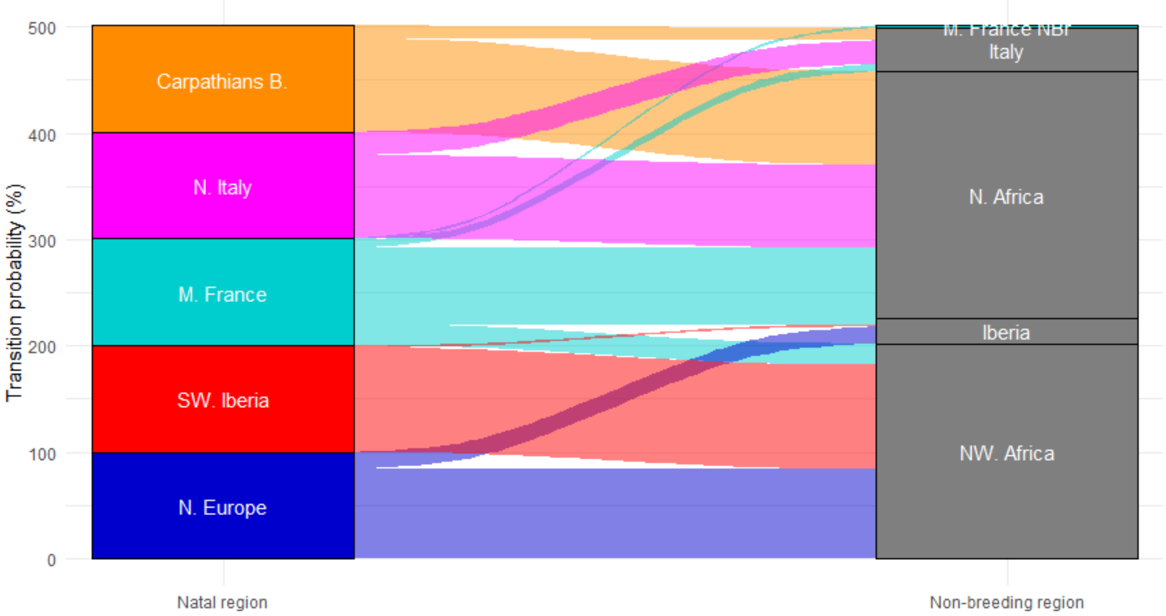

Fig. 4 – Transition probability of juveniles from breeding (i.e. natal in the case of juveniles) to non-breeding region (the grey colour non-breeding regions, indicates birds with multiple Natal *origin*). Estimates based on the most-supported model (Table 2, Model 9). For more details on these parameters (e.g. confidence intervals of each estimate) please see the Appendix (Table A7.5).

Immatures transitions are not presented due to potentially being severely biased due to our modelling constraints (see discussion). Overall, adults in the same breeding region exhibited similar probability of transition to the same non-breeding regions, with most transitioning to an African non-breeding region (Fig. 5). The exceptions to these patterns were natal Northern European adults, which had a higher chance of transitioning to Iberia when departing from the Northern Europe breeding region compared to natal Mediterranean France birds in the same region, and adults in the Mediterranean France and Northern Italy breeding regions transitioning to Italy non-breeding region.

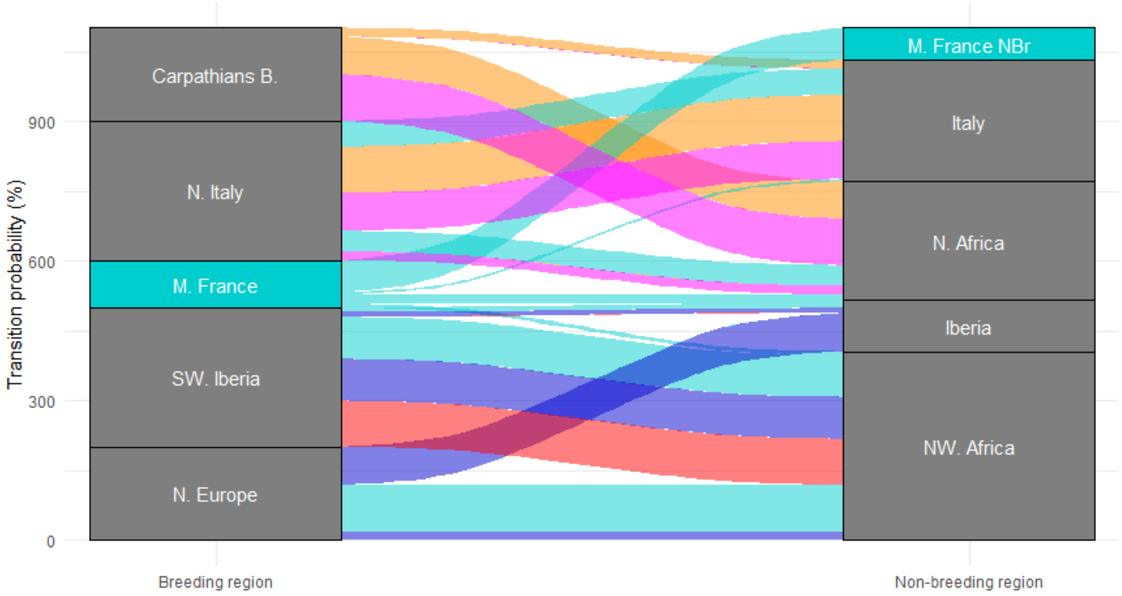

Fig. 5 – Transition probability of adults from breeding to non-breeding region (the grey colour of non-breeding regions indicates birds with multiple *Natal origin*). Estimates based on the most-supported model (Table 2, Model 9). For more details on these parameters (e.g. confidence intervals of each estimate) please see the Appendix (Table A7.5).

In general, there was a higher chance of immatures transitioning to other breeding regions than returning to their natal breeding region (Appendix, Table A7.5). Adult birds showed a high tendency to be attracted to regions located on route to their more northerly natal breeding region. Specifically, natal adults from the Carpathian Basin and Mediterranean France transitioning to Northern Italy and natal adults from Northern Europe and Mediterranean France transitioning to Southwest-Iberia (Table 3).

Table 3. Transition probability of adult spoonbills from non-breeding to breeding region. Estimates based on most-supported model (Table 2; Model 9). Those highlighted in red indicate a higher chance of dispersal than returning to their natal region and those highlighted in green the reverse. Impossible transitions in our model due to absent or insufficient data supporting such transition are noted with a hyphen.

Natal origin	*Non-breeding →*	*Breeding*	*Transition (%)*	*2.5%*	*97.5%.*
Carpathian Basin	Italy	Carpathian Basin	41%	29%	55%
		Northern Italy	59%	45%	71%
		Mediterranean France	-	-	-
	Northern Africa	Carpathian Basin	94%	79%	88%
		Northern Italy	6%	2%	21%
		Mediterranean France	-	-	-
Northern Italy	Italy	Carpathian Basin	0%	0%	0%
		Northern Italy	100%	100%	100%
		Mediterranean France	-	-	-
	Northern Africa	Carpathian Basin	61%	53%	70%
		Northern Italy	39%	30%	47%
		Mediterranean France	-	-	-
Mediterranean France	Italy	Carpathian Basin	-	-	-
		Mediterranean France	12%	4%	31%
		Northern Italy	88%	69%	96%
	Northern Africa	Carpathian Basin	-	-	-
		Mediterranean France	74%	44%	91%
		Northern Italy	26%	9%	56%
	Iberia	Mediterranean France	90%	60%	98%
		Northwest Europe	2%	0%	13%
		Southwest-Iberia	8%	1%	40%
	Northwest Africa	Mediterranean France	37%	29%	46%
		Northwest Europe	6%	3%	10%
		Southwest-Iberia	57%	48%	65%
Southwest-Iberia	Iberia	Mediterranean France	-	-	-
		Northwest Europe	-	-	-
		Southwest-Iberia	100%	100%	100%
	Northwest Africa	Mediterranean France	-	-	-
		Northwest Europe	-	-	-

		Southwest-Iberia	100%	100%	100%
Northwest Europe	Iberia	Mediterranean France	-	-	-
		Northwest Europe	96%	93%	98%
		Southwest-Iberia	4%	2%	7%
	Northwest Africa	Mediterranean France	-	-	-
		Northwest Europe	33%	20%	27%
		Southwest-Iberia	77%	73%	80%

Juveniles had a consistently lower survival rate than adults and strongly differ between breeding regions, with estimates being exceptionally low for juveniles from the Carpathian Basin followed by juveniles in Southwest-Iberia (Fig. 6). During the period between breeding and non-breeding seasons, adults had different survival rates according to their breeding region, but not related to *Natal origin* (Fig. 6). However, during the period between non-breeding and breeding seasons, adult survival was similar and independent of non-breeding region and *Natal origin* [$\Phi_{ad} = 0.94$, 95%CI (0.91–0.96)].

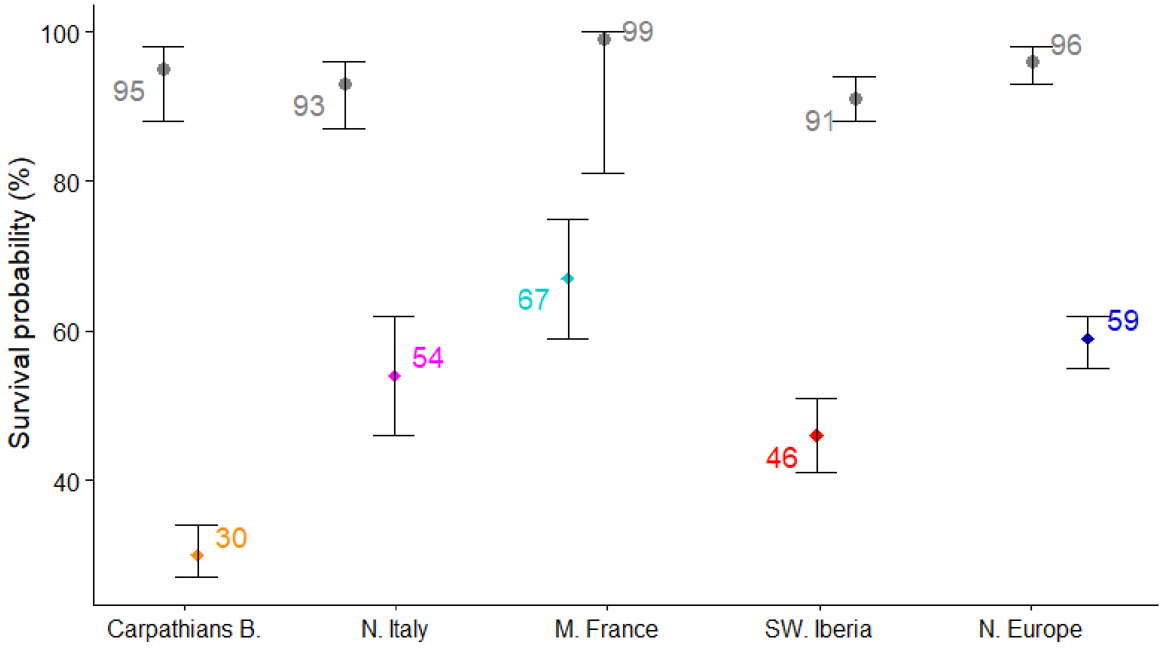

Fig. 6 – Variation on survival probability (± 95% CI) of juvenile (diamonds) and adult (circles) spoonbills during the six months from breeding to non-breeding periods according to *Region* (the grey colour for adults is used as survival includes bird from multiple natal regions). Estimates based on the most-supported model (Table 2; Model 9).

Immature survival was substantially less precise than other age classes, and particularly low in North Africa (Fig. 7).

