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MECHANISMS COSTRAINING THE DISTRIBUTION OF JUVENILE SPOONBILLS *Platalea leucorodia*

Dissertação de Mestrado em Ecologia, orientada pelo Doutor Pedro Miguel Araújo (Investigador do MARE, Marine and Environmental Sciences Centre) e pelo Professor Doutor Jaime Albino Ramos (Universidade de Coimbra) apresentada ao Departamento de Ciências da Vida da Universidade de Coimbra

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Mechanisms explaining the distribution of juvenile Spoonbill *Platalea leucorodia*

Dissertação apresentada à Universidade de Coimbra para cumprimento dos requisitos necessários à obtenção do grau de mestre em Ecologia, realizada sob a orientação científica do Doutor Pedro Miguel Araújo (investigador do MARE, Marine and Environmental Sciences Centre) e do Professor Doutor Jaime Albino Ramos (Universidade de Coimbra).

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Abstract

Wetlands are habitats of ecological importance because they provide unique and vital functions for the ecosystems, hold an enormous biodiversity and provide several ecosystem services. Wetland areas and associated wildlife are declining at fast rate, however, in Europe, some waterbird species are, unexpectedly, increasing their numbers. A remarkable example is the Eurasian Spoonbill (*Platalea leucorodia*) whose numbers increased sharply in the last 50 years which enabled the (re)colonization of several areas across their range. With this work we aimed to understand the drivers behind the colonization of Portuguese areas by spoonbills and their population expansion. To address this, we focused on three major aspects: 1) analysed the Portuguese database of coloured marked spoonbills re-sightings, 2) compared the diet and trophic ecology of spoonbill in traditional and recently established colonies, and 3) tracked the movements of juveniles of a traditional colony to study their habitat selection and spatial ecology.

This work unravelled unknown aspects of spoonbills' ecology in Portugal. Ria Formosa, Ria de Alvor and Tejo estuary were the most important wetlands for foreign spoonbills during the wintering season, and those that sheltered more juveniles during dispersal movements. Throughout the breeding season, Spanish and Dutch spoonbills were common in Ria Formosa, Paúl do Boquilobo, Ria de Alvor and Sado estuary. Migratory connectivity between European breeding colonies and Portuguese wetlands was low for the largest breeding populations (Netherland 0.04 and Spain -0.14). In Ria Formosa (traditional colony), spoonbills rely more on crustaceans, that are more abundant and easy to catch, than fish. In Tejo estuary, a more recent colony, they feed on the Louisiana Crayfish (*Procambarus clarkii*), which supports the idea that this invasive species may contribute to the growth of waterbirds populations. Carbon isotopic values of feathers and blood from chicks of both colonies were different but in accordance with differences between areas which indicates that spoonbills feed their chicks in its vicinity. Juvenile spoonbills of Ria Formosa use several habitat types, including anthropogenic habitats, mainly intertidal wetlands (28%), salt evaporation ponds (28%) and rice fields (23%). Juveniles showed heterogeneity of movements, migratory and dispersal patterns, and home range sizes.

Overall, we conclude that the expansion of spoonbills in Portugal can be promoted by: a) the possibility of preying on invasive species in recent colonies, b) the use of anthropogenic habitats that can act as substitute for the traditional wetland habitats, c) the great heterogeneity in dispersal and spatial movements, and d) the immigration of breeding spoonbills from the older European colonies. This reinforces the need to protect wetlands, the need to correctly manage anthropogenic habitats to benefit waterbird species, and finally, the importance of studying populations in the view of the metapopulation theory, conserving and taking measures across the entire range of species, and including breeding, migration and wintering seasons.

Key-words: migratory connectivity, stable isotopes, dynamic brownian bridges, expansion, juvenile dispersal.

Resumo

As zonas húmidas são habitats de elevada importância ecológica dado que desempenham funções únicas e vitais para os ecossistemas, albergam uma enorme biodiversidade e fornecem vários serviços de ecossistema. As zonas húmidas e a vida selvagem a elas associadas estão a diminuir a grande ritmo, no entanto, na Europa, várias espécies de aves aquáticas estão, inesperadamente, a aumentar os seus números. Um exemplo notável é o do Colhereiro Europeu (*Platalea leucorodia*) cujos números aumentaram abruptamente nos últimos 50 anos, o que permitiu a (re)colonização de vários locais dentro da sua área de distribuição. Com este trabalho pretendemos perceber as razões por detrás da colonização de áreas Portuguesas pelos colhereiros e do seu aumento de população. Para isto, focámo-nos em três aspetos: 1) analisámos a base de dados Portuguesa de avistamentos de colhereiros marcados com anilhas coloridas, 2) comparámos a dieta e a ecologia trófica entre colhereiros de uma colónia tradicional e de uma recente, 3) seguimos com GPS os movimentos de juvenis de uma colónia tradicional para estudar a sua seleção de habitat e ecologia espacial.

Este trabalho revelou vários aspetos da, quase desconhecida, ecologia dos colhereiros em Portugal. A Ria Formosa, a Ria de Alvor e o estuário do Tejo são as zonas húmidas mais importantes para colhereiros estrangeiros durante o Inverno e também as que abrigaram mais juvenis durante os movimentos dispersivos. Durante a época de reprodução, colhereiros Espanhóis e Holandeses foram comuns na Ria Formosa, Paúl do Boquilobo, Ria de Alvor e Estuário do Sado. A conectividade migratória entre colónias reprodutoras europeias e zonas húmidas portuguesas é baixa para as maiores populações (Holandesas 0.04 e Espanholas -0.14). Na Ria Formosa (colónia tradicional), os colhereiros consomem principalmente crustáceos, que são mais abundantes e fáceis de capturar, do que peixes. No Tejo, uma colónia recente, predam o Lagostim vermelho do Louisiana (*Procambarus clarkii*), o que suporta a ideia de que esta espécie invasora pode contribuir para o crescimento de populações de aves aquáticas. Os valores dos isótopos de carbono das penas e do sangue das crias de ambas as colónias foram diferentes, mas de acordo com as diferenças entre os locais, o que indica que os colhereiros alimentam as crias na proximidade das colónias. Os colhereiros juvenis da Ria Formosa usam vários tipos de habitat, incluindo artificiais, principalmente zonas húmidas intertidais (28%), poços de evaporação de sal (28%) e campos de arroz (23%). Os juvenis apresentaram heterogeneidade de movimentos, de padrões de migração e dispersão, e de tamanho das áreas vitais.

No geral, concluímos que a expansão dos colhereiros em Portugal pode ser promovida pela possibilidade de predar espécies invasivas nas colónias recentes, pelo uso de habitats artificiais que podem funcionar como habitats substitutos nas colónias tradicionais, pela grande heterogeneidade de movimentos espaciais e de dispersão, e pela imigração de colhereiros reprodutores provenientes das colónias Europeias mais antigas. Com este trabalho reforçamos a necessidade de proteger as zonas húmidas, a necessidade de gerir corretamente os habitats artificiais para que beneficiem as espécies de aves aquáticas e, por fim, a importância de estudar populações sob a luz da teoria das metapopulações, protegendo e impondo medidas de conservação ao longo de toda a área de distribuição das espécies e durante todo o ano (épocas de reprodução, migração e de invernada).

Palavras-chaves: conectividade migratória, isótopos estáveis, pontes brownianas dinâmicas, expansão, dispersão de juvenis.

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List of abbreviations:

CEMPA – Centro de Estudos de Migrações e Proteção de Aves

INCF – Instituto da Conservação da Natureza e das Florestas

GPS – Global Position System

GSM – Global System for Mobile Communications

RF – Ria Formosa

TE – Tejo Estuary

MC – Migratory Connectivity

BLC – Before leaving the colony

ALC – After leaving the colony

UD- Utilization Distribution

dBBMM – Dynamic Brownian Bridge Movement Model

CLC – Corine Land Cover

Psi – Proportional Specialization index

IS – Individual Specialization

NSD – Net Squared Displacement

TAC- Mean turning angle correlation

RT- Mean Residence Time

TtoR – Mean Time to Return

VI – Mean Volume of interception of monthly home range

MNSD – Maximum Net Squared Displacement

INTRODUCTION

Wetland loss and associated biodiversity decline

Wetland ecosystems hold an enormous biodiversity, and are among the most productive ecosystems in the world (Tiner 1989, Keddy 2010). The importance of wetlands is clearly visible due the first sedentary human civilizations originated in the vicinity of large rivers and their wetlands, where people found food, water and fertile lands to develop agriculture. Wetlands provide many ecosystem services, being particularly important as a source of fresh water, food resources, as barriers to protect upland areas from extreme climatic events (Millennium Ecosystem Assessment 2005, Nellemann and Corcoran 2010). Overall, contributing to regulate climate by sequestering large amounts of CO2 while also playing an important role in the cycle of water and nutrients (Millennium Ecosystem Assessment 2005, Nellemann and Corcoran 2010).

There are many definitions and many types of wetlands, but the definition provided by the Ramsar Convention in 1971, encompasses most wetland areas: "Areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or saline, including areas of marine water, the depth of which at low tide does not exceed six metres" (Barbier et al. 1997). Despite the great importance of wetlands for biodiversity and their recognized value in providing ecosystem services, wetland degradation and conversion are of major concern worldwide (Nellemann and Corcoran 2010, Sutherland et al. 2012). Construction of dams and dikes, drainage of wetlands, changes in rivers streams, conversion into agricultural land, pollution and introduction of alien species are the main threats to wetlands, mostly driven by human population growth (Millennium Ecosystem Assessment 2005, Van Asselen et al. 2013). Davidson (2014) estimated that 87% of the world's wetlands were lost since 1700, with peak loss occurring in the second half of the 20th century. Moreover, many of the remaining wetland areas are degraded and currently suffering the cited pressures (Davidson 2014).