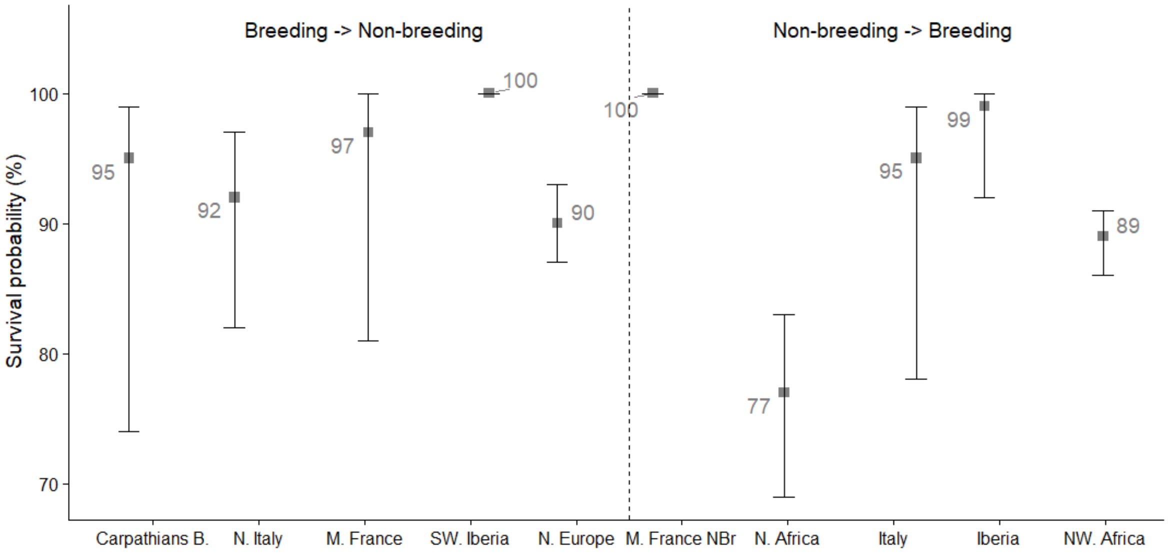

Fig. 7 – Variation on survival probability (± 95% CI) of immatures spoonbills during the six months from breeding to non-breeding periods (and vice-versa) according to *Region* (the grey colour is used as survival includes birds from multiple natal regions). Estimates based on the most-supported model (Table 2; Model 9).

Discussion

In this study, we show that juveniles have different survival rates depending on their natal region, which may explain the contrasting population trends observed across the spoonbill European breeding range, specifically the decreasing trend of the CEF population may be partially driven by the low survival rates of the Carpathian Basin juveniles, which are the lowest recorded across all age classes and regions (Fig. 6). Furthermore, we confirmed that juveniles from both flyways are more likely to winter in Africa than in Europe (Lok et al., 2011; Pigniczki, 2022). In addition, and contrary to what was previously known for this species (Lok et al., 2011, 2015), but in accordance with the results from Chapter 6, no effect of *Region* (or *Natal origin*) on adult survival rates was detected during the period between non-breeding and breeding seasons, thus reinforcing that spoonbills become better able to overcome the challenges of return migration with age (Chapter 6). While differences in adult survival from breeding region to non-breeding region were detected, no clear pattern was apparent. In general, adults in non-breeding sites had a higher chance of transitioning into breeding regions located *en route* to their northern natal region and potentially former breeding region. Detection rates were higher in the breeding regions than in the non-breeding regions and, contrary to our prediction, in the same breeding regions, the probability of detecting immigrant recruits (i.e., with a different breeding region from their natal breeding region) was considerably lower than of detecting spoonbills breeding in their natal region. As for non-breeding regions, spoonbills with different *Natal origin* generally had similar probabilities of being detected.

Limitations on immature rates

The lower detection rates of immatures (compared to adults) and their high movement to non-natal breeding regions (compared to natal regions), may be explained by immature behaviour given the species biology and the structure of the models used. During the breeding season, resightings were conducted within a radius of up to 60 km around breeding colonies. However, immatures tend to remain outside the breeding colonies (both in the non-breeding regions and further than the 60 km defined breeding regions) until they reach maturity (ca., 3-4 cy; Cramp and Simmons, 1977), although in some cases they may be resighted visiting breeding colonies likely to gather social information (Lok et al., 2013b; Tenan et al., 2017). In spoonbills, as described in other long-lived species, immatures may wander over extensive foraging areas, staying for varying lengths of time if a given foraging site is suitable, or perform long journeys prospecting for potential breeding sites as they approach the age of first breeding (Reed et al., 1999). However, to avoid overparameterisation that would result in non-estimable parameters, the models restricted birds from remaining in non-breeding regions, such as those in Africa, during the breeding season. This modelling approach “forced” immatures to “move” to one of the designated breeding regions, whilst in reality, most remain in non-breeding regions (Lok et al., 2013b). This discrepancy results in lower detection rates of immatures in breeding regions, as a higher number of individuals was expected to be present (i.e. resighted) by the models. Consequently, detection and transition rates of immatures obtained in the most parsimonious model must be interpreted with caution, as this methodology restriction violates the assumption that every marked individual alive in the population has equal likelihood of being detected (Lindberg, 2012). For example, immatures in European non-breeding regions that have not moved, are more likely to be resighted, than those that remain in Africa or those that display explorative behaviour, given our imposed restriction. Therefore, the detection probability obtained in our model for this age class includes both individuals available for detection and those unavailable for detection that are outside the study regions. In summary, we acknowledge that detection, survival, and transition rates for immatures are biased. In any case, such biases are not expected to affect adult estimates which are the main focus of this study.

Spoonbills from different *Natal origin* but in the same breeding and non-breeding *Region* were predicted to have similar chances of being detected. However, the most parsimonious model supported significant differences in detection rates between spoonbills of different *Natal origin*. By allowing the models to account for *Natal origin,* possible variation between monitoring programmes was accounted for. For example, the higher detection of individuals from Mediterranean France in Northwest Africa might be related to the fact that the rings used by the French programme (i.e., four-letter code) may be easier to resight than those used by the Northwest European and Iberian programmes (i.e., colour schemes; see Appendix, Table A7.2). But as individuals from different natal regions (where they are ringed) generally mix in non-breeding regions and, this pattern is only noticeable in Northwest Africa, any potential effect of ring type is likely to be attenuated. Nevertheless, it is indeed possible that differences in detection rates, at least in non-breeding regions, may also be due to heterogeneity in certain non-breeding regions, where spatial segregation by *Natal origin* may occur. This is the case in Italy non-breeding region, where Mediterranean French spoonbills are mainly resighted in Sardinia, while Carpathian Basin individuals are mainly found along the Southeastern coast of Italy (Fig. 2). However, such differences in detection rates (ca. 13 to 35 times higher detection rates of natal individuals versus immigrants in the same breeding region) were not expected in the breeding regions and may be due to the reported difficulty of estimating immature detectability in these regions rather than an underlying biological reason. Future analysis should therefore consider excluding a *Natal origin* effect in breeding regions, forcing similar detection rates between all adults in the same breeding regions. Such parametrisation is expected to allow further testing of transitions to non-natal regions (Table 4),which will either support the high philopatry previously reported for this species (Brouwer, 1964; Müller, 1984), or align with our results and provide further evidence that philopatry is lower than previously though. It should be noted that previous studies (Brouwer, 1964; Müller, 1984) reporting philopatry did not employ employed CMR methods, nor considered metapopulations level datasets, which may contribute to the novel results presented here.

Transition rates and natal dispersal

Although it is known that juvenile spoonbills in the EAF are more likely to spend the non-breeding season in Africa than in Europe (Lok et al., 2011; Pigniczki, 2022), this is now reported here for the entire Western Palearctic. Spoonbills are social birds (de Goeij et al., 2012; Lok et al., 2019; Navedo and Garaita, 2012) and similar to what was described in other species, like the Lesser spotted eagle (*Clanga pomarina*) (Meyburg et al., 2017) and the White stork (*Ciconia ciconia*), individuals are likely to follow older conspecifics during migration to benefit from their knowledge (e.g. navigation skills, location of stop-over sites) (Meyburg et al., 2017). Considering that Northwest European spoonbills were known to mainly winter in Northwest Africa (Lok et al., 2011), although recent analysis suggest a northward shift toward European non-breeding regions (Lok et al., 2013a), while Carpathian Basin spoonbills mainly winter in Northern Africa (Pigniczki, 2022), it is unsurprising that a higher proportion of juveniles follow older conspecifics to African rather than European regions.

As suggested by the low number of emigration cases detected during data exploration, we predicted high philopatry of spoonbills to their "natal breeding" region. However, while this was certainly true in certain regions (e.g., North European spoonbills in Iberia showed a higher probability to move to Northwest Europe breeding region than to recruit in Southwest-Iberia), several exceptions were also detected. In fact, natal adults from northern regions, displayed a high chance of transition to southern breeding regions (Northern Italy and Southwest-Iberia) located *en route* to their more northern natal region. This result is surprising, but it should be taken with care due to potential limitations. First, since some breeding regions are *en route* to more northern regions, we cannot rule out the possibility that some birds were misclassified if resighted during migration rather than at their actual northern breeding region. Such misclassifications can occur because long-distance migrants (those returning to northern breeding regions) typically arrive at their breeding sites later in the season (General discussion; Lok et al., 2013b). Second, as mentioned above, it is not possible to rule out the possibility that biased detection rates may have influenced the estimates of transition rates. Nevertheless, if low philopatry reflects a genuine behaviour and natal dispersal, it may result from high conspecific attraction, a trait characteristic of social species, which may indeed reduce philopatry by attracting individuals into non natal breeding regions (Brown et al., 1990; Forbes and Kaiser, 1994). Juvenile-led recruitment processes have been observed in other systems (Gill et al., 2019; Verhoeven et al., 2018), and conspecific attraction has been identified as the main driver of colony growth for spoonbills in Italy (Tenan et al., 2017). It should also be noted that the low number of known cases of immigration into southern breeding regions could be due to the low resighting effort in the Southwest-Iberian breeding region (< 20%). It is therefore plausible that, at least to some extent, recruiting spoonbills may indeed follow older conspecifics to southern breeding regions instead of proceeding with migration to their northern natal regions.

Survival rates and its influence on population trends

As expected, juvenile survival rates were lower than that of immatures and adults, due to their lower experience and performance of basic functional behaviours such as foraging and movement (Anders et al., 1997; Corbeau et al., 2020; Harel et al., 2016; Rotics et al., 2016; Sullivan, 1989). Among these, juveniles from the Carpathian Basin breeding region have the lowest survival (Fig. 7). This is likely due to the poor conditions on some of the breeding colonies in this region. For example Croatian breeding sites, which are classified as Natura 2000, are becoming increasingly degraded due to the mismanagement of fishponds, which are being “reconstructed” to intensify fish production (funded by the European Union), severely affecting the Croatian spoonbill breeding population (Mikuska et al., 2023). Similarly, Hungary breeding sites are currently severely threatened by anthropogenic activities, specifically by water drainage which is further exacerbated by climate change due to ongoing reduction of groundwater levels. Indeed, a decline of approximately 25% of the Hungarian and Croatian breeding populations has been documented from 2007 to 2022 (Champagnon and Kralj, 2023). The low survival rates estimated here suggest that the survival of juvenile during their first migration plays a role in the observed decline of the CEF meta-population (Champagnon et al., 2019a). However, further studies, particularly applying a matrix model, should be developed to further test this pattern (Caswell, 2001). The degradation of breeding sites can also explain the low survival rates estimated for Iberian juveniles. The over-exploitation of groundwater in Doñana for intensive agriculture (e.g. rice fields and berry production) together with climate change, specifically warming temperatures (Bustamante et al., 2016; de Felipe et al., 2023; Díaz-Paniagua and Aragonés, 2015), andd the transformation of wetlands in agricultural production areas such as strawberry farms (Vansteelant, 2023) have greatly reduced the quality of this wetland (Acreman and Salathe, 2022; de Felipe et al., 2023; Díaz-Paniagua and Aragonés, 2015). Therefore, our results support that inexperienced juveniles likely have severe difficulties in sustaining themselves in a landscape where wetland habitats are disappearing and becoming or lower quality.