A direct consequence of wetland loss is the large decline in biodiversity on those areas (Lemly et al. 2000, Bunn and Arthington 2002). There are many studies documenting the decline in amphibian species richness (M'Closkey 1996, Lehtinem (1999), in aquatic mammal populations, such as the Otter (*Lutra lutra*) (Macdonald, & Mason 1994), and in birds populations (Boere et al. 2006a). Wetland destruction particularly affected waterbirds (Boere et al. 2006b) and regular census of these birds only became frequent and accurate in the 70’s and 80’s (mostly in the Palearctic), due to the increasing awareness regarding wetlands destruction raised by the Ramsar Convention. Although the population trends of waterbirds was inexistent or inaccurate before then (Kushlan 1997, Boere et al. 2006a, Kuijken 2006), it is now very obvious that wetland birds declined over the last decades (Millennium Ecosystem Assessment 2005). In Australia, Kingsford et al. (2004) assessed the effects of water resource development and wetland destruction in floodplains, reporting a decline of almost 90% in waterbird populations after water was diverted into agriculture usage. Furthermore, an iconic bird species in Europe associated with temporary and permanent wetlands, the white stork *(Ciconia ciconia*), declined strongly throughout the 20th century until the 1970´s (Dallinga and Schoenmakers 1987) and became locally extinct in several northern European countries, Sweden, Switzerland and Belgium (Luthin 1987). Similarly, all European heron species declined with widespread destruction of wetlands, mainly in the 19th and 20th centuries. The purple heron (*Ardea purpurea*), for example, decreased across all Europe, and particularly in Netherlands, where the number of pairs decreased from 900 to 210 between 1970 and 1991 (Marion et al. 2000). Likewise, the Eurasian bittern (*Botaurus stellaris*) became extinct in northwest countries as Sweden and England (Day 1981). However, from the 1980’s the populations of several waterbird species began to recover throughout Europe (Table AI), despite wetland recovery being marginal (Wetland International 2016). Even though some progress has been processed towards wetland restoration in Europe, namely with the implementation of the Water Framework Directive (EC, 2000), the recovery of waterbird species in Europe precedes such large-scale wetland habitat improvement. This suggests some alternative causes for the increasing trends recorded for many waterbirds species, but such drivers of population increase remain currently unknown.

Why are waterbird populations increasing in Europe?

Understanding the key drivers of waterbird recovery for those populations which are currently increasing and expanding is essential to inform future conservation of these species and others with similar ecology. In addition, these species enable to study processes such as colonization of new sites and range expansion, which are poorly known.

There are several potential drivers to explain waterbird population increases throughout Europe in recent decades:

Rice field expansion: Conversion of wetland areas for agriculture is very common and widespread globally, especially for the cultivation of rice (*Oryza sp*.). In 2014, an area of 641.988 ha was harvested in Europe, with southern Europe being responsible for more than half of rice production area (394.567 ha) (Food and Agriculture Organization of the United Nations 2012). Despite the fact that conversion of wetlands into agricultural areas has been one major factor for habitat destruction and consequently biodiversity decline, some forms of agricultural methods present characteristics that allow birds to use them as substitute habitats. Rice fields are a notable example, because the need to have the fields flooded for a great period of the year creates habitats and conditions favourable for waterbirds (Fasola and Ruiz 1996). Therefore, rice fields have been indicated as good alternative habitats for waterbirds (Fasola and Ruiz 1996, Navedo et al. 2015) through a variety of forms: a) Elphick (2000) tested the differences between semi-natural wetlands (areas that were altered in the past but are currently similar to natural wetlands) and flooded rice fields. The predation risk was higher in semi-natural wetlands, but all the other factors were similar (food abundance, feeding performance and time allocated to different behaviours), thus supporting the idea that flooded rice fields are good alternative habitats for waterbirds; b) Czech et al. (2002) stated that most heron species in Europe that forage in rice fields breed in nearby wetlands. Additionally, species, such as the Black-winged stilts (*Himantopus himantopus)* and Common Moorhen (*Gallinula chloropus)*, use the rice fields as breeding sites (Fasola and Ruiz 1996); c) In Portugal, Marques and Vicente (1999) indicated a peak on food abundance in the Sado rice fields, between February-March and September, coinciding with the timing of migration of several waterbirds species that use Iberian rice fields to refuel during migratory stop-overs (e.g. Alves et al. (2010), Lourenço and Piersma (2009)).

Despite the potential benefits of rice fields as alternative wetland habitats, natural wetlands are preferred whenever available. For example, Tourenq et al. (2001) compared species richness and abundance of waterbirds in natural wetlands and rice fields in Camargue (France), and showed that the abundance and species richness was consistently lower in the rice fields, with several species being exclusively recorded in natural wetlands. Similarly, Campos et al. (2001) found that the Purple Heron, despite foraging occasionally in rice fields, spent the majority of the time foraging along rivers preying on fish (80,5%), which is more caloric than prey available in rice fields, such as the Louisiana crayfish (*Procambarus clarkii)*.

The introduction of Louisiana crayfish: this is a crustacean natural from north-east Mexico and central-southern North America that was introduced in Europe for aquaculture. It was firstly introduced in Badajoz and Guadalquivir (South Spain), in 1973 and 1974 respectively, for commercial proposes due to its high economic value (Gherardi 2006). But it quickly escaped from captivity and colonised several nearby wetlands and expanded to new areas. This expansion was also facilitated by fishermen that distributed them to several sites across Spain and, thereafter, throughout southern Europe (Gherardi 2006). Despite its invasive status, and recognized negative consequences for wetland ecosystems, namely the devastation of subaquatic vegetation, which negatively affects the trophic chain and the clearness of the water (Rodríguez et al. 2005, Gherardi 2006), it also became a food resource for several predator species, most noticeably waterbirds: a) In Portugal, Louisiana crayfish became part of the diet of several aquatic species such as the otter and several waterbirds (night heron *(Nycticorax nycticorax)*, little egret (*Egretta garzetta*), grey heron (*Ardea cinerea*), purple heron, etc (Correia 2001)). Some of these waterbirds forage more frequently on this prey during the breeding season (purple heron and little egret), others rely on this item throughout the non-breeding season, although not in a regular way, whereas the white stork preys on crayfish during all year (Correia 2001); b) Salazar et al. (2005) compared diets of the cattle egret (*Bulbucus ibis*) and the little egret in S'Albufera Natural Park in Mallorca (Spain) and found that both species feed on the Louisiana crayfish, but in small amounts; c) Montesinos et al. (2008) studied the diet of chicks of night heron and of purple heron in Guadalquivir marshes, Spain, and found that the chicks of both species were not fed crayfish by the adults, even though the adults feed on this prey throughout the year; d) Conversely Poulin et al. (2007) studied the diet of Eurasian bittern in Camargue (France) during 3 years (2002-2004) and found that bitterns feed their nestlings almost exclusively crayfish (95,4% found in pellets and 84,9% found in regurgitates), and adults also fed on crayfish during the winter. Therefore, the increase in Eurasian bittern population in Camargue was caused, at least in part, by the increase of crayfish population; e) Rodríguez et al. (2005), found that, contrary to other bird species, mostly waterfowl, grey heron, cattle egret and white stork increased their populations in Chozas Lake (NW Spain) after the invasion of the Louisiana crayfish. However they report also a slightly decrease in the population of little egret; f) Tablado et al (2010) studied the relation between crayfish abundance and population trends of vertebrates in Guadalquivir marshes, and found that top predators that included crayfish in their diet had increased in numbers both in breeding and wintering seasons, whereas herbivorous species, even with the increase of legal protection, did not show similar trends, increasing at a much slower rate.

Increasing waste landfill availability: The increasing Human population in Europe during the 20th century lead to the creation of large waste landfills which can provide foraging opportunities for several bird species. For example, in recent years the populations of white stork has been increasing (Thomsen and Hötker 2006) and this is linked to the usage of wasteland fields. Tortosa et al. (2002) showed that white storks breeding in areas closer to landfill sites experience higher breeding success. In winter this species forages also in landfills (Tortosa et al. 1995, Kruszyk and Ciach 2010). In Poland the number of white storks feeding on landfills has increased where natural resources are low (Kruszyk and Ciach 2010). The use of landfills as a food source has also changed the migratory behaviour of several species, such as white storks, which used to be migratory in Europe, but currently use and protect the nesting sites throughout the year, in locations where they can forage in landfills, and no longer migrate to the traditional wintering areas in Africa (Gilbert et al. 2016). Even though the stork population increased and changed the migratory behaviour promoted by the occurrence in landfills, this does not seem to have influence on waterbird species not recorded in landfill sites.