Due to the methodological limitations mentioned above, a high uncertainty in immature survival rates was expected. Furthermore, even if the survival of immatures might have a major impact on population dynamics (Gaillard et al., 1998; Penteriani et al., 2005), the large spatial variation in immature distribution, their exploratory dispersal behaviour, and the associated difficulty in tracking them, limits our capacity to assess how different factors influencing different sites may affect immature survival rates (Grande et al., 2009). These difficulties were apparent in our modelling as it was not possible to estimate immature survival according to their behaviour (immatures remaining in the non-breeding regions vs immatures that moved to breeding regions) and *Natal origin*. Despite these above limitations, it is nonetheless interesting to note that our present estimates for this age class are aligned with the prediction of a negative effect of ecological barriers, which had been suggested by the lower survival rates of migratory spoonbills from Mediterranean France (though not supported by the most parsimonious model in Chapter 6, likely due to the small sample size of individuals with known non-breeding location in that chapter). Indeed, both African regions appear to have the lowest immature survival rates among non-breeding regions (despite the overlapping CIs between Italy and Northern Africa; Fig. 7), which is likely due to the crossing of major ecological barriers (Chapter 6; Lok et al., 2015). Crossing the Sahara, which several spoonbills travelling to Northwest Africa must undertake, poses a significant challenge (Lok et al., 2015), and one that immatures travelling to Northern Africa do not have to overcome. It would therefore be expected that survival for immatures in Northwest Africa non-breeding region [$\Phi_{Imt} = 0.89$, 95%CI (0.86–0.91)] would be lower than that of immatures in Northern Africa [$\Phi_{Imt} = 0.77$, 95%CI (0.69–0.83)], which was not the case. This may be due to ongoing wetland degradation in the Northern Africa non-breeding region. In Tunisia, for example, more than 50% of wetlands have been destroyed in the last century, and the remaining ones are under intense pressure from urban development, industrial activities, and unsustainable agricultural practices (e.g., excessive use of pesticides, retention and removal of water from wetlands for agriculture) (OTEDD, 2016). Tunisia is known to be one of the most important non-breeding areas for CEF individuals, as confirmed by recent work assessing the non-breeding distribution of Hungarian birds, with 74% of Hungarian birds with a known non-breeding location being present in Tunisia (Pigniczki, 2022). Therefore, the impact of wetland degradation in Tunisia on the survival and population trends of the CEF may be greater than initially thought.

In birds and mammals, the conditions experienced in early life are known to have a significant effect on the quality of the individual and, consequently, their survival rates (Lindström, 1999). Therefore, it could be expected that individuals born in apparently low-quality habitats such as the Carpathian Basin (according to juvenile and immature survival rates), would also experience lower adult survival rates compared to conspecifics from other natal regions. But, contrary to our prediction, adult survival between the non-breeding and breeding seasons was not dependent on *Region* or *Natal origin*. Conversely, it supports the hypothesis that, with age, spoonbills are increasingly able to respond successfully to multiple challenges, regardless of the non-breeding region used. Older individuals are likely more experienced, leading to improved performance (e.g. in foraging and migration) as suggested in Chapters 3 and 6 of this thesis. This is further supported by the fact that adults in the Carpathian Basin breeding region (and associated migration routes) have similar survival to adults from other breeding regions, whilst this is depressed in other age classes. The high adult survival in the Carpathian Basin may also suggests that spoonbills prioritise survival over reproduction, when faced with adverse environmental conditions. Promoting survival as a response to periods of environmental instability , is typical of long-lived species (Rolland et al., 2009; Sæther and Bakke, 2000), which adopt a bet-hedging strategy by maintaining high adult survival rates to ensure future reproductive opportunities under more favourable conditions (Nevoux et al., 2010). Although an effect of *Region* on adult survival was included in the most parsimonious model, adult survival rates in different breeding regions appear to overlap without a clear pattern (Fig. 7), and it is therefore to identify an underlying biological explanation for this result.

Mark-capture-recapture analyses are challenging, and although this dataset contained a unique and impressive amount of information in both time and space, it is still challenging to test and interpret biological rates such as survival, natal philopatry and breeding site fidelity. Nevertheless, and despite some limitations, this study successfully overcomes some of the challenges encountered in Chapter 6 (and in other survival studies) and, while reenforcing the potential impacts of wetland degradation and ecological barriers on survival, it also highlights the capacity of spoonbills to cope with adversity as they age. Interestingly, while the raw data indicated high rates of philopatry, the most parsimonious model revealed a potential high level of dispersal (likely natal but not possible to distinguish from breeding dispersal with current modulization) to breeding regions that lay on route to the more northern breeding regions. This result should be further scrutinized by subsequent exploration of the dataset as it continues to expand, in order to reduce modelling limitations and estimates. For example, since the probability of using a particular site is likely to depend mainly on the site previously used by an individual, it is possible to account for such past events by applying memory models that track both the current non-breeding region and the previous breeding region of an individual (Brownie et al., 1993; Cole et al., 2014; Rouan et al., 2009).

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Ethics approval

All ringing sessions were conducted in accordance with national legislation, animal welfare, and by experienced ringers.

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Appendices A7

Table A7.1. Number of spoonbills ringed per year of birth (since 2003) and specified country. Only individuals ringed as chicks considered and those resighted in different flyways from the flyway of ringing are also given on this table (but were excluded from the analysis, see Methods for further details on data cleaning).

		Ringing program							
Year of birth	Total ringed per year	France	Croatia	Hungary	Italy	Netherlands	Portugal	Servia	Spain
2003	1054	0	33	74	96	300	0	38	513
2004	1331	0	62	108	87	391	0	101	582
2005	918	0	104	65	39	395	0	154	161
2006	1429	0	37	91	43	478	0	20	760
2007	1493	0	97	127	61	481	0	133	594
2008	1238	30	35	189	152	579	0	31	222
2009	1148	55	9	154	193	491	0	39	207
2010	1226	140	74	70	233	296	0	0	413
2011	1732	240	64	166	155	328	0	118	661
2012	968	224	110	141	76	398	0	0	19
2013	1545	262	113	222	125	412	0	0	411
2014	1341	542	0	128	97	510	0	37	27
2015	1412	382	0	215	188	524	25	0	78
2016	1558	452	32	169	232	627	38	0	8
2017	1674	368	0	198	209	594	25	0	280
2018	1548	171	26	178	168	658	14	0	333
2019	1279	426	0	59	75	498	27	0	194
2020	833	281	0	152	17	354	29	0	0
2021	1610	569	0	85	93	666	29	0	168
Total per country	25337	4142	796	2591	2339	8980	187	671	5631

Table A7.2. Description of ringing scheme details per ringing program.

Ringing program	Colour-ring type	Colour-ring colour	Colour-ring code	First letter	Contact
Croatia	Flag: combination of uncoded flag and legring(s)	Red flag			werkgroeplepelaar@gmail.com
Croatia	Legring: one, coded	White [W]	3 alpha-numeric code	C	tibor.kopacki.rit@gmail.com
France	Legring: one, coded	White [W]	4 alpha code	A or F	baguage@tourduvalat.org
Hungary	Flag: combination of uncoded flag and legring(s)	Blue flag			werkgroeplepelaar@gmail.com
Hungary	Legring: one, coded	White [W]	4 alpha-numeric code	J	csaba.spoonbill@gmail.com
Italy	Legring: one, coded	Black (Niger) [N]	3 alpha-numeric code		recoveries@isprambiente.it
Italy	Legring: one, coded	Black (Niger) [N]	4 alpha code	I	recoveries@isprambiente.it
Netherlands	Legrings: combination of uncoded (both legs)				werkgroeplepelaar@gmail.com
Netherlands	Legring: one, coded	White [W]	4 alpha code	N	werkgroeplepelaar@gmail.com

Netherlands	Flag: combination of uncoded flag and legring(s)	yellow flag (Yf) or black flag (Nf)			werkgroeplepelaar@gmail.com
Netherlands/ Croatia/ Serbia/ Hungary	Legrings: combination of coded		2 alpha-numeric code		werkgroeplepelaar@gmail.com
Portugal	Flag: combination of uncoded flag and legring(s)	light blue flag			werkgroeplepelaar@gmail.com
Serbia	Legring: one, coded	White [W]	3 alpha-numeric code	E	daliborka@nhmbeo.rs antun.zuljevic@gmail.com
Serbia	Legring: one, coded	White [W]	4 alpha code	B	daliborka@nhmbeo.rs antun.zuljevic@gmail.com
Spain	Legrings: combination of uncoded	white, yellow and red			anillamiento@ebd.csic.es
Spain	Legring: one, coded	Red [R]	3 alpha-numeric code		anillamiento@ebd.csic.es
Spain	Legring: one, coded	White [W]	3 alpha-numeric code		anillamiento@ebd.csic.es

Table A7.3. Number of different spoonbills resighted during each breeding season. Only one resighting per individual was considered in each year ($n_{Resighting}$ = 15 675).

Year	Carpathian Basin	Southwest-Iberia	Northern Italy	Mediterranean France	Northwest Europe
2004	2	18	17	0	15
2005	6	25	10	0	28
2006	21	105	13	0	95
2007	41	85	32	0	190
2008	30	126	30	0	211
2009	30	73	45	0	317
2010	23	171	79	3	417
2011	43	154	78	11	553
2012	71	113	67	25	417
2013	59	104	95	6	405
2014	72	151	105	83	444
2015	93	110	136	95	521
2016	101	233	146	259	654
2017	111	149	152	272	763
2018	116	98	160	377	751
2019	113	112	119	348	824
2020	127	54	120	339	969
2021	159	139	127	534	980

Table A7.4. Number of different spoonbills resighted during each non-breeding season per region. Only one resighting per individual was considered in each year ($n_{Resighting}$ = 6 673).

Winter	Atlantic France	Iberia	Italy	Mediterranean France	Northern Africa	Northwest Africa
´03 -´04	0	13	8	0	1	26
´04 -´05	10	43	12	0	11	17
´05 -´06	9	50	28	0	19	39
´06 -´07	14	35	22	0	11	94
´07 -´08	20	109	17	0	18	162
´08 -´09	25	102	10	0	28	137
´09 -´10	21	68	24	0	30	44
´10 -´11	38	112	6	0	47	100
´11 -´12	56	118	27	0	40	104
´12 -´13	42	146	4	1	100	97
´13 -´14	51	125	22	0	144	95
´14 -´15	33	179	26	0	84	144
´15 -´16	58	160	31	0	61	130
´16 -´17	59	216	95	19	60	149
´17 -´18	44	208	53	15	74	128
´18 -´19	30	235	42	28	169	59
´19 -´20	57	179	25	2	21	108
´20 -´21	48	130	17	11	58	86
´21 -´22	54	288	14	3	117	114

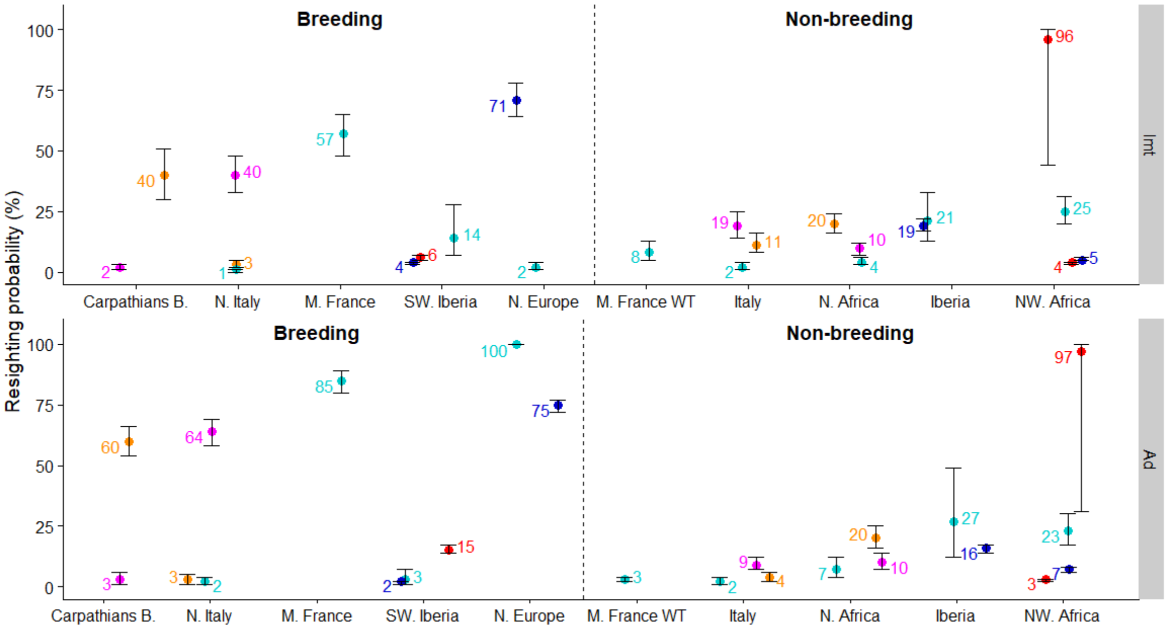

Fig. A7.1 – Resighting probability (± CI) of spoonbills according to *Age* classes and *Natal origin* in each *Region*. Estimates are based on most-supported model (Model 9; Table 2).

Table A7.5. Transition probability of spoonbills from different age classes from breeding to non-breeding region (and vice-versa). Estimates are based on the most supported model (Model 9; Table 2).

From	*To*	*Age*	Natal *origin*	*Est.*	*Min.*	*Max.*	*Period*
Carpathian Basin	Italy	Juvenile	Carpathian Basin	12%	7%	19%	Br -> NBr
Carpathian Basin	Northern Africa	Juvenile	Carpathian Basin	88%	81%	93%	Br -> NBr
Carpathian Basin	Italy	Immature	Carpathian Basin	67%	52%	79%	Br -> NBr
Carpathian Basin	Northern Africa	Immature	Carpathian Basin	33%	21%	48%	Br -> NBr
Carpathian Basin	Italy	Adult	Carpathian Basin	19%	10%	34%	Br -> NBr
Carpathian Basin	Northern Africa	Adult	Carpathian Basin	81%	66%	90%	Br -> NBr
Carpathian Basin	Italy	Immature	Northern Italy	5%	0%	33%	Br -> NBr
Carpathian Basin	Northern Africa	Immature	Northern Italy	95%	67%	100%	Br -> NBr
Carpathian Basin	Italy	Adult	Northern Italy	0%	0%	0%	Br -> NBr
Carpathian Basin	Northern Africa	Adult	Northern Italy	100%	100%	100%	Br -> NBr
Iberia	Mediterranean France	Immature	Mediterranean France	36%	22%	53%	NBr -> Br
Iberia	Northwest Europe	Immature	Mediterranean France	12%	3%	36%	NBr -> Br
Iberia	Southwest-Iberia	Immature	Mediterranean France	53%	36%	68%	NBr -> Br
Iberia	Mediterranean France	Adult	Mediterranean France	90%	60%	98%	NBr -> Br
Iberia	Northwest Europe	Adult	Mediterranean France	2%	0%	13%	NBr -> Br
Iberia	Southwest-Iberia	Adult	Mediterranean France	8%	1%	40%	NBr -> Br
Iberia	Northwest Europe	Immature	Northwest Europe	69%	62%	75%	NBr -> Br
Iberia	Southwest-Iberia	Immature	Northwest Europe	31%	25%	38%	NBr -> Br
Iberia	Northwest Europe	Adult	Northwest Europe	96%	93%	98%	NBr -> Br
Iberia	Southwest-Iberia	Adult	Northwest Europe	4%	2%	7%	NBr -> Br
Iberia	Southwest-Iberia	Immature	Southwest-Iberia	100%	100%	100%	NBr -> Br

Iberia	Southwest-Iberia	Adult	Southwest-Iberia	100%	100%	100%	NBr -> Br
Italy	Mediterranean France	Immature	Mediterranean France	31%	24%	40%	NBr -> Br
Italy	Northern Italy	Immature	Mediterranean France	69%	60%	76%	NBr -> Br
Italy	Mediterranean France	Adult	Mediterranean France	12%	4%	31%	NBr -> Br
Italy	Northern Italy	Adult	Mediterranean France	88%	69%	96%	NBr -> Br
Italy	Carpathian Basin	Immature	Carpathian Basin	93%	71%	99%	NBr -> Br
Italy	Northern Italy	Immature	Carpathian Basin	7%	1%	29%	NBr -> Br
Italy	Carpathian Basin	Adult	Carpathian Basin	41%	29%	55%	NBr -> Br
Italy	Northern Italy	Adult	Carpathian Basin	59%	45%	71%	NBr -> Br
Italy	Carpathian Basin	Immature	Northern Italy	5%	1%	22%	NBr -> Br
Italy	Northern Italy	Immature	Northern Italy	95%	78%	99%	NBr -> Br
Italy	Carpathian Basin	Adult	Northern Italy	0%	0%	0%	NBr -> Br
Italy	Northern Italy	Adult	Northern Italy	100%	100%	100%	NBr -> Br
Mediterranean France	Northwest Africa	Juvenile	Mediterranean France	20%	16%	26%	Br -> NBr
Mediterranean France	Iberia	Juvenile	Mediterranean France	6%	4%	9%	Br -> NBr
Mediterranean France	Italy	Juvenile	Mediterranean France	7%	3%	13%	Br -> NBr
Mediterranean France	Mediterranean France NBr	Juvenile	Mediterranean France	2%	1%	3%	Br -> NBr
Mediterranean France	Northern Africa	Juvenile	Mediterranean France	66%	58%	72%	Br -> NBr
Mediterranean France	Northwest Africa	Immature	Mediterranean France	7%	4%	13%	Br -> NBr
Mediterranean France	Iberia	Immature	Mediterranean France	8%	4%	14%	Br -> NBr
Mediterranean France	Italy	Immature	Mediterranean France	12%	6%	23%	Br -> NBr
Mediterranean France	Mediterranean France NBr	Immature	Mediterranean France	66%	54%	75%	Br -> NBr
Mediterranean France	Northern Africa	Immature	Mediterranean France	8%	3%	19%	Br -> NBr
Mediterranean France	Northwest Africa	Adult	Mediterranean France	8%	5%	12%	Br -> NBr

Mediterranean France	Iberia	Adult	Mediterranean France	7%	3%	16%	Br -> NBr
Mediterranean France	Italy	Adult	Mediterranean France	5%	2%	12%	Br -> NBr
Mediterranean France	Mediterranean France NBr	Adult	Mediterranean France	69%	56%	79%	Br -> NBr
Mediterranean France	Northern Africa	Adult	Mediterranean France	12%	5%	25%	Br -> NBr
Northern Africa	Mediterranean France	Immature	Mediterranean France	2%	1%	5%	NBr -> Br
Northern Africa	Northern Italy	Immature	Mediterranean France	98%	95%	99%	NBr -> Br
Northern Africa	Mediterranean France	Adult	Mediterranean France	74%	44%	91%	NBr -> Br
Northern Africa	Northern Italy	Adult	Mediterranean France	26%	9%	56%	NBr -> Br
Northern Africa	Carpathian Basin	Immature	Carpathian Basin	18%	10%	28%	NBr -> Br
Northern Africa	Northern Italy	Immature	Carpathian Basin	82%	72%	90%	NBr -> Br
Northern Africa	Carpathian Basin	Adult	Carpathian Basin	94%	79%	98%	NBr -> Br
Northern Africa	Northern Italy	Adult	Carpathian Basin	6%	2%	21%	NBr -> Br
Northern Africa	Carpathian Basin	Immature	Northern Italy	79%	69%	87%	NBr -> Br
Northern Africa	Northern Italy	Immature	Northern Italy	21%	13%	31%	NBr -> Br
Northern Africa	Carpathian Basin	Adult	Northern Italy	61%	53%	70%	NBr -> Br
Northern Africa	Northern Italy	Adult	Northern Italy	39%	30%	47%	NBr -> Br
Northwest Europe	Northwest Africa	Immature	Mediterranean France	100%	100%	100%	Br -> NBr
Northwest Europe	Iberia	Immature	Mediterranean France	0%	0%	0%	Br -> NBr
Northwest Europe	Northwest Africa	Adult	Mediterranean France	100%	100%	100%	Br -> NBr
Northwest Europe	Iberia	Adult	Mediterranean France	0%	0%	0%	Br -> NBr
Northwest Europe	Northwest Africa	Juvenile	Northwest Europe	84%	81%	86%	Br -> NBr
Northwest Europe	Iberia	Juvenile	Northwest Europe	16%	14%	19%	Br -> NBr
Northwest Europe	Northwest Africa	Immature	Northwest Europe	15%	11%	20%	Br -> NBr
Northwest Europe	Iberia	Immature	Northwest Europe	85%	80%	89%	Br -> NBr

Northwest Europe	Northwest Africa	Adult	Northwest Europe	18%	15%	21%	Br -> NBr
Northwest Europe	Iberia	Adult	Northwest Europe	82%	79%	85%	Br -> NBr
Northern Italy	Italy	Immature	Mediterranean France	74%	59%	85%	Br -> NBr
Northern Italy	Northern Africa	Immature	Mediterranean France	26%	15%	41%	Br -> NBr
Northern Italy	Italy	Adult	Mediterranean France	56%	33%	77%	Br -> NBr
Northern Italy	Northern Africa	Adult	Mediterranean France	44%	23%	67%	Br -> NBr
Northern Italy	Italy	Immature	Carpathian Basin	25%	16%	37%	Br -> NBr
Northern Italy	Northern Africa	Immature	Carpathian Basin	75%	63%	84%	Br -> NBr
Northern Italy	Italy	Adult	Carpathian Basin	100%	100%	100%	Br -> NBr
Northern Italy	Northern Africa	Adult	Carpathian Basin	0%	0%	0%	Br -> NBr
Northern Italy	Italy	Juvenile	Northern Italy	22%	15%	32%	Br -> NBr
Northern Italy	Northern Africa	Juvenile	Northern Italy	78%	68%	85%	Br -> NBr
Northern Italy	Italy	Immature	Northern Italy	81%	69%	89%	Br -> NBr
Northern Italy	Northern Africa	Immature	Northern Italy	19%	11%	31%	Br -> NBr
Northern Italy	Italy	Adult	Northern Italy	81%	71%	89%	Br -> NBr
Northern Italy	Northern Africa	Adult	Northern Italy	19%	11%	29%	Br -> NBr
Northwest Africa	Mediterranean France	Immature	Mediterranean France	10%	6%	16%	NBr -> Br
Northwest Africa	Northwest Europe	Immature	Mediterranean France	89%	83%	93%	NBr -> Br
Northwest Africa	Southwest-Iberia	Immature	Mediterranean France	1%	0%	34%	NBr -> Br
Northwest Africa	Mediterranean France	Adult	Mediterranean France	37%	29%	46%	NBr -> Br
Northwest Africa	Northwest Europe	Adult	Mediterranean France	6%	3%	10%	NBr -> Br
Northwest Africa	Southwest-Iberia	Adult	Mediterranean France	57%	48%	65%	NBr -> Br
Northwest Africa	Northwest Europe	Immature	Northwest Europe	7%	5%	10%	NBr -> Br
Northwest Africa	Southwest-Iberia	Immature	Northwest Europe	93%	90%	95%	NBr -> Br

Northwest Africa	Northwest Europe	Adult	Northwest Europe	23%	20%	27%	NBr -> Br
Northwest Africa	Southwest-Iberia	Adult	Northwest Europe	77%	73%	80%	NBr -> Br
Northwest Africa	Southwest-Iberia	Immature	Southwest-Iberia	100%	100%	100%	NBr -> Br
Northwest Africa	Southwest-Iberia	Adult	Southwest-Iberia	100%	100%	100%	NBr -> Br
Southwest-Iberia	Northwest Africa	Immature	Mediterranean France	0%	0%	0%	Br -> NBr
Southwest-Iberia	Iberia	Immature	Mediterranean France	100%	100%	100%	Br -> NBr
Southwest-Iberia	Northwest Africa	Adult	Mediterranean France	90%	72%	97%	Br -> NBr
Southwest-Iberia	Iberia	Adult	Mediterranean France	10%	3%	28%	Br -> NBr
Southwest-Iberia	Northwest Africa	Immature	Northwest Europe	77%	73%	80%	Br -> NBr
Southwest-Iberia	Iberia	Immature	Northwest Europe	23%	20%	27%	Br -> NBr
Southwest-Iberia	Northwest Africa	Adult	Northwest Europe	90%	85%	93%	Br -> NBr
Southwest-Iberia	Iberia	Adult	Northwest Europe	10%	7%	15%	Br -> NBr
Southwest-Iberia	Northwest Africa	Juvenile	Southwest-Iberia	98%	97%	98%	Br -> NBr
Southwest-Iberia	Iberia	Juvenile	Southwest-Iberia	2%	2%	3%	Br -> NBr
Southwest-Iberia	Northwest Africa	Immature	Southwest-Iberia	99%	99%	99%	Br -> NBr
Southwest-Iberia	Iberia	Immature	Southwest-Iberia	1%	1%	1%	Br -> NBr
Southwest-Iberia	Northwest Africa	Adult	Southwest-Iberia	99%	98%	99%	Br -> NBr
Southwest-Iberia	Iberia	Adult	Southwest-Iberia	1%	1%	2%	Br -> NBr
Mediterranean France NBr	Mediterranean France	Immature	Mediterranean France	100%	100%	100%	NBr -> Br
Mediterranean France NBr	Mediterranean France	Adult	Mediterranean France	100%	100%	100%	NBr -> Br

Appendices B7

Goodness-of-fit analysis

The dataset was first split in two considering breeding and non-breeding events, and ringing region of the individual (group) was not considered. Nevertheless, we considered multiple states in the model according to the region where the individuals were resighted.

Breeding dataset

In the U-care programme, the first occasion was suppressed to account for the lower probability of survival and detection of juveniles, compared to the other age classes, when performing goodness-of-fit.