The increase of spoonbills in Europe

Like most waterbird populations, the Eurasian Spoonbill (*Platalea leucorodia*) decreased drastically in Europe at the start of the 20th century, and by 1950 only two breeding sites were active, one in Spain and another one in the Netherlands. After intense recovery programs this population is currently increasing in most of northwest Europe (Overdijk 2013), and is now categorized as Least Concern (LC) in the European Red List (BirdLife International 2015). The (re)colonization of breeding areas is ongoing across Europe and, in most cases, this occurs due to habitat creation or restoration of traditional breeding sites with re-colonization events or colonization of new sites by individuals from traditional colonies. Dispersal and emigration is usually low in colonial nesting birds (Nager et al. 1996, Aguilera 1997, Serrano et al. 2001, Balkiz et al. 2010), but it can be levelled up by density dependence factors. When colonies reach higher number of animals resources may become limiting and the stronger competition may lead individuals to disperse to inhabited sites or to sites with lower density (Matthysen 2005, 2012, Oudman et al. 2017). Moreover, the fast growth of some recent colonies may be promoted by immigration following the conspecific-attraction theory (Stamps 1988, Reed and Dobson 1993, Tenan et al. 2017). For example, in Serbia the breeding spoonbill population of Vojvodina declined due to habitat degradation reaching its minimum in 1970, with only one breeding area in Obedska bara. After two fish farms were created and vegetation grew, spoonbills started breeding there and population increased at a steep rate since 2001, likely due to dispersal of individuals from colonies in adjacent countries like Hungary and Croatia (Tucakov 2004). In France, by 1992 there was only one breeding area for spoonbills in Grand-Lieu, but in 2011 there were a total of 14 breeding sites in the country. The main reasons for this expansion is immigration from Dutch colonies, associated to the increase of feeding areas, the presence of the invasive crayfish, and in some places, the low level of human disturbance (Marion 2013). In Donãna, Spain, colonial waterbirds (including Eurasian spoonbills) show positive trends since 1996 (Ramo et al. 2013). The main causes contributing for such increase was the protection of breeding areas, lack of human disturbance, creation of fish ponds, and management of vegetation (e.g. fencing marshes and planting trees) (Ramo et al. 2013).

Spoonbill is listed as vulnerable in Portugal (Cabral et al. 2005) but the Portuguese breeding population is considered stable (Overdijk et al. 2013). Despite historical breeding records from the 18th century (Tait 1924) the species was absent as a breeding bird in the country until 1988, when the first successful breeding pairs were recorded in Paúl do Boquilobo (Pereira 1989). In Ria Formosa, the first breeding pair was recorded in 1993, even though Ria Formosa has historically been a very important area for spoonbills both in winter and as a stopover during migration periods (Farinha and Trindade 1994). Similarly, wetlands of Castro Marim have also been a very important area during the non-breeding season, particularly between June and July, when a large number of dispersive spoonbills (mostly juveniles and non-breeding birds) from Spanish colonies were recorded (Farinha and Trindade 1994), which suggests that breeding spoonbills in Portugal likely originated from breeding colonies in southern Spain. By 1995 there were three breeding colonies in Portugal: 1 in the Tejo basin (Paúl do Boquilobo), 1 in Alentejo (Pêro Pião) and other in the Algarve (Ria Formosa) (Cardoso 1998). One year later, another colony was located along the river Tejo (Açude de Muge) (Farinha and Encarnação 1996). Portugal became also an important area for spoonbills in winter, with numbers increasing exponencially (Fig.1), reaching ca. 1650 in 2016 (CEMPA, ICNF). The population increase and northward expansion has been dramatic (Fig. 1) with new four breeding colonies created in 8 years, and the most recent one was established in 2012 (Paul do Trejoito) (Encarnação 2014). A minimum twelve-fold breeding population increment, increasing from 43 pairs in 1996, to 92-99 in 2002 and 540 in 2014 (Farinha and Trindade 1994, Farinha and Encarnação 1996, Equipa Atlas 2008, Encarnação 2014).

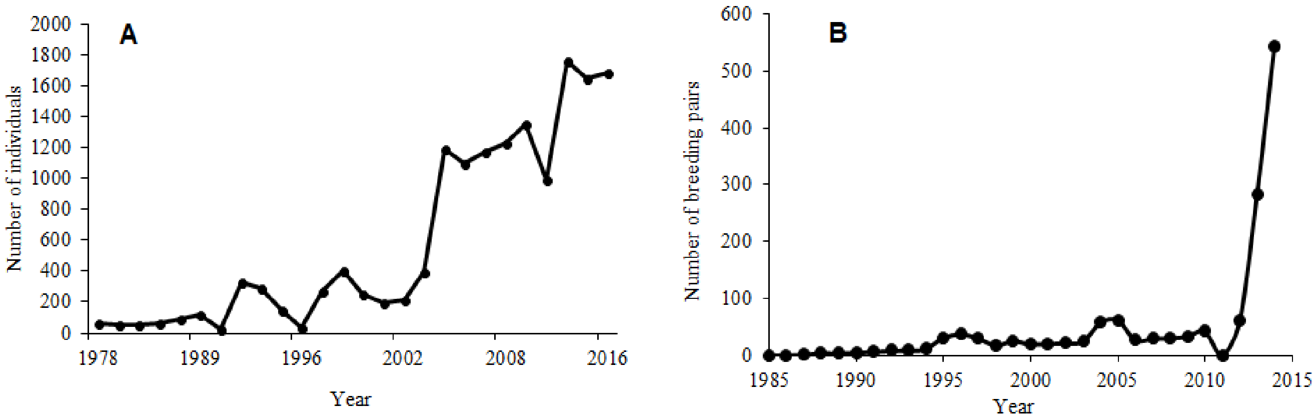

Figure 1: A) Number of spoonbills in Portugal during winter along the years; B) Number of breeding pairs of spoonbills along the years in Portugal; (Numbers from CEMPA/ICNF).

Eurasian Spoonbill ecology

Spoonbills are migratory waterbirds, and the subspecies *Platalea leucorodia leucorodia*, breeds exclusively in Europe and winters in south Europe and north Africa (Overdijk et al. 2013). The breeding season activity starts in March/April and autumn migration occurs generally in August/September, with spring migration occurring in February (Triplet et al. 2008, Lok et al. 2013a). Spoonbills usually breed in colonies, using nests built in the ground or in trees (Hancock et al. 1992). They start to breed with an average age of 3.6 years, lay clutches of 2-6 eggs and sometimes have a second clutch (Triplet et al. 2008). The incubation takes 24 to 28 days and after that both parents feed and care for the young chicks until they fledge at ca. 42 days (Triplet et al. 2008). During this post fledging period, juveniles make exploratory movements in surrounding wetlands and these journeys can reach distances higher than 100 km away from the natal colony (Hancock et al. 1992, Aguilera 1997, Volponi et al. 2008, Jelena et al. 2012). After that period, juveniles either migrate to southern wintering areas or stay in the vicinity of the colony, particularly birds from south Europe (Bauchau et al. 1998, Triplet et al. 2008, Volponi et al. 2008, Lok et al. 2013a). In some cases, birds that migrate south only return to the breeding colonies with 2 years or older (Aguilera 1997, Triplet et al. 2008). Spoonbills are considered philopatric birds, with a very low percentage (less than 5%) of birds breeding more than 100 km away from their natal colony (Aguilera 1997, Bauchau et al. 1998, De Voogd 2005). Although, populations originating from less stable areas, like the ones in central Europe, usually have higher proportion of dispersive birds, which indicates they attempt to establish in more favourable breeding sites (Pigniczki and Végvári 2015, Pigniczki 2017, Tenan et al. 2017). The low percentage and short range of dispersive spoonbills is usually associated with the slow formation and growth of new colonies, generally not very distant from original breeding sites (Pigniczki and Végvári 2015, Oudman et al. 2017, Tenan et al. 2017).

Aims of the present work

Spoonbills are considered umbrella and flagship species, and thus are indicators of good quality wetlands (Jin et al. 2008, Lorenz et al. 2009, Overdijk and Navedo 2012, Pigniczki and Végvári 2015). Therefore, it is crucial to understand the mechanism and drivers of their recent expansion to identify and protect key wetland areas for this species and consequently for a large number of other aquatic species. Studying the spoonbills is a good opportunity to understand the recent process of range expansion and colonization/recolonization of new sites. With this work, we aim to evaluate the recent expansion of Spoonbill in Portugal, particularly during the breeding season, exploring 3 main factors:

(i) Migratory behaviour and dispersal ecology: Quantify the numbers of individuals coming from colonies outside Portugal to winter and breed, and the level of juveniles dispersing into Portugal during their first winter (seasons between 1974 and 2015). These will be used to estimate overall connectivity between Portugal and European colonies, and also to understand from which European colonies spoonbills are dispersing to breed and colonise areas in Portugal.

(ii) Diet and trophic ecology: Identify the diet of spoonbill chicks in a traditional colony (Ria Formosa) and in a more recently occupied colony (Tejo), to test the hypothesis that Louisiana crayfish or other invasive species will likely be more relevant in recent colonies, whereas fish and other crustaceans should be most important prey in traditional colonies. In addition, we will explore the trophic ecology and dietary changes during chick development by analysing carbon and nitrogen stable isotopes on different tissues. We will be able to understand if the diet varies in relation to phases of the chick rearing period and colony.

(iii) Native juvenile dispersal and use of resources: Studying the spatial movements of juvenile spoonbills after fledging and identify which areas are they using, following the movements of tracked juveniles born in a traditional colony (Ria Formosa). Furthermore, we will be able to understand: a) the nature of the movements; b) the level of migration and dispersal of juveniles; c) areas that they select to forage and rest.

METHODS

Study species

Eurasian spoonbill is a white bird with a very uncommon bill in a spatular form. It measures between 65/80cm and has a wing-span between 115/145cm. Males are usually bigger than females but, apart from this, both sexes are equal. Adults display a crest during the breeding season and the lower throat become more yellow (Hancock et al. 1992).

They are wading birds that feed in low depth waters, being salty, brackish or fresh, so they are usually found habiting estuarine, coastal areas and marshlands. They mainly feed on fish, amphibians, crustaceans and others small invertebrate, usually during the night (Hancock et al. 1992).

Study sites

Two Eurasian Spoonbill breeding colonies were selected based on their historical colonization (one traditional and one recent) in order to sample juveniles for diet and movement analysis. Both colonies were visited in the period between May and July of 2017 for sample collection, color-ring marking and GPS/GSM tag deployment.

The traditional colony where the species breeds since at least 1993, is situated in **Ria Formosa** (RF) (36º 59’N, 7º 55’W), a lagoon system, with 18000 ha, protected from the Atlantic Ocean by a system of small islands and sand banks composed by several habitats such as marshes, fresh and brackish lagoons, salt evaporation ponds, dune banks and agricultural fields. Ria Formosa is a wetland of national importance being a Natural Park since 1987 and a Special Protection Area (SPA) for birds defined under de the bird directive of European Union and part of Rede Natura 2000. It has also international importance being part of the Ramsar Convention. Eurasian spoonbills breed in saltmarsh islands in a mixed colony with Little Egret. In this marsh *Spartina maritima* is the dominant plant species, but others like *Arthrocnemum perenne*, *Arthocnemum fruticosum*, *Salicornia nitens* and *Suaeda vera* are also common (Costa et al. 1996).

The more recently colony is located in the brackish salt marshes and reed-beds of **Tejo Estuary Natural Reserve** (TE) (38º 49’N, 8º 59’W), one of the most important and the largest wetland in Portugal, also included in the list of wetlands protected by the Ramsar Convention. It is a national protected zone and a SPA for birds of Rede Natura

2000. The Reserve extends for an area of 44772 ha and comprises a large diversity of habitats, including estuarine open waters, intertidal flats, alluvial agriculture fields, where the rice is one important culture, salt marshes and reed beds. This last habitat is where Eurasian Spoonbills breed in a mixed colony with several heron species, such as Grey Heron and Cattle Egret. The dominant vegetal species in that zone are *Phragmites australis* and *Scirpus maritime* (ICNF 2018).

Dispersal, settlement and migratory connectivity

We used the Portuguese re-sightings database of colour-ringed spoonbills (data kindly provided by CEMPA/ICNF) to identify the natal country of the birds that were re-sight in Portugal since 1974. We excluded from the analysis re-sightings without information on the country of birth or the data of ringing (N=12). This information is required to define the status of the bird (Breeding or Non-breeding) based on the month of the re-sighting (Breeding: April to July; Non-breeding: September to March; August was excluded because of the presence on the country of birds on several distinct periods (post-breeding dispersion, birds starting migration, birds on stopover)) and in its age (individuals up to 3 years of age recorded during breeding period were considered non-breeders). A total of 272 re-sightings were included in the analysis.

All spoonbills colour ringed from schemes across Europe were marked prior to fledging, and we therefore quantified the percentage of: i) individuals that dispersed to breed in Portugal (adults only) and ii) individuals that settled to winter in Portugal (juveniles and adults), originating from breeding colonies outside the country.

Non-breeding records were also used to estimate connectivity between European breeding colonies and Portuguese wintering areas. Migratory connectivity is a measure of how connected breeding and wintering areas are of a given migratory species or population. In general, if a population that breeds spatially together also shares the same wintering areas it is considered as being strongly connected. Conversely, a population that breeds together but whose individuals migrate to occupy diverse and spatial distant wintering areas, usually mixed with other species and/or populations, is thus considered as having weak migratory connectivity (Webster et al. 2002, Finch et al. 2017).

Recently, a new method to estimate migratory connectivity was developed (Cohen et al. 2018) that has several advantages compared with the Mantel test (R_M) (Ambrosini et al. 2009), the most used method (e.g. Cormier et al. (2013), Trierweiler et al. (2014)). This new metric, *Migratory Connectivity* (MC), is an extension from R_M, and accounts for uncertainty in sample errors and samples sizes that are not proportional to real abundance in origin areas. This method also has the advantage of being applicable to different types of migratory data (e.g., tracking with GPS systems, ring recovery) and different taxa, which makes comparisons among different studies more straightforward (Cohen et al. 2018). Estimating MC requires to: a) define origin and target regions coordinates (in this work, breeding and wintering regions, respectively), b) build two matrixes, one with distances between breeding areas and another with distances between wintering areas, c) build a matrix with species-specific probabilities of transition between all breeding areas to all wintering areas, d) have data of the abundance of each breeding area. Additionally, and optionally, it is possible to use the sample size, which is helpful when accounting for samples different from abundance (Cohen et al. 2018). We used the re-sightings database to define the breeding and wintering areas, calculated the distances matrixes between localizations with the "geosphere" package in R (Hijmans et al. 2017), using the Haversine method. To obtain the relative abundance for the breeding colonies of France, Spain and Netherlands we retrieved information from the online "Critical Sites Network" database (BirdLife International and Wetlands International 2010), and for Germany we used data available in Triplet et al. (2008), which is the most reliable datasource, despite the fact that it presents information on numbers relative to 2000's. Subsequently, with all this information, we could use the estMC function in the "MigConectivity" package (Hostetler and Hallworth 2018) to estimate migratory connectivity. The resulting values of estMC function range from -1 to 1, where higher positive values indicate strong connectivity, meaning that individuals breed and winter close together, values close to zero mean that there is no relation between distances in breeding and wintering areas, and, lastly, negative values imply that birds that breed close spend winter in diverse and distanced areas (Cohen et al. 2018).

Field work: bird biometrics, biological sampling and tagging

During the breeding season of 2017 we captured pre-fledged spoonbill chicks from nests in both colonies, Tejo and Ria Formosa. We ringed the birds with metallic rings (CEMPA), marked them with coloured rings, each with a unique combination, and collected biometric measurements (tarsus-length, head/bill-length and body mass) (Fig.2) to infer date of hatching based on previously established growth rate equations for the species (Lok et al. 2014). In addition, we collected the following biological samples, 150µl of blood from the brachial vein (Fig. 2) and the 5th primary feather that were cut from the base for stable isotope analysis. Blood was stored in 70% of alcohol and feathers were stored in individual plastic bags.

Figure 2: Field work in Ria Formosa colony. A) Measuring head/bill length. B) Collecting blood from the brachial vein. C) Spoonbill chick with colour rings and GPS/GSM tag (photo courtesy of Silvério Lopes).

As Spoonbills chicks frequently regurgitate spontaneously when handled (Lok 2013), we collected all regurgitations during handling for diet reconstruction. However, because adult spoonbills typically feed chicks during night or early in morning, and visits to the island colonies were only possible during high tides, which in our case was during the afternoon, we only could collect 1 sample in Tejo (TE) and 14 in Ria Formosa (RF) colony. These were complemented with faeces collected fresh (when a chick defecated $N_{TE} = 5$, $N_{RF} = 6$) or collected dry ($N_{RF}=11$) when deposited in the nest (Veen et al. 2012). All regurgitations and faeces samples were stored in plastic bags and frozen until laboratory analysis.

In the breeding seasons between 2015 and 2017 we equipped 10 juveniles from Ria Formosa with solar-powered GPS/GSM transmitters (Movetech Telemetry) attached to the birds' back with Teflon ribbons: 3 in 2015, 2 in 2016, and 5 in 2017. Birds were selected based on their development stage and only those with enough body mass to have the transmitter weight (17.6-19 g), well below the threshold of 3% body mass, were tagged (1461.25± 279.36 g), as recommended to avoid interferences with the wellbeing and natural movements of each tagged individual (Phillips et al. 2003, Casper 2009).

Diet reconstruction and stable isotope analyses

In order to reconstruct the diet of juvenile spoonbills from both colonies, we unfrozen faeces and regurgitations samples and searched for prey items, that were then stored in alcohol (70%) for identification. Given that remains from faeces were very degraded and were very small, we used a stereomicroscope (Wild Heerbrugg M3B) to avoid missing microscopic items, specially otoliths, (Veen et al. 2012). All fish otoliths found were identified, and other remains were divided by colour with stronger red tones being considered parts of Louisiana crayfish (*Procambarus clarkii*), that has a dark red exoskeleton, and orange ones being considered parts of other crustacean (shrimps, prawns or crabs). For prawn identification we used the identification key by González-Ortegón and Cuesta (2006) and identified them until the lowest possible taxonomic level. Other Decapode crustaceans were identified with the aid of available databases (WoRMS Editorial Board 2017). To identify fish we used mainly otoliths following published sources (Assis 2004, Tuset et al. 2008). For cases when fish was found well preserved we were able to identify it without searching for otoliths. The remaining contents of regurgitations such as small gastropods, bivalves and vegetal material where not identified as these were probably ingested accidentally.