Table B7.1. GOF results for the breeding dataset, when considering a multistate Arnason-Schwarz model with 19 breeding occasions and five states (corresponding to the five breeding regions). Colors indicate adequate overdispersion effects (green); high but acceptable overdispersion (orange); and strong violation of GOF assumptions (red).

	χ_2 stat.	*df*	*c-hat*	*P-value*
Test WBWA	141.90	38.00	**3.73**	< 0.001
Test 3G.SR	619.93	72.00	**8.61**	< 0.001
Test 3G.SM	460.58	292.00	**1.58**	< 0.001
Test M.Itec	6512366.21	78	**83491.87**	< 0.001
Test M.Ltec	78.59	30	2.62	< 0.001

Memory, transience and trap dependence effects were detected. The memory effect was significant, which was predicted given the high fidelity displayed by spoonbills (Lok et al., 2013). Rather than accounting for this effect during modelling, which would result in over-parameterisation due to the creation of a large number of additional parameters to estimate (i.e., survival, detectability, and transition) to our multiregional dataset (Rouan et al., 2009), we accounted for the overdispersion associated with this effect by including it in the overdispersion correction (i.e. *c-hat*). Despite suppressing the first encounter, we still had a strong transience effect, likely caused by immature birds that do not systematically return to breeding sites (1-3.5 cy). We accounted for this by including three age classes (0.5 cy, 1-3.5 cy, >3.5 cy) in the model and therefore discarded the Test3G.Sr component from the calculation of the overdispersion effect (Pradel et al., 1997). Finally, the large trap dependence component may have been caused by within-region variation in resighting effort, such that some individuals (using regions where observers are more active) are much more likely to be resighted than others. To explore this effect in more detail, we grouped the data by ringing region. The trap-dependence test of Arnason-Schwarz model is not available when considering a group effect associated with ringing region (*Natal origin*). As there are too few movements of breeders from one region to another, as an approximation, we performed a GOF test on CJS model (i.e., without considering a potential effect of resighting region).

Table B7.2. GOF results for the trap-dependent component Test2.CT applied to breeding dataset only, when considering a CJS model with 19 breeding occasions and five different groups (i.e., five breeding regions). Colors indicate adequate overdispersion effects (green); high but acceptable overdispersion (orange); and strong violation of GOF assumptions (red).

	χ_2 stat.	*df*	*c-hat*	*P*-value
Mediterranean France	12.065	9	**1.34**	0.210
Carpathian Basin	35.792	15	**2.39**	0.002
Northern Italy	24.323	15	**4.07**	0.060
Northwest Europe	409.414	15	**27.29**	0.000
Southwest-Iberia	17.372	15	**1.16**	0.297

Trap dependence effect is mainly caused by the birds marked in the Northwest Europe Region. To account for this dependence effect, *Natal origin* classes were considered in the detectability component of competing models.

Non-breeding dataset

The non-breeding dataset started at the first winter resighting of an individual. We started by first testing the Arnason-Schwarz model:

Table B7.3. GOF results for the non-breeding dataset, when considering a multistate Arnason-Schwarz model with 19 breeding occasions and six states (corresponding to the six different non-breeding regions). Colours indicate adequate overdispersion effects (green); high but acceptable overdispersion (orange); and strong violation of GOF assumptions (red).

	χ_2 stat.	*df*	*c-hat*	***P*-value**
Test WBWA	47.08	18.00	**2.62**	0
Test 3G.SR	515.90	86.00	**6.00**	0
Test 3G.SM	296.70	210.00	**1.41**	0
Test M.Itec	94.58	16.00	**5.91**	0
Test M.Ltec	18.49	6.00	**3.08**	0

We detected a memory effect (test WBWA) for the non-breeding dataset that was likely due to the high fidelity of spoonbills to their non-breeding sites (Lok et al. 2011). As above the transience (Test 3G.SR) was accounted for by considering two age classes (1-3.5 cy, >3.5 cy) in our model. Due to their exploratory behaviour, greater heterogeneity in immature detection rates during the non-breeding period was expected, and thus trap-dependence is accounted for by also considering two age classes (1-3.5 cy, >3.5 cy). Thus, the Test 3G.SR and Test M.Itec components were discarded from the calculation of overdispersion effect (Kentie et al., 2023; Pradel et al., 1997b). Finally, the Test M.Ltec component was significant but accounted for in the overdispersion correction (i.e. *c-hat*).

In summary, by adding χ_2 from the breeding and non-breeding datasets we accounted for a strong memory and trap dependence effects, and obtain our overdispersion effect (*c-hat)* which was accounted in the different competing models (Table B7.8).

Table B7.4. Estimation of overdispersion effect. Green colours mean acceptable overdispersion effects.

	SUM (WBWA;TES3G.SM; Test M.LTec) of all groups	***SUM (degrees of freedom)***	***c-hat* (overdispersion correction)**
Breeding	681.07	360	**1.89**
Non-breeding	362.28	234	**1.55**
Total	1043.35	594	**1.76**

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CHAPTER 8

General discussion

Spoonbills, Camargue, 2021.

Spoonbills are between 65-80 cm in length, have a wingspan of 115 to 145 cm, and weigh approximately 1700-2000 g. On average, males are 12% larger than females.

General discussion

In this thesis, I investigated how local and global changes across the migratory range of a waterbird species may affect demographic parameters at different phases of the annual cycle and life stages. This knowledge improves our current understanding of how resilient these species may be, and help predict how biodiversity may respond to ongoing and future global changes. The present thesis specifically contributes to a broader understanding of the links between anthropogenic activities and environmental change on breeding phenology, productivity, body condition, habitat use, migratory behaviour, and survival rates at population and meta-population levels, of a colonial migratory waterbird that has undergone a remarkable population recovery after years of decline, the Eurasian spoonbill (*Platalea leucorodia*). Here, I discuss the main findings of each previous chapter, together with the possible limitations of each study, providing a species-level and general overview and suggestions for future research in those topics.

1. Local and global impacts of anthropogenic activities on spoonbills

1.1. *Direct and local impacts of anthropogenic activities*

Despite increasing awareness of the importance of wetlands, many of those still present are degraded and/or currently under severe anthropogenic pressure (Davidson, 2014; Gardner and Finlayson, 2018). For instance, the spread and abundance of artificial materials in the environment continues to increase (Borrelle et al., 2020; Geyer et al., 2017), as do reports of direct impacts of artificial materials on wildlife (Derraik, 2002; Gregory, 2009; Kühn and van Franeker, 2020; Laist, 1997), including their presence on bird nests (de Souza Petersen et al., 2016; Hanmer et al., 2017; Jagiello et al., 2018; Suárez-Rodríguez and Macías Garcia, 2017; Townsend and Barker, 2014; Witteveen et al., 2017). During data collection for **Chapters 2** and **3**, the presence of artificial materials in spoonbill nests was abundantly evident. However, what drives spoonbills to collect such materials, and their potential effects with respect to breeding success were unclear, even after reviewing the existing literature. In **Chapter 4,** I found that spoonbills demonstrated a clear preference for sheet-like plastics of white transparent colour. Given the high availability of different artificial materials throughout Camargue (Almeida et al., 2023) and the tendency of Pelecaniformes species, such as spoonbills, to collect materials in close proximity to their nests (namely from nests of conspecifics) (Grant et al., 2018; Nelson, 2006), if these materials are collected accidentally (e.g., Brown noddy – *Anous stolidus*; Ryan, 2020) or simply because they are more readily available than natural materials (e.g., Great grey shrike – *Lanius excubitor*; Antczak et al., 2010), I would therefore expect either greater variability in the type and colour of artificial materials on nests, or that those materials would resemble natural ones. The fact that more than half of all artificial materials identified were of the same type and colour, which does not resemble natural materials, suggests that these may have a specific role in spoonbill nests. However, while the potential functional role of sheet-like plastics in spoonbill nests cannot be ruled out, it is nevertheless possible that the higher frequency of these materials could be related to the species spoon-shaped bill. This bill shape might facilitate the transport of such materials (Fig. 1), compared to smaller or heavier materials (e.g., strings, metals), which might require greater bill agility or strength.

Fig. 1 – Eurasian spoonbill arriving with sheet-like plastic. © Tour du Valat

Artificial materials found by deconstructing the nests at the end of the breeding season (Fig. 2), corresponded to a residual proportion of the total nest weight and were predominantly present in the nest lining. To confirm the role of artificial materials in the nest lining and to overcome the challenge of recording spoonbill nest temperature, in **Chapter 4**, I recommended the use of temperature loggers embedded in artificial eggs, as demonstrated by Hope et al. (2018). However, to correlate nest lining with the temperature measured by the artificial eggs, visual monitoring (e.g., photos of the nest taken once a week; following the protocol developed by Dumas et al. (2009) and adapted in **Chapter 4**), would be necessary to avoid observation bias in the wild.

Fig. 2 – Artificial material present in a deconstructed nest. © Carolina Hadden

Given that nests, which were initially considered to have no artificial material lining when the loggers were deployed, subsquently had artificial materials added to their lining.

It is also worth noting that, despite the abundance of artificial materials on the nests, there are currently no documented cases of spoonbill mortality due to entanglement or suffocation of chicks or adults by nest material. Nevertheless, this is entirely possible as seen in Fig. 3, and as reported in other species (Lavers et al., 2014; Luna et al., 2018; Ryan, 2018; Seacor et al., 2014; Votier et al., 2011). Mortality events should therefore be recorded and reported as part of the artificial materials monitoring protocol mentioned above.

Fig. 3 – Although death of this individuals was likely not caused by artificial materials, the presence of a bottle ring in the chick neck could have impaired the chick from swallowing, and eventually lead to death by starvation, as the chick grows, and the ring tightens around its neck (© Hugo Ferreira/Tour du Valat).

The presence of unexpected materials (e.g., surgical masks, condoms, and biodegradable materials, Fig. 4) in spoonbill nests across the species breeding range (the presence of artificial materials has also been observed in other countries such as Greece and Portugal), should also be monitored, as it highlights how current global events, such as Covid pandemic and other environmental policies, directed to biodegradable products directly impact animals and the environment.

Fig. 4 – Unexpected material found at spoonbill nests: (a) Surgical mask (© Sara Veríssimo); (b) condom (© Hugo Ferreira/Tour du Valat); (b) Biodegradable tag stating, "*I think in the environment, I use biodegradable bag*s" (© Carolina Hadden/Tour du Valat). It should be noted that biodegradable materials may take a long time to biodegrade, despite eventually reach that stage.

To further explore the impact of these materials, it would also be interesting to conduct necropsy analyses, following the protocol used by Almeida et al., (2023), to assess the presence of macro and microplastics in spoonbill digestive tracts. Identifying the nature of those, could unravel potential long-term effects of such materials on their survival rates, physiology, and/or breeding performance (Derraik, 2002; Gregory, 2009; Herzke et al., 2016; Kühn and van Franeker, 2020; Laist, 1997; Lavers and Bond, 2016; O'Hanlon et al., 2017; Teuten et al., 2009).

To conclude, the fact that spoonbills seem to actively collect certain types of artificial materials, suggests that other species, with a broader collection spectrum, may be better suited to act as sentinels of overall plastic pollution in wetland nesting sites. Nevertheless, studies such as this one are important to understand how humans are impacting wetlands and their biodiversity. In addition, studying such materials and how animals respond to their presence, could potentially provide insights into how to mitigate their negative impact in the environment (Avery-Gomm et al., 2018; Jagiello et al., 2019; Sergio et al., 2011). Finally, the potential role of artificial materials as lining highlights the capacity of a moderately specialised species to respond to current local and global changes (i.e., further explored in **Chapters 2** and **5**).

1.2.Continent-wide impacts of anthropogenic activities

In **Chapter 2**, I tested how multiple breeding parameters change along longitudinal and latitudinal gradients. By assessing how breeding phenology, investment and productivity relate to the different environmental conditions experienced locally across different breeding colonies at continental scale, it is possible to gain insights into how some species might respond to changes in habitat and/or climatic patterns in one part of their range, which will in the future likely resemble the conditions already present in other parts of their range. Thus, this information can be potentially very helpful in predicting species responses to changing environmental conditions. Eurasian spoonbill is an extensively monitored waterbird species and the subject of several long-term colour ringing programmes across a wide geographical distribution (Jin et al., 2008; Lorenz et al., 2009; Schneider-Jacoby, 2008; Sergio et al., 2006, 2008; Triplet et al., 2008). In **Chapter 2,** Manuela Rodrigues and I amassed and combined breeding data from across its European range and confirmed that some South-European sites (i.e., France and Italy) had an earlier 1st laying date than North-European sites (i.e., Belgium, United Kingdom, and The Netherlands), likely influenced by better environmental conditions at lower latitudes. Nevertheless, this was not the case for the Portuguese or Greek colonies. Thus, the early laying in France and Italy may be driven by a combination of factors, namely favourable environmental conditions (linked with lower latitudes) and higher food availability (during laying period). Additionally, in **Chapter 2**, no evidence was found for overall gradients in breeding patterns (e.g., egg volume and hatching success) and phenology (e.g., laying peak) along geographical or climatic axes, which suggests that local factors such as density dependence, food availability, predation and/or local quality of breeders, may be more important in driving breeding parameters and phenology of spoonbills. In any case, the influence of global patterns such as latitude/longitude and climatic gradients on other demographic parameters such as survival, and how spoonbills may be able to thrive in a changing world, is further explored in the **Chapters 3**, **5**, **6**, and **7**.