Diet reconstruction was done mostly from recent samples providing details on food items (mainly animal prey) whereas stable isotope analysis allows comparing diet in different periods: for chicks sampled with few weeks (in this work with an average of 25 days) blood will encompass almost all their period of life (Hobson 2005, Cherel et al. 2014), while different sections of feathers will reflect the earliest and the most recent days (Mizutani et al. 1990, Thompson and Furness 1995, El-Hacen et al. 2014). In order to compare the diet between chicks developing in both colonies, we used Carbon and Nitrogen stable isotope analysis to extend the comparative period. Stable isotope values of N and C in the tissues of predators are related to those of their prey in a predictable manner allowing to extract information regarding the trophic level, as Nitrogen $\delta^{15}N$ increases about 3 to 5 parts for thousand between consecutive trophic levels (Schoeninger and DeNiro 1984, Hobson and Welch 1992, Post 2002), and also to distinguish between freshwater and marine prey, as Carbon $\delta^{13}C$ is higher in marine than in freshwater habitats (Craig 1953, Fry et al. 1983, Fry 2002, Barrett et al. 2007). However, and to compare isotopic values in different tissues (and consequently in different periods), we applied the general discrimination factor for birds in both feathers and blood samples, proposed by Caut et al. (2009). In the laboratory, blood samples were dried during 48h leaving hole blood solid particles. Each 5th primary feather was cut in two sections, one section at the base of the feather (close to the quill) and another at the tip. With this procedure we were able to explore potential differences between earlier and later development stages (El-Hacen et al. 2014). Feathers sections were cleaned in a solution of chloroform and methanol in a proportion of 2:1 with the objective of removing any possible impurity. Each section was immersed in this concentration for a total of 15 minutes (divided in periods of 5 minutes in subsequent cleaner solutions). After that, feathers were dried for 24 hours at 60ºC. Ending that process, we encapsulated blood and feather samples to be combusted and then had their nitrogen and carbon isotopic ratios measured by Continuous Flow Isotope Ratio Mass Spectrometry (CF-IMRS). Outcome was expressed in δ (‰) as result of the equation:

$$\boldsymbol{\delta^{13}C \text{ or } \delta^{15}N = [(R\text{sample}/\ R\text{standard}) - 1] \times 1000,}$$

where $R={}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ and standards are the PeeDee Belemnite (PDB) in the case of $\delta^{13}C$, and atmospheric nitrogen (N_2) in the case of $\delta^{15}N$. Carbon and nitrogen measurements had an analytical precision of 0.2‰.

Lastly, and to examine the results, $\delta^{13}C$ and $\delta^{15}N$ values of feathers and blood were compared using MANOVAs (Wilk's lambda). We also performed one-way analysis of variance (ANOVA) of $\delta^{13}C$ and $\delta^{15}N$ ratios individually. Post hoc Tukey tests were used to analyse the differences in carbon values of tissues of both colonies. To evaluate the isotopic niche of spoonbills in the different periods and colonies (Jackson et al. 2011), we used "SIBER" (Stable Isotope Bayesian Ellipses in R) to calculate the area of standard ellipses (SEAc). Furthermore, and to correct for different sample sizes between colonies, we estimated the Bayesian estimate of the standard ellipse (SEA_B) to compare the isotopic niche width among different samples (Jackson et al. 2011). We used the metrics of "SIBER" implemented in the package "siar" (Parnell et al. 2010) in R environment (R Core Team 2017).

GPS tracking and data filtering

GPS/GSM transmitter tags were programmed to record fixes at 30 minutes intervals with an error below 3 meters. Besides timestamp, latitude and longitude, loggers of 2017 and one of 2016 also recorded acceleration in 3 axis (x,y,z). Unfortunately, the quality of 2015 and 2016 transmitters was lower which produced records of inferior quality. We excluded from the analyses two spoonbills of 2015 given the low quality of their GPS data, and although two other GPS tags collected less than 2 months of data, we included the information in some sections of the analysis (see below). Tracked spoonbills were named for a better understanding of the movements of each individual (Table 1).

Table 1: Identification of juvenile spoonbills and GPS related information

ID	Year	Date of GPS/GSM attachment	First GPS record date	Last GPS record date	Days of data recording	Age at first time out of colony (days)	Age at last time on colony (days)
Castula	2015	22/07/2015	24/07/2015	14/08/2015	22	56	68
Mira	2016	14/06/2016	21/06/2016	07/02/2017	231	55	59
Nembus	2016	14/06/2016	20/06/2016	13/08/2016	49	59	70
Polaris	2017	23/06/2017	23/06/2017	12/10/2017	111	46	67
Atlas	2017	23/06/2017	23/06/2017	05/11/2017	135	45	72
Rigel	2017	23/06/2017	23/06/2017	01/12/2017	162	54	55
Sirius	2017	23/06/2017	23/06/2017	01/03/2018	251	58	80
Vega	2017	23/06/2017	23/06/2017	02/03/2018	252	42	50

Data obtained from GPS tags was filtered by removing repeated data/hour localizations and removed the flying fixes, acceleration value >1 m/s, (only for loggers that had this information). We used ArcGis combined with R software (R Core Team 2017) to perform all the spatial data analysis and visualization of geographical data.

Home range estimation

With the objective of estimate home ranges for spoonbill chicks tagged between 2015 and 2017, we firstly established the limits of the breeding colony by considering it to be the entire island, even if the nest locations occupy only part of it, although variable between years. We considered the first position outside the colony to indicate the ability of flying and thus divided the tracking in two distinct periods: Before leaving the colony (BLC) and After leaving the colony (ALC), defining the moment of leaving the colony as the last time that the bird visited the island to estimate home range separately for both periods.

Home range and Utilization Distribution (UD) of the tracked juveniles were estimated using the Dynamic Brownian Bridge Movement Model (dBBMM). This method follows the principles of the Brownian Bridges that are movement models which consider the localization of starting and ending points, as well as, the time between relocations and the characteristics of the movement, such as speed and direction (Horne et al. 2007). The dBBMM is an improved home range and UD estimator method compared with the "traditional" ones (e.g. kernel density estimation), because it reflects not only the spatial localization of the points, but also the elapsed time between them and is thus able to estimate the path taken by the animal even during periods that include different behavioural movements (Horne et al. 2007, Kranstauber et al. 2012). The model requires the localizations associated with timestamp, the error of localization (from the GPS system), and the Brownian motion variance (σ^2_m), related with the characteristics of the movement, that varies along the path in accordance with the changes in movement of the animal (e.g. foraging, flying) (Kranstauber et al. 2012). We thus used the package "move" (Kranstauber and Smolla 2014) in R software to define the sliding window size and margin and calculate the home range. The sliding windows are consecutives subsets of the tracking where the program searches for changes in the movement parameters to estimate separated and adequate σ^2_m values and the margin must be equal or higher than 3, since the model requires at least 3 positions to detect changes in movements. We used a window size of 23, which corresponds to a period of c.a. eleven and a half hours, and a margin of 9 following Kranstauber et al. (2012). We calculated the 50% and 95% contours from the UDs to represent the core and foraging/exploratory areas, respectively for two distinct periods: BLC and ALC.

Habitat use and Specialization

To explore the use of different habitats by juvenile spoonbills in Ria Formosa we used the most recent version of Corine Land Cover (CLC) data accessible from Copernicus land cover monitoring services (Bossard et al. 2000) that has information from the use of soil in 2012. In addition, we complemented the soil usage map using satellite images (ESRI 2018) from 2018 to reclassify outdated regions. Corine Land

Cover has 48 different habitat categories, but we only considered those present in the study area (including all tracked spoonbill locations) and grouped some at higher levels of organization resulting in 6 final habitat categories (table 2). We also excluded from the analysis some locations that occurred in urban areas, considering those to be either errors in the localization of GPS or of CLC and satellite images or scales.

Table 2: Corine land cover (CLC) corresponding to habitat categories analysed.

Habitat categories	Correspondent CLC categories
Intertidal wetlands	Salt marshes Intertidal flats Coastal lagoons Estuaries
Salt evaporation ponds	---
Inland wetlands	Inland marshes Water courses Water bodies
Water waste treatment plant (WWTP)	---
Agricultural areas	Non-irrigated arable land Permanently irrigated land Fruit trees and berry plantations Pastures Annual crops associated with permanent crops Complex cultivation patterns
Rice fields	---

To investigate how individual habitat use varied during the first period of life, we quantified the weekly frequency of usage of each habitat type by dividing the number of localizations in a given habitat type in a week by the total number of localizations in that week. The first week considered in this analysis started when the spoonbill visited the colony for the last time (ALC). For the spoonbill Polaris which migrated to Africa we only calculated the frequency of habitat use when it was in Europe. As we noticed an apparent trend in the frequency of usage of intertidal wetlands along time, we tried to fit a tendency line to the use of this habitat category. We tested several equation types to evaluate which fitted the data best based on the lowest Akaike Information Criterion (AIC) and on the value of the multiple r squared (R^2). This analysis was carried out with R package “basicTrendline”(Mei et al. 2018).

To explore the degree of Specialization of juveniles in terms of habitat use we calculated the proportional specialization index (PSi), that is a measure which quantifies the mean pairwise overlap between each individual and the population related to resources utilization (Schoener 1968, Bolnick et al. 2002b). Psi fluctuates from 0 to 1, where 0 is the value of an extremely specialized individual and 1 is from a generalist that uses all the resources of the population (Bolnick et al. 2002b, Navarro et al. 2017). Calculating the mean of all Psi values, provides the prevalence of Individual Specialization (IS) in the population (Bolnick et al. 2002b, Navarro et al. 2017). Monte Carlo resampling was used to test whether observed Psi results diverged significantly from randomized values extracted from the entire population (Navarro et al. 2017). We calculated Psi for 2 different periods of time (ALC) corresponding to early and late exploration phases: late Summer (August and September) (6 individuals); and Autumn (between mid-September and November) (4 individuals). All the above analysis were made with the R package "RInSp" (Zaccarelli et al. 2013).

Movement patterns analysis

To study the movement patterns of tracked spoonbills we first estimated Net Squared Displacement (NSD), a useful metric for studding proprieties of movements. NSD measures the distance in a straight line between each point of the trajectory and the initial point (Kareiva and Shigesada 1983, McCulloch and Cain 1989, Bunnefeld et al. 2011). Several studies defined different movements categories based in the graphical displays of their NSD: a) migratory animals usually show a NSD annual cycling curves characterized by rapidly increasing and decreasing rates of NSD in early spring and early autumn, respectively, followed by stationary phases were the NSD slope is almost zero (Kölzsch and Blasius 2008, Bunnefeld et al. 2011), b) central foragers animals with stable home ranges frequently display stable NSD curves with almost no slope (Moorcroft et al. 1999, Börger et al. 2008), c) dispersing animal's NSD curves tend to be stationary and close to zero at the beginning but then increase during exploratory movement until becoming stable due to stationary behaviour (Börger and Fryxell 2012), d) nomad animals, moving in a random way, will show an ever increasing NSD curve (Turchin 1998, Börger et al. 2008). We calculated the NSD in the package "adehabitatLT"(Calenge 2011a) in R.

In addition, and to classify the movements of juveniles in movement syndromes, we calculated 4 more movement metrics following Abrahms et al. (2017): a) Mean turning angle correlation (TAC), where turning angle is the angle between the line of a point and the previous point and the line of the trajectory until that same previous point (Dray et al. 2010), b) Mean Residence time (RT), that is the amount of time an individual stays inside an circle of a defined radius centred in each point of the trajectory (Van Moorter et al. 2016) c) Mean Time to return (TtoR), the time that an individual takes to return to a circle of a determined radius (Van Moorter et al. 2016), d) Mean Volume of interception of monthly home range (VI), that measures the overlap between 95% kernel home ranges of different months for the same individual (Millspaugh et al. 2004, Fieberg and Kochanny 2005). We used the packages "adehabitatLT" (Calenge 2011a) and "adehabitatHR" (Calenge 2011b) to calculate these metrics. Following the method suggested by Abrahms et al. (2017) we carried out a Principal Component Analysis (PCA) with the results from the above metrics and the maximum NSD (MNSD) in R (R Core Team 2017) with the function *prcom*, and then used the results to perform cluster analysis with Ward's method that agglomerate the most similar points based on their Euclidean distance (Gordon 1987). We used the function *hclust* in R software (R Core Team 2017) to perform the cluster analysis.

RESULTS

Analysis of migratory connectivity and settlement

We compiled a total of 280 re-sightings, from 7 countries corresponding to 217 individuals (Table 3). The mean percentage of re-sighted birds per total number of ringed bird in each country was of 1.15 ± 0.68 (SD). Of spoonbills marked outside Portugal, 13.7% where recording during the breeding season, Spanish and Dutch (and one French not included in the data), mainly in Ria Formosa (including Castro Marim, 33.3%), Paúl do Boquilobo (18.2%), Ria de Alvor (15.2%) and the Sado Estuary (15.2%). Considering juveniles only, most where recorded in Ria Formosa (43.5%) which was also the area where 100% of Spanish juveniles were recorded (Fig. 3), followed by Ria de Alvor (15.3%) and the Tejo estuary (14.1%). During winter (Fig. 4) the areas with most records were Ria Formosa (38%), Ria de Alvor (18%), and the Tejo estuary (12%).

Table 3. Number of spoonbills colour-ringed in European countries and re-sighted in Portugal. Re-sights includes all visual records of the same Individual. Percentage of re-sights per number of ringed birds in each country since the start of ring programs was low (ca: 0.5-3%). Possible breeding individuals include birds sighted between April to July and older than 3 years. Percentage of juveniles also includes young birds recorded in August, (that were usually excluded from other categories). Results of estimated Migratory Connectivity test were presented only for four countries that had more than 10 records of spoonbills in Portugal. (NA = not applicable).

Country	**Individuals**	**Re-sights**	**% recorded during breeding**	**% of recorded during winter**	**% of juveniles**	**Migratory Connectivity (MC)**
Germany	14	19	0	100.0	21.4	0.77
Denmark	4	4	0	100.0	75.0	N.A.
Spain	57	59	40.4	36.8	29.8*	-0.14
France	10	13	10.0	80.0	50.0	0.56
Belgium	1	1	0	100.0	0	N.A.
Netherlands	131	184	10.0	91.6	45.8	0.04
Total (N)	217	280	34	185	86	N.A.

Migratory connectivity was positive for German and French populations, for Netherlands it was almost zero, and was negative for the Spanish population (Table 3).

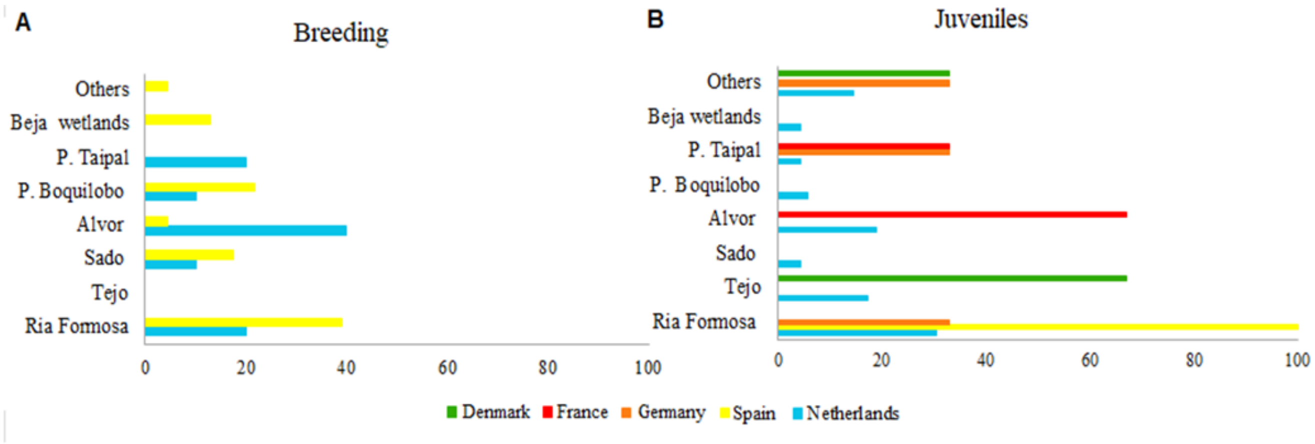

Figure 3: Percentages of Spanish and Dutch breeding and juvenile spoonbills in different wetlands of Portugal

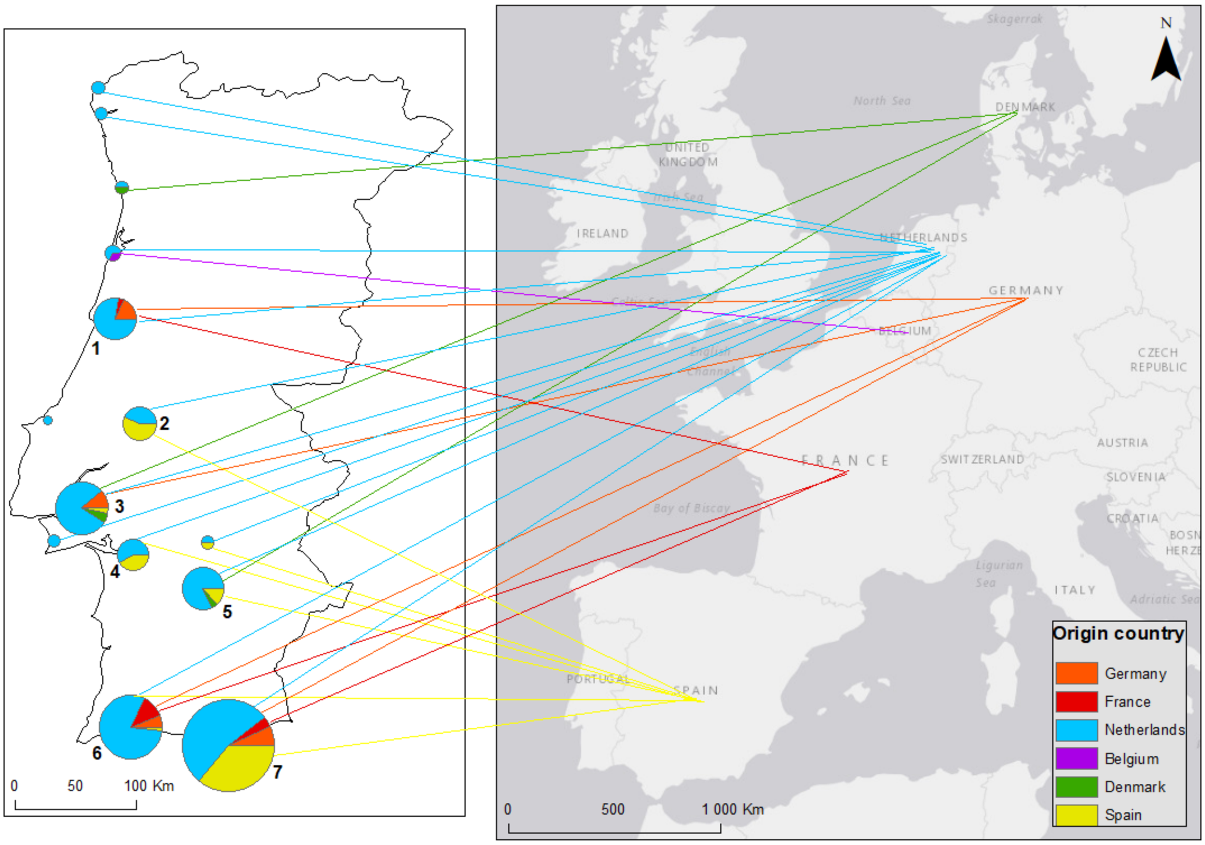

Figure 4: Spoonbills from European countries wintering in Portuguese wetlands (1: Paúl do Taipal, 2: Paúl do Boquilobo, 3: Tejo estuary, 4: Sado estuary, 5: Beja wetlands, 6: Ria de Alvor, 7: Ria Formosa). Relative size of pie charts is proportional with the number of re-sights of coloured spoonbills in each wetland. Only wetlands with more than 10 wintering birds are considered in the legend.