In **Chapter 2**, our results should be interpreted with caution due to the small sample sizes for longitudinal and latitudinal gradients, as well as some differences in methodology between monitoring programmes. These factors may have limited our capacity to detect and interpret geographical patterns, and their possible explanation and association with other environmental factors, at local or large scales. The difficulty of accessing and monitoring spoonbill colonies, and the fact that spoonbills breed in few specific sites, can make geographical gradient studies challenging. However, standardised protocols and collaborative studies like the one presented in **Chapter 2**, allow other important variables such as population trends and colony specific productivity trends to be tested. Therefore, together with the co-authors of this study, I recommend that the Eurasian Spoonbills International Expert Group (ESIEG) continues to strengthen collaboration among its experts by developing standardised monitoring protocols (e.g., to measure body condition, egg volume, fledging and hatching success), on which to build more years of data and conduct more robust analyses to understand how global changes might affect spoonbill breeding phenology and productivity. Good quality and informative data are essential for the ESIEG group's objective, which is the conservation of the Eurasian spoonbill. The descriptive parameters collected by the different programmes and compiled in **Chapter 2**, can serve as a starting point and a baseline for future collaborative work, monitoring efforts and targeted actions undertaken by ESIEG members, and can be extended to other groups, working with other waterbird species.

2. Spoonbill as social seasonal migrant

Throughout this thesis, I discuss on several occasions the consequences of different behaviours (e.g., timing of breeding, use of artificial materials in the nest), with particular attention to different migratory behaviours (e.g., migration route, location of the breeding or wintering site). Migratory behaviour is particularly important as it can significantly influence survival and productivity (Alerstam et al., 2003; Alves et al., 2013; Boyle, 2008; Chapman et al., 2011; Gillis et al., 2008; Harrison et al., 2011; Lok et al., 2015; Newton, 2008; Norris, 2005; Swift et al., 2020).

2.1.Drivers of Spoonbill migration

Migratory birds are one of the taxa most negatively affected by global environmental changes (Kirby et al., 2008; Rosenberg et al., 2019; Xu et al., 2019). The Spoonbill is a particularly interesting model species to explore how different migratory behaviours may affect survival or productivity rates, as it is a partial migrant, where individuals from the same breeding population vary in their migratory behaviour by several thousand kilometres and even flyways. But before I discuss the relationships between non-breeding site and survival or productivity rates, it is important to discuss the drivers of spoonbill migration.

In certain social migratory species (e.g., Lesser spotted eagles - *Clanga pomarine*; Meyburg et al., 2017), younger individuals often rely on social cues from older individuals (either from family members or not) to undertake migration (Berthold, 1996; Byholm et al., 2022; Gill, 2019; Harrison et al., 2010; Sutherland, 1998). Therefore, the timing of breeding may have consequences for chick migratory behaviour, as experienced migrants may have left the breeding sites by the time later-born chicks are able to migrate, which therefore have more limited access to those social cues (Cresswell, 2014; Gill et al., 2014, 2019; Gunnarsson, 2006; Meyburg et al., 2017; Nightingale, 2023). Spoonbills are social birds (de Goeij et al., 2012; Lok et al., 2019; Navedo and Garaita, 2012), however the influence of social interactions in their behaviour remains mostly unknown.

Spoonbills are known to exhibit a migratory paradox, where a considerable proportion of Dutch spoonbills migrates along the East Atlantic Flyway, adopting a long-distance migratory behaviour, which is associated with the lowest survival rates (Lok et al., 2011a). Similarly, a considerable proportion of Camargue spoonbills also adopts a long-distance migratory behaviour (**Chapter 6)**. In **Chapter 3**, and although chick body condition had no effect on migratory behaviour, I found a link between the timing of breeding and juvenile migratory behaviour. Specifically, later-born chicks tended to undertake less challenging migration than earlier-born chicks, suggesting that spoonbills do rely on social cues to migrate. The fact that later-born chicks are also able to undertake migrations that involve crossing major ecological barriers and/or covering the longest distances (as do most early hatched/born chicks) was explained by social migration. If social migration cues are available at the breeding site and/or as they encounter experienced individuals at stopovers sites during their first fall migration, later-born chicks may indeed still be able to “catch up” and follow older, more experienced individuals, and thus also undertake migrations that involve crossing major ecological barriers and/or covering the longest distances (as do most early hatched/born chicks). Such behaviour, has also been observed in other bird species, like Short-toed snake eagles (*Circaetus gallicus*) where juveniles appear to learn detours to complete trans-Mediterranean migrations from older individuals encountered during migration (Agostini et al., 2017). Finally, the absence of social cues during the first winter of late hatched/born chicks can also explains why a considerable number of immature spoonbills remain in France and Iberia during this period, but migrate to more distant locations in the following winters, once social cues (i.e. experienced adults) become available to them (Blanchon et al., *unpublished data*; Lok et al., 2011). A socially driven migratory behaviour would thus resolve the Spoonbill paradox identified by Lok and collaborators (2011), as the reliance of inexperienced spoonbills on social cues to migrate would explain both the tendency of first year birds wintering in Africa and the fact that some birds that have wintered in Europe during their first wintering period would shift to Africa in their second wintering period.

Social behaviour and transmission is widespread in waterbird species (Byholm et al., 2022; Cresswell, 2014; Gill et al., 2014, 2019; Gunnarsson, 2006; Méndez et al., 2020, 2021; Meyburg et al., 2017; Nightingale, 2023) and could lead to population range shifts. Nevertheless, spoonbills are also known to show high fidelity to their breeding and non-breeding sites (De Voogd, 2005; Lok et al., 2011b, 2013a; Pigniczki and Karcza, 2013). Therefore, strongly conservative social migratory behaviour to suboptimal sites (indicated by the lower survival of long-distance migration) could potentially delay or prevent an adaptive shift of the spoonbill wintering range in response to rising temperatures (Barrett et al., 2019; Keith and Bull, 2017; Kokko and Sutherland, 2001; Whitehead and Richerson, 2009). For example, in continental Black-tailed godwits (*Limosa limosa*) while new recruits drove a population shift in the proportional use of spring passage sites, adults kept using previously occupied stopover sites (Verhoeven et al., 2018). Similarly adult site-fidelity was also reported for this species with regards to non-breeding sites (Gill et al., 2019).

2.2.. Effects of migratory behaviour on breeding phenology and productivity

There is a clear impact of migratory behaviour on survival, but less is known about the potential effects of migratory behaviour on productivity. Overall, birds that breed earlier in the season tend to achieve higher reproductive success (including better quality chicks), than those that breed later (Alves et al., 2019; Benharzallah et al., 2015; Both et al., 2006; Costa et al., 2021; Daan et al., 1989; Drent et al., 2003; Kentie et al., 2015; Klomp, 1970; Lok et al., 2017; Morrison et al., 2019; Perrins, 1966; Smith and Moore, 2005). Thus, if long-distance migrants arrive later and are likely to breed later than short-distance migrants (and residents), I expect the existence of multiple laying peaks in spoonbill colonies and a negative impact of more distant migration in productivity rates. In **Chapter 2**, together with Manuela Rodrigues, we noted the existence of multiple laying peaks, within the same breeding colony (usually two to three), and discussed the possibility that the multiple laying peaks are related to age demographics and migratory behaviour in each colony. In the case of the Dutch breeding population, short-distance migrants are known to arrive and lay earlier than long-distance migrants (Lok et al., 2017); however in South-European sites such as Camargue, this discrepancy could be less evident as distance between breeding and wintering sites is smaller, or even non-existent (i.e., resident individuals). As a proxy of the distance and the difficulty of migration, I tested if breeders that do not cross any major ecological barrier (i.e. wintering in Iberia and France, including residents; see below) arrive earlier than migrants which cross at least the Mediterranean Sea and/or the Sahara Desert. I considered the migratory behaviour of 166 Camarguese breeding individuals and resighting information collected over 14 years. The results confirmed that individuals with shorter and less challenging migrations (i.e., migrants that do not cross any or only one major ecological barrier) arrive significantly earlier than those undertaking more challenging and longer migrations (i.e., migrants crossing multiple ecological barriers) (Fig. 5).

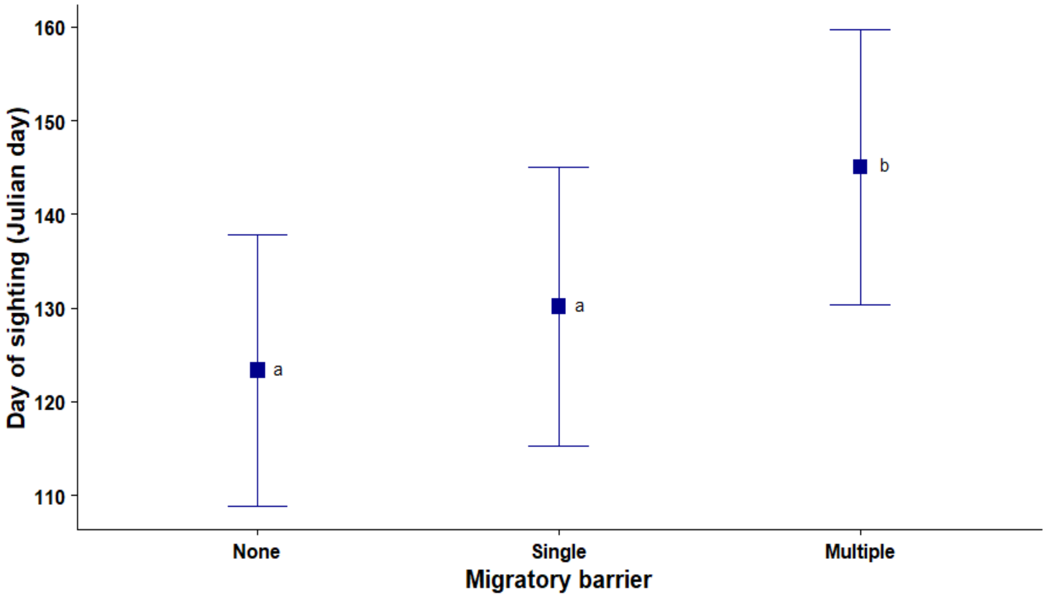

Fig. 5 – Post-hoc comparison of estimated marginal means of the first day (on each year) that a given individual was resighted in Camargue as a breeder (*Day* ~ *Barrier*; $n_{Breeder} = 166$), according to its migratory behaviour that imply crossing varying numbers of ecological barriers (None – residents and migrants which do not cross any major ecological barrier; Single – migrants which cross the Mediterranean Sea; Multiple – migrants which cross the Mediterranean Sea and the Sahara Desert). Vertical lines indicate 95% confidence, and different letters indicate significant differences between groups.

To further explore the consequences of later laying on productivity, in **Chapter 3**, I show that older spoonbills not only arrive earlier to Camargue, but also tend to breed earlier than younger individuals, and that early breeders are more likely to produce chicks with higher body condition than late breeders. Thus, it may be possible that with increasing age and experience spoonbills improve their parental skills (e.g., brooding, provisioning, and chick guarding), resulting in chicks with better body condition. The beneficial impact of age on productivity has also been widely reported in other bird groups (e.g., aerial insectivores – Costa, 2020; Steven, 1978; Passeriformes – Desrochers, 1992; Enoksson, 1988; Franks and Thorogood, 2018; Jansen, 1990; waterbirds – Pyle et al., 1991). For example in the case of European shags (*Phalacrocorax aristotelis*), older pairs consistently outperformed younger ones when breeding under similar environmental conditions, due to intrinsic differences in brood rearing capacity (Daunt et al., 1999). Note that it is often difficult to disentangle the role of experience from age, especially in long lived species (Desprez et al., 2011; Pradel et al., 2012).