Diet reconstruction

Samples from spoonbill chicks in the Tejo Estuary contained only evidence for consumption of the Louisiana crayfish (Table 4). Samples collected in the colony of Ria Formosa were more diverse with consumption of Crustaceans (all exoskeleton fragments from faeces were orange), Fish, Gastropodes and Isopodes (Table 3). Crustaceans were also the most consumed prey that was present in all samples (regurgitations and faeces) and constituting 80.7% of all prey consumed, followed by fish, present in 52.2% of samples but composing only 9.3% of prey consumed (Table 3). The most consumed crustaceans were shrimps of genus *Palaemon*, mainly *Palaemonetes varians* (19.3%). Fish were mostly from genus *Atherinidae* and *Gobiidae*, and were identified mainly by their otoliths that were of small size and some of them were very degraded, particularly in faecal samples. Other prey items found were gastropods (mainly molluscs) and isopods. Vegetal matter was also found in samples from both colonies.

Table 4. Percentage of occurrence of each prey item in chicks regurgitations and faeces (NRF=23, NTE=5) and numerical frequency of prey items (N_{RF}=280, N_{TE}=10) from spoonbills chicks of Ria Formosa (RF) and Tejo (TE).

Prey	Ria Formosa		Tejo	
	% Occurrence	**Numerical frequency**	**% Occurrence**	**Numerical frequency**
Fish	52.2	9.3	0	0
Atherinidae	21.7	0.0	0	0
Batrachoididae	4.3	0.4	0	0
Sparidae	13.0	4.3	0	0
Gobiidae	39.1	4.3	0	0
Soleidae	4.3	0.0	0	0
Mugilidae	8.7	0.4	0	0
Unidentified	8.7	0.0	0	0
Crustacean	100.0	80.7	100.0	100.0
Crangonidae	4.3	3.2	0	0
Palaemonidae	26.1	54.3	0	0
Portunidae	8.7	2.5	0	0
Cambaridae	0.0	0.0	100.0	100.0
Unidentified	91.3	20.7	0	0
Gastropod	13.0	8.9	0	0
Isopod	4.3	1.1	0	0

Stable Isotopes

Stable isotope signatures from spoonbill chicks of both colonies (Table 5) showed differences between colony sites (MANOVA, Wilk's lambda, $F_{1,82}$= 524.43, p<0.0001) and tissues (MANOVA, Wilk's lambda, $F_{1,82}$= 7.78, p=<0.0001). However, these differences were only significant for δ^{13}C (colony $F_{1,82}$=1056.88 p<0.0001, tissue $F_{2,82}$=16.10 p<0.0001) and not for δ^{15}N (colony $F_{1,82}$=1.48 p=0.23, tissue $F_{2,82}$=1.68 p=0.19).

Table 5: Stable isotope δ15N and δ13C (mean ± SD) values for blood and feathers from juveniles of Ria Formosa and Tejo. SEA_B is the Bayesian estimate of the standard ellipse area and its P value indicates if the sizes of ellipses of both colonies are statistically different. N is the number of each tissue samples analysed.

Tissue	Ria Formosa							Tejo							SEA_B P
	N	δ13C	±	SD	δ15N	±	SD	N	δ13C	±	SD	δ15N	±	SD	
Blood	13	-14.46	±	0.62	13.2	±	0.62	11	-24	±	1	12.43	±	1.43	< 0.001
Feather tip	28	-12.74	±	1.09	14.04	±	0.83	4	-23	±	1	14.41	±	1.02	0.3053
Feather base	28	-12.97	±	1.1	14.37	±	0.99	4	-23	±	0	13.58	±	1.1	0.6625

Table 6: P values from Post-hoc Tukey for both colonies comparing signatures of Carbon isotope between blood and different sections of feathers (tip and base) samples. * signals significant differences.

Ria Formosa / **Tejo**	Blood	Feather base	Feather tip
Blood	----	0.006*	0.058
Feather base	0.002*	----	0.985
Feather tip	0.016	0.963	----

Post-hoc Tukey test revealed only significant differences between carbon signature in blood and in the base of feathers for both colonies (table 6). Niche width estimated as SEAc is represented in Figure 5, and SEA_B, corrected for different sample sizes was only higher (P = < 0.001) in blood isotope signature of the Tejo estuary compared with Ria Formosa (Table 5).

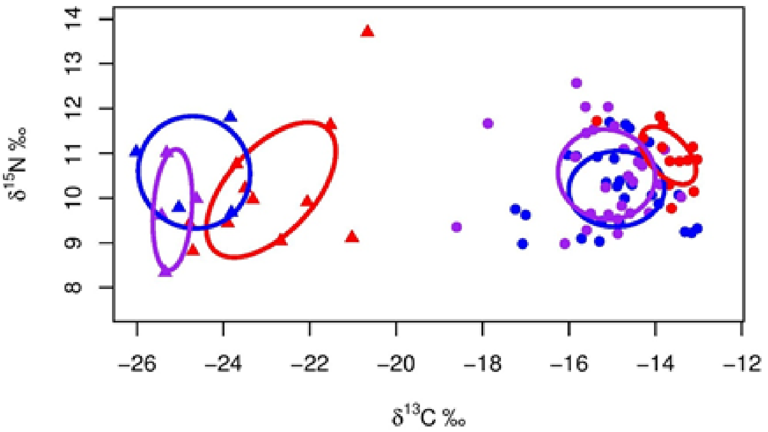

Figure 5: Isotopic niches of spoonbill juveniles in Ria Formosa (circles) and Tejo (triangles) based on Jackson et al. (2011) applied to Stable Isotopic ratios in blood (red) and feathers tip (earlier stage – blue) and base (later stage - purple) sections. The area of the standard ellipses (SEAc) is represented.

Home range, habitat use and specialization

On average each GPS tag recorded 152 ± 89.14 SD days, corresponding to about 5 months of tracking data, but the maximum period recorded was about 8 months (although data collection continued past that time) and the minimum corresponding to less than a month (with transmission stopping or the bird dying). The mean number of fixes per day per tag was 37.20 ± 0.71 SD. On average, spoonbills left the colony with 52 ± 6.53 SD days and visited it for the last time at 65 ± 9.8 SD days after hatching. (Table 1). All spoonbills stayed in Iberia, except Polaris that migrated to North Africa (Morocco). All others remained in Portugal, but Sirius travelled to South of Spain. Three spoonbills from 2017 (Polaris, Atlas and Rigel) died during the period of study, two were found dead in advanced decomposing state, being impossible to determine cause of death (José Silvério, *pers. comm.*), and one was presumably shoot in Africa, as final stationary tag locations were from a house whilst immediate previous fixes showed common movement patterns in a remote wetland area.

Home range varied considerably among juvenile spoonbills (Fig 6), both for core (50%UD) and for foraging/exploratory (95%UD) areas, before and after leaving the colony. The core home range for BLC ranged between 0.02km and 0.59km, while for ALC it increased its upper limit to 4.15km. For foraging home range, the minimum area was 0.02km for BLC and ALC but the maximum was larger for ALC than BLC, with 175.80km and 13.26km, respectively.

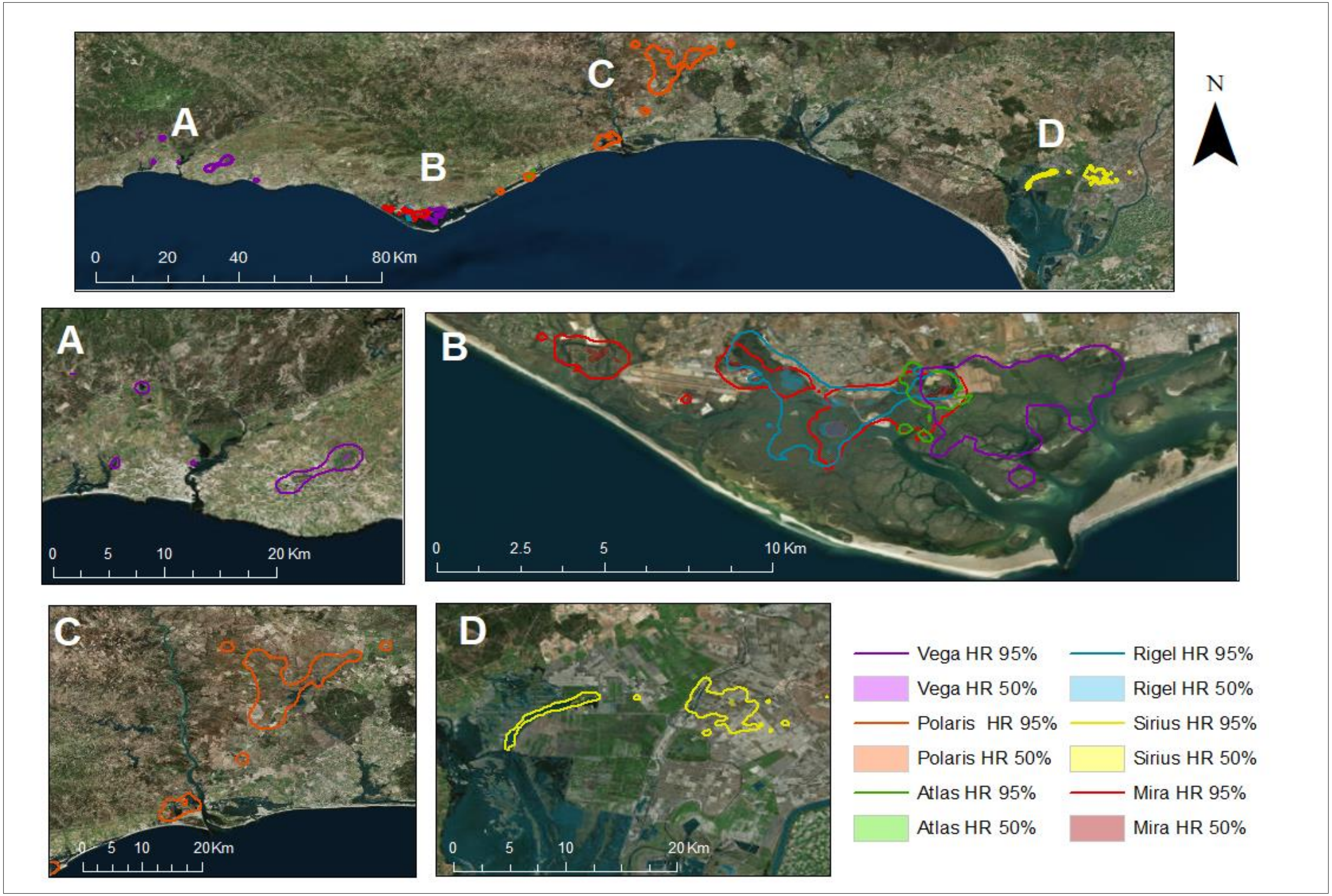

Figure 6: Home range of spoonbills in Southern Iberia Peninsula. Lines represent exploratory range (Home range 95%), and Semi-transparent polygon represent core areas (Home range 50%).

Juvenile spoonbills selected a broad range of habitats (Table 2) and used them in different proportions across weeks (Fig 7). Overall the most used habitats were intertidal wetlands (0.28), salt evaporation ponds (0.28), and rice fields (0.23). The best fitted model (Fig 8) to describe the use of intertidal wetlands per week was a logarithmic model (Table A2) (AIC= 47.22, $p<0.0001$, $R^2= 0.384$, $y=-0.251 \ln (x) +0.904$). In the first weeks ALC all juveniles used intertidal wetlands but as they aged this habitat was less frequently used and replaced by others habitat types, mostly rice fields (0.75) and salt evaporation ponds (0.10).

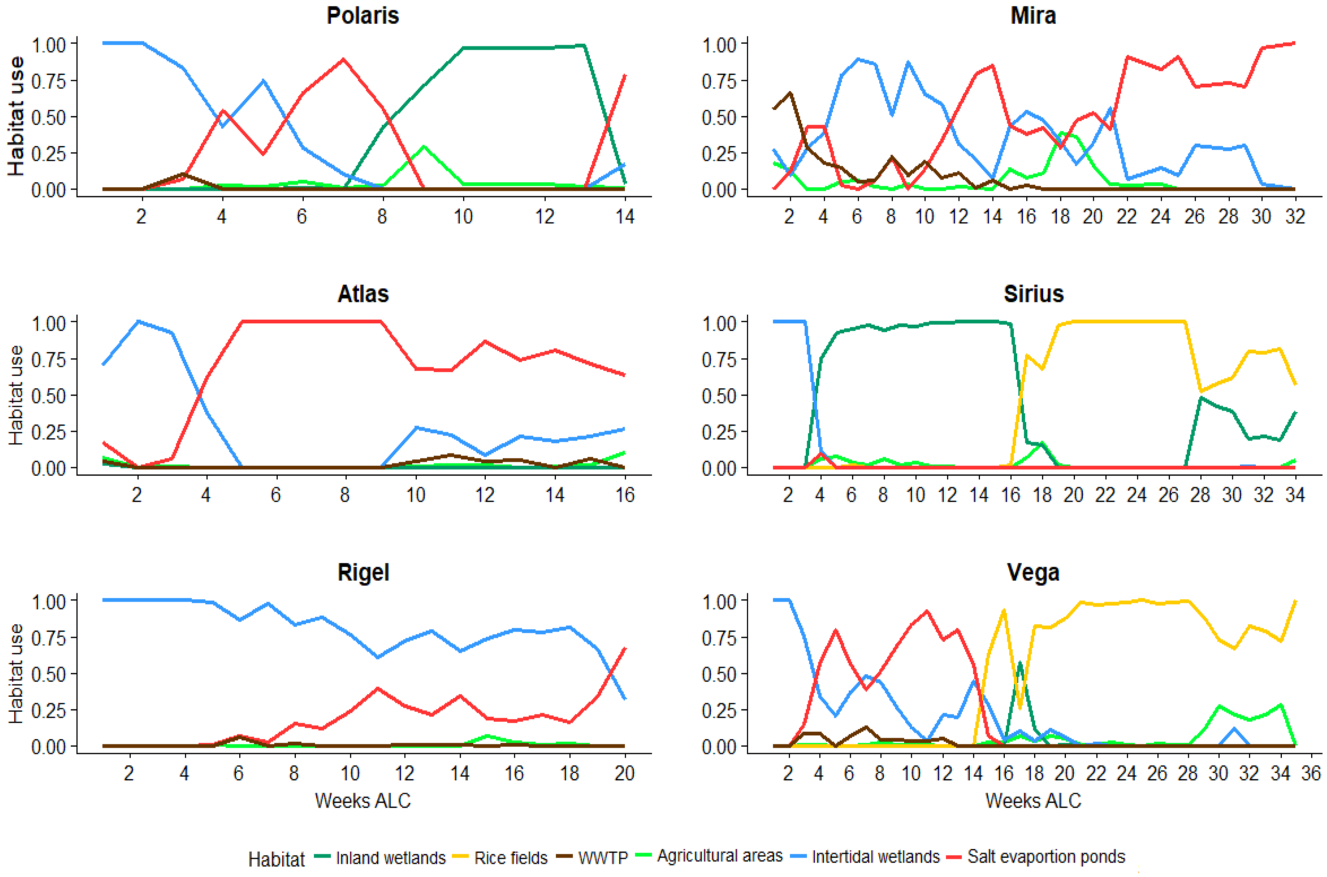

Figure 7: Juvenile Spoonbill's frequency of use of each habitat type on south Iberian Peninsula per weeks after leaving the colony (ALC).

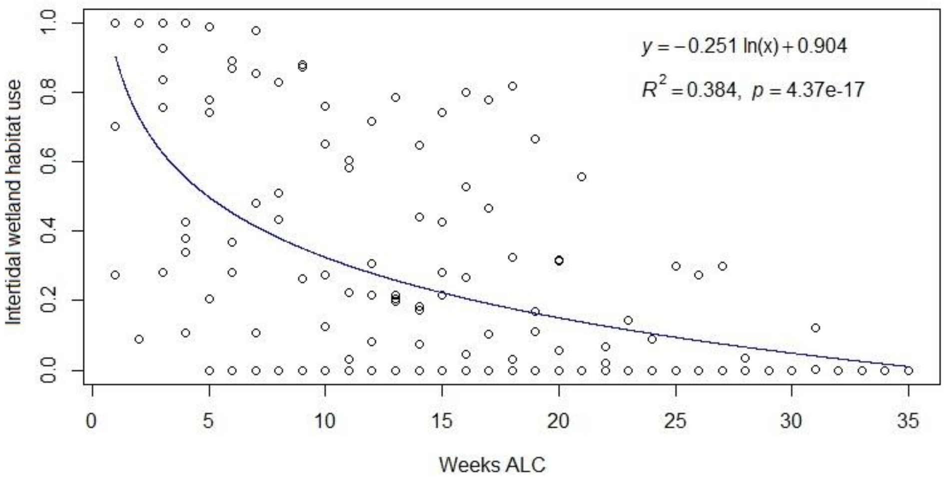

Figure 8: Variation on juvenile spoonbill's frequency of use of intertidal wetlands with weeks after leaving the colony.

Psi levels for late Summer ranged between 0.25 and 0.75, and in Autumn between 0.4120 and 0.5790 (Fig 9). Using Monte Carlo