2.3.Impact of migratory behaviour on survival

Assessing the effects of migratory behaviour in survival can provide the necessary insight not only to understand contrasting population trends (e.g., between migratory flyways or wintering sites), but also to identify wetlands of critical conservation importance. In **Chapter 6**, I examine five main migratory behaviours displayed by the population breeding in Camargue, in which individuals can vary both in terms of migratory flyway (East Atlantic vs. Central European) and migration distance (long-distance vs. short-distance vs. resident). There was no evidence supporting a correlation between survival and flyway, but there was a negative effect of migration distance on survival. However, the relationship between survival and distance, is likely to be explained by the crossing of major ecological barriers, such as the Mediterranean Sea and the Sahara Desert, which increase in number at discrete intervals as migration distance increases once suitable non-breeding habitats are not continuous in any flyway for any waterbird species. As is often the case with survival studies, some common challenges (e.g., mortality and emigration are confounded) constrained the survival estimates obtained in **Chapter 6** and limiting their interpretation. Therefore, in that chapter, I also tested the possibility that the lower apparent survival rates of longer distance migrants may be due to a higher probability of permanent emigration to other breeding sites (Cilimburg et al., 2002; Lebreton et al., 1992; Lindberg et al., 2007). This did not appear to be the case, as there were few known records of Camargue spoonbills that could potentially have recruited to other breeding sites and long-distance migration remained the behaviour with the lowest survival rate. Nevertheless, to further strengthen the results of **Chapter 6**, a larger-scale analysis would be valuable in order to overcome and formally consider the aforementioned limitations, such as the difficulty in separating mortality from permanent emigration, as well as the relatively small sample size (despite higher than in other survival studies) of marked birds with known wintering site location (i.e., outside of the West-African wintering range), which leads to larger confidence intervals.

In **Chapter 7**, I do exactly that! In that chapter, I attempt to overcome the challenges reported above by combining data from several interconnected spoonbill breeding populations across Europe and thus including two flyways (EAF and CEF). From raw data, I found that there were only a few cases per breeding population of spoonbills that had permanently emigrated from their natal breeding region. This low emigration rate, in itself, supports the hypothesis that the differences in survival rate estimates attained in **Chapter 6** are indeed caused by the lower survival rate of long-distance migrants. However, despite its limitations, the most parsimonious model in **Chapter 7** suggested a high probability of emigration to southern breeding regions, located on route to the most distant breeding regions on each flyway (i.e., Northern Italy is on route for Carpathians and Mediterranean France, whereas Southwest-Iberia is on route for Northern Europe and Mediterranean France). This may have previously been overlooked due to the low detectability of spoonbills in these regions (at least in Southwest-Iberia). Although this unexpected result could be due to methodological limitations further discussed in **Chapter 7**, it is still strongly suggested that wetland degradation impacts spoonbills survival. This is evidenced by the lower survival of juveniles and immatures from the Carpathian breeding region, in addition to the lower survival of immatures in the Northern Africa non-breeding region, linked to both wetland degradation in the Carpathian (e.g., Hungarian and Croatian; Champagnon et al., 2019; Mikuska et al., 2023) and Northern African regions (e.g., Tunisia; OTEDD, 2016). Finally, although no flyway effect was found in **Chapter 6**, in **Chapter 7**, the overall lower survival of birds from CEF regions compared to EAF is consistent with the decreasing trend of the CEF population and the contrasting increasing trend of the EAF. Revealing a mechanistic relationship between demographic rates, as described on Fig 1 of **Chapter 1**.

As shown in **Chapters 6** and **7**, spoonbills seem to be increasingly able to cope with the challenges of migration and non-breeding conditions with age, with significant differences in survival rates between migratory behaviours only occurring during the interval between the first non-breeding range sighting and the subsequent breeding period, or during the first years of life. Once, spoonbills (independently of age class), return to the breeding site, no differences in apparent survival among migratory behaviour are detected, suggesting an improved migratory performance with experience, once one migratory cycle has been completed. This result contradicts previous results obtained for the Dutch population, showing lower survival rates of adults performing long-distance migrations (Lok et al., 2011b, 2015). However, in **Chapter 7**, I considered a larger sample size that previous spoonbill survival analysis, as well as multiple breeding sites, to approximate estimates to “true survival”, as it is less likely that permanent emigration and mortality are confounded and confirmed the absence of differences in adult survival between the non-breeding and breeding seasons. Thus, supporting **Chapter 6** result of an improved migratory performance. An improved performance of adult spoonbills is also supported by the fact that adult survival in the Carpathian breeding region is as high as in other breeding regions, while this is not so for the younger age classes. In fact, juveniles and immatures appear to have a localize difficulty to survive in this breeding region, as evidenced by their lower survival compared to other breeding region.

3. The importance of protected areas for highly mobile species: the role of managed wetlands

Over the past 50 years, human development gains have largely been achieved at the cost of habitat loss and degradation (IPBES, 2019). For example, increased demand for arable land over the last century has led to extensive land conversion for agriculture, and water reservoirs have become more common and larger, with water retention quadrupling since then (IPBES, 2019; MEA, 2005). As habitat degradation and fragmentation increasingly threaten the ability of even highly mobile species to find suitable habitat (Freemark and Merriam, 1986; MEA, 2005; Piersma et al., 2016; Taylor and Stutchbury, 2016), the designation, management, and restoration of protected habitats is considered essential for the sustainability of these species (Braun et al., 1978; Dobkin et al., 1998; Geldmann et al., 2019, 2013; Leberger et al., 2020; Manning et al., 2011; Murray and Hamilton, 2010; Weller, 1999). However, as introduced in the **Chapter 1** and discussed in **Chapter 5**, some species are also likely to have benefited from increasing food sources and the complementary role of wetlands managed for recreational or economic objectives (e.g., rice fields or waterfowl hunting grounds; Guillemain et al., 2010; Hafner and Fasola, 1997; Tourenq et al., 2001). Specifically, in **Chapter 5**, using GPS data from spoonbills tracked in the Camargue over a period of eight years, I found that they were mainly present in areas managed to promote the presence of waterbirds for economic and recreational purposes (e.g., agriculture, ecotourism and hunting activities), or for conservation purposes (i.e., strongly protected areas, such as National and Regional Reserves).

Given that the whole of the Camargue is protected to some extent (Lefebvre and Moncorps, 2010; Vallecillo et al., 2023), it is not surprising that strongly protected areas did not appear to be selected overall (**Chapter 5**). In Camargue, several private areas are actively managed to provide space and food resources for the influx of wintering waterfowl (e.g., artificial flooding, creation of artificial ponds, manipulation of water levels, and scattering of seeds as bait) (Brochet et al., 2009; Davis et al., 2014; Mathevet and Guillemain, 2016; Vallecillo et al., 2019). On the other hand, strongly protected areas in Camargue are managed differently to provide optimal conditions for species of conservation interest, considering climatic conditions, the annual cycle, and the biology of the target species (e.g., flora – *Tolypella salina*; birds –*Botaurus stellaris*; insects – *Lestes macrostigma*; amphibians – *Pelophylax kl*.; reptiles – *Emys orbicularis*; mammals – *Lutra lutra*; Stamm, 2023), and as such, are not necessarily managed to provide constant ideal conditions for waterbirds. Thus, the results of **Chapter 5,** suggest that privately managed areas play a complementary role to areas manage for conservation in Camargue, and likely provide more suitable foraging habitat for spoonbills (and other waterbirds) than is available in strong protection areas at certain periods of the year. Reliance on privately managed areas can have serious consequences for species that are highly dependent on them, as these areas can potentially become ecological traps (Central Valley Joint Venture, 2006; Champagnon et al., 2023a; Fasola et al., 2022; Pernollet et al., 2015). Nevertheless, as shown in **Chapter 5,** privately managed areas can also provide foraging opportunities within fragment landscapes, which may partly explain how opportunistic foragers such as the spoonbills thrive in changing environments. To further explore the potential complementarity between wetlands managed for economic or recreational activities and wetlands managed for conservation, behavioural data (e.g. collected by accelerometers) can be used to determine the functional role of each habitat (e.g., foraging, roosting) and how this role is affected by different management decisions (i.e., practice of "*assec*", see **Chapter 5** for further details).

In **Chapter 5**, I also confirmed that the spoonbill is a moderate specialised species that benefits from some current outcomes of global changes (e.g., the use of invasive species as new food sources; land use changes and the use of wetlands managed for economic and recreational activities) and thrives in highly fragmented landscapes. While such a flexibile and opportunistic foraging might explain the recovery of this and other waterbirds, many wetlands' habitats are threatened (e.g., cases further developed in **Chapter 1** and **7**), and as such, the results obtained in Camargue may not be representative of how global changes affect spoonbills across their range.

4. Future of Camarguese spoonbill

The exponential growth of spoonbills in Camargue shows no signs of slowing down, with unoccupied islets being increasingly colonised, while the main colonies continue to grow in numbers, including in 2023 where 420 breeding pairs have a nest in 6 different islets. In **Chapter 3** and **5**, I discuss how the abundance of food sources in the area specifically in. temporary and permanent marshes, is likely to have supported the expansion of this population until now. Nevertheless, the population cannot grow indefinitely and will eventually reach its limit. A capacity limit is likely to affect the body condition of spoonbill chicks, for example if currently abundant food resources become highly contested (Bechet and Johnson, 2008; Forero et al., 2002; Lack, 1954; Lok et al., 2013b, 2017), which could possibly lead to increase competition for nesting sites and potentially to the emergence of new breeding colonies in Southern France. In fact, emergence and development of new colonies in Southern France occurred since 2019 with the colony of Planasse reaching 26 breeding pairs in 2023, ca. 130 km from Camargue. The colonisation of Planasse may have occurred due to limiting nesting locations and/or food abundance, and its growth may be promoted by conspecific attraction (**Chapter 6**, Tenan et al., 2017). Spoonbills en route to Camargue breeding islets, pass through or near the Planasse colonies, so less experienced individuals may be attracted by conspecifics to breed in these newer colonies instead of proceeding to Camargue.

In **Chapters 3, 6,** and **7**, I discuss how long-distance migration involving the crossing of ecological barriers can be costly to the survival and productivity of spoonbills. The current deterioration of non-breeding sites in Africa, could further amplify the difficulties of undertaking such migration (Brochet et al., 2016). In Tunisia, for example, more than 50% of wetlands have been destroyed in the last century and the remaining ones are under intense pressure from urban development, industrial activities, and unsustainable agricultural practices (e.g. excessive use of pesticides, retention and removal of water from wetlands for agriculture) (OTEDD, 2016). In contrast, conditions in Europe appear to be improving for these species in recent decades, due to changes in water management, enforced wetland protection (e.g., European Union’s Birds and Habitats Directives; Water Framework Directive—2000/60/EC) and rising temperatures (Klein et al., 2002; Lok et al., 2013b; Shukla et al., 2019). Due to their poor binocular vision, which reduces their capacity to detect and avoid obstacles (Triplet et al., 2008), as well to their high philopatry (**Chapter 7**; Lok et al., 2013a; Pigniczki and Karcza, 2013), spoonbill migration is further threatened by the emergence of new barriers along their migratory route. Energy infrastructure, particularly offshore wind farms, is increasingly being built or developed along the Atlantic coast, and there are several projects both in the Mediterranean and the Adriatic seas (Gauld et al., 2022), adding to the cumulative challenges of long-distance travelling. Consequently, if these cumulative challenges lead to increased mortality of birds undertaking such routes, this may further influence the previously mentioned northward shift of the spoonbills' (and other waterbirds) nonbreeding range (Chen et al., 2011; Parmesan and Yohe, 2003; Pecl et al., 2017; Thurman et al., 2020).

While some spoonbill populations, such as the one in Camargue, appear to be growing and not under any immediate major threat, populations such as those breeding in Spain and Croatia, show how quickly the scenario can change. The greater Doñana ecosystem is a major wetland, that is currently being threatened by climate change and water diversion for agriculture and government projects (Camacho et al., 2022; Navedo et al., 2022) (for further details also see **Chapter 1** of this thesis). As for the Croatian breeding population, although spoonbills breed in fishponds located in Natura 2000 sites, the mismanagement of these sites, due to "reconstruction works" for the purpose of intensifying fish production (funded by the European Union), is causing habitat degradation and negatively impacting the Croatian breeding population (Mikuska et al., 2023). Therefore, management such as that of the Vigueirat National Nature Reserve (in Camargue), a strongly protected area of 1,200 ha, where water levels are actively managed to provide optimal conditions for waterbirds, considering climatic conditions, the annual cycle, and the biology of the targeted species (e.g., ducks in winter, *Ardeidae*, terns, waders and spoonbills in summer; see **Chapter 5** for further details), may be essential to maintain species resilience (Kokko and Sutherland, 2001). Indeed, while waterbirds (and other species) might benefit from wetland management for conservation, the broader reality involves competing land use claims that often place conservation and economic interests in opposition (Davidson, 2014; Eppink et al., 2004; Sponsel, 2013). Thus, the fast speed at which a suitable area for waterbirds can be lost or transformed into an unsuitable one, further exposes the potential problem of species losing natural habitats and becoming extremely dependent on highly managed areas, such as fishponds and agricultural fields (Champagnon et al., 2023a; Mikuska et al., 2023; Rodrigues et al., 2023a; Vansteelant, 2023). Finally, the potential impact of land use change also highlights the importance of public support and engagement to go against unsustainable developments that may threaten the remaining wetlands and their biodiversity. In Portugal, plans to build the capital's new airport by the Tagus Estuary, Portugal's most important wetland and a vital refuge for millions of migratory bird (Alves and Dias, 2020), were stopped by the combined efforts of non-profit organizations (e.g., ClientEarth), societal groups (e.g., Portuguese Society of Bird Studies), Non-governmental agencies, Research groups (e.g., EcoFlyway) and the general public. However, success stories are rare and would not be possible without societal engagement. As many in our society still consider wetlands as *wastelands* that can and should be exploited for economic gain, innovative ways are needed to build societal engagement and awareness for the conservation of critical wetlands is needed.

5. The importance of citizen engagement and of new technology in the study of waterbirds

Citizen science is a term used to describe projects that involve the general public in scientific research activities, in order to generate new knowledge or develop a better understanding of an ongoing processes. Typically, participants help with data collection, but they can also be involved in defining research questions, co-designing investigations and data applications. Such approaches can therefore have great potential for raising public awareness for specific conservation or environmental issues. Resighting data collected by ornithologists and nature enthusiasts across the spoonbill range was fundamental for this thesis, namely in **Chapters 3, 6**, and **7**. In addition to co-managing the Camargue spoonbill database for six years, together with Tour du Valat staff, during my PhD I have developed a participatory science project on the Zooniverse platform (www.zooniverse.org) to further promote data applications with the general public (**Chapter 1**). Although, the project did not succeed in making a long and tedious task more efficient, as the participants needed ca. eight months longer than the experts to classify all the photos, it succeeded in creating substantial engagement with the species (Fig. 6). Currently, more than 5,900 registered participants have performed more than 400,000 classifications and created more than 600 discussion topics. Additionally, several international schools have contacted the Tour du Valat requesting the use of our project in their classrooms.

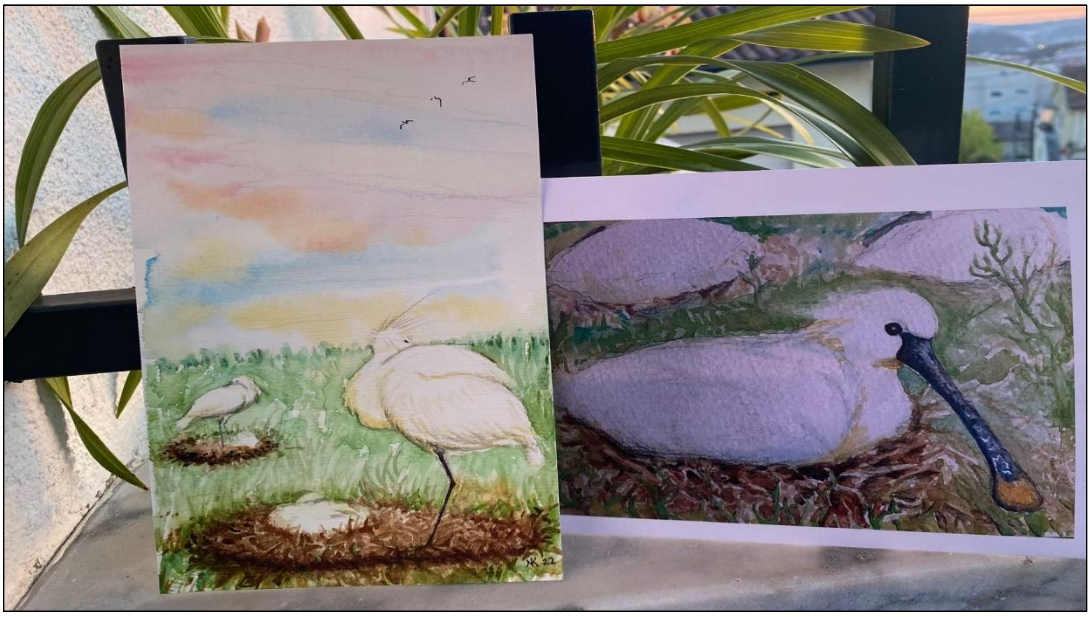

Fig. 6 – Spoonbill drawings by one of the "*Where is Spoony*" participants (©Nicole_WiltedLotus).

The potential for citizen science projects such as "*Where is Spoony*", to generate public engagement is substantial and critical. Such engagement can potentially help mitigate the level of direct anthropogenic environmental change caused by public or private developments such as large infrastructure (e.g. airports, harbours, etc) and/or by agricultural practices that may threaten waterbirds and wetlands (e.g., projects mentioned above for Spain and Croatia). In addition, data collected through citizen science can be used for machine learning techniques which will make data processing significantly faster and more efficient. In the case of "*Where is Spoony*", ring classifications made by participants were used to train artificial intelligence to identify spoonbills marking rings (Bourbon, 2024). This approach may be adapted in the future to other markings, species, or even programmed to identify other parameters, such as specific behaviours of marked individuals (e.g., breeding behaviour).

The development of new or existing technologies is a powerful tool in ecological studies (Cagnacci et al., 2010; Robinson et al., 2010; Shamoun-Baranes et al., 2012; Shepard et al., 2008; Wilmers et al., 2015). Tracking devices and camera traps have helped to overcome challenging tasks, such as following individuals through their annual cycle and assessing their performance (e.g., survival and productivity) (Alerstam et al., 2006; Brønnvik et al., 2022; Campioni et al., 2020; Corbeau et al., 2020; Robinson et al., 2010), while reducing potential disturbance by allowing remote and faster data acquisition. For example, in **Chapter 4**, photos of the nest lining provided a way to quantify the use of artificial materials by spoonbills, while also being an effective intermediate solution to the precision-disturbance trade-off (Rodríguez et al., 2023; Ryan, 2020). In **Chapter 7**, the detection rate of spoonbills in Camargue was of 85%, significantly higher than most regions and likely driven by the high use of camera traps. Furthermore, since information is obtained in form of a photo, it allows for the storage of a "*digital dodo*" (Nightingale, *in prep.*), where information collected is permanently stored and readily available for future analysis.

Although GPS tracking data had a smaller role in this thesis, in **Chapter 5**, it allowed the identification of important areas in Camargue and how their use by spoonbills changes throughout the annual cycle. In addition, the current use of GPS tracking data is providing important insights to disentangling the role of genes and early-life social influences on spoonbill migration (Lok, 2022). GPS technology is also proving fundamental for environmental assessment of the potential impact of new infrastructures along the migratory route of animals (Gauld et al., 2022). For example, the Migralion project funded by the French Biodiversity Agency, aims to characterize the flying characteristics of migratory birds (altitudes, directions) and the functionalities of marine areas for marine fauna at the scale of the Gulf of Lion. This can help to improve the implementation of public policies towards limiting adverse effects on bird species (OFB, 2021). Nevertheless, it is important to coordinate this and similar projects at a larger scale, as several migratory waterbirds (and others), face the cumulative impacts of such structures in multiple points of their journey, which effects are often not possible to account by local initiatives.

In **Chapters 6** and **7**, it was clear that individuals (likely inexperienced) adopting long-distance migratory behaviour have a lower survival than those wintering in Europe. However, important rare events (that did not occur during the study period but are known to take place at larger time scales), could add an additional layer of complexity to the results. In particular, exceptionally long droughts (e.g., drought in Doñana) and cold spells in Europe, which generally occur every 25 years in Southern France during winter, may significantly reduce the survival of locally wintering spoonbills, as it is the case for flamingos (Deville et al., 2014). Thus, when considering the future trends of spoonbills, it is important to acknowledge the occurrence of extreme weather events and therefore to maintain long-term monitoring programmes. And, once sufficient data have been collected, to assess how survival and/or productivity trends change in those years. Further analysing long-term data will help to unravel the mechanisms underlying waterbird survival given annual variation and provide clues as to how they may respond to future global changes given the current predictions of future climatic scenarios and trends from annual variation in survival with climatic variables as co-variates.

6. Future directions: where to go from here

The spoonbill populations considered in **Chapter 2** are all populations that either experienced exponential growth and are now stabilising (e.g., Netherlands), or are still growing (e.g., France and Italy) (Champagnon and Kralj, 2023). It would therefore be interesting to understand how populations that have experienced opposing trends, declining and now stabilising (e.g., Croatia and Hungary), or are currently declining (e.g., Romania, Spain, and Ukraine), compare with those in terms of breeding performance. With reduced food availability due to habitat degradation and land use change (Champagnon et al., 2023b; Kralj et al., 2023; Mikuska et al., 2023), breeding parameters such as hatching success and chick body condition are expected to be lower than in populations displaying positive trends. At the same time, egg laying dates and laying peaks may be highly variable, as spoonbills seek new and more suitable breeding areas given ongoing land use changes. Furthermore, several of these populations still lack adequate protection and are dependent on poorly managed sites (Mikuska et al., 2023), being therefore likely to continue to show negative trends for the foreseeable future.

In animals that are able to improve their breeding performance with age or experience, such development usually occurs during the first breeding attempts, (and the same may occurs regarding migratory performance) followed by maximum output and stabilisation, before a decline in performance in old age due to senescence (Clutton-Brock, 1988; Forslund and Pärt, 1995; Martin, 1995; Sæther, 1990). An increasing number of studies have examined senescence in birds (Balbontín et al., 2007; Froy et al., 2013; Kim et al., 2011; McCleery et al., 2008; Rebke et al., 2010; Reed et al., 2008; Sæther, 1990; Zhang et al., 2015) but never in relation to migration, except a recent study in Greater flamingo. That study suggest that Camargue resident flamingos have lower basal mortality than migrants in early life, but higher actuarial senescence and lower late-life breeding success than migrants (Roques et al., *submitted*). Spoonbills are a long-lived species which can reach ca. 30 years in captivity (Brouwer et al., 1994) and while 43 individuals in **Chapter 3** were over ten years old, only one was 13 and another 14 years old. Therefore, once sufficient time has elapsed since the implementation of the Camargue monitoring programme, it would be ideal to examine the effects of senescence in spoonbills to unravel how productivity declines with age. Such understanding can potentially improve population trends prediction and to disentangle the effects of age and experience. Finally, some species are known to delay the timing of breeding at older ages (Balbontín et al., 2007; McCleery et al., 2008), and given the high survival rates of adult spoonbills as estimated in **Chapters 6** and **7**, it would be interesting to explore how survival rates or migratory performance may decrease with age, which could improve predictions of population trends and contribute to understanding the resilience of species or to delineate effective conservation management actions.

In **Chapter 5**, I further discuss how spoonbills are likely benefiting from the current global changes and thriving in highly fragmented landscapes because they are opportunistic foragers with high diet flexibility (El-Hacen et al., 2014; Enners et al., 2020; Rodrigues et al., 2023b). Their capacity to improve their migratory and breeding performance is further highlighted in **Chapter 3**, **4**, **6,** and **7**. Thus, despite spoonbill macro level habitat selection, highlighted by the patchy distribution of the species and the need of large and undisturbed wetlands for breeding, both their diet flexibility and their capacity to learn might explain the resilience and recovering trends of this species. The system studied here applies to the waterbird community which thrives in mosaic landscapes such as the Camargue (Galewski and Devictor, 2016) and more globally, has benefitted from conservation measures initiated in the last century (Amano et al., 2018). However, we should keep in mind that some more specialised species fail to adapt in highly fragmented landscapes (Devictor and Robert, 2009), as well as habitat-specialist species that have suffered from land-use change, such as farmland birds (Rigal et al., 2023).

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Hide to observe spoonbill colony, Camargue, 2018.

Where is Spoony? Is a project that allows you to immerse yourself in a colony of an emblematic waterbird, and help us to understand how birds cope with the long migration routes they undertake every year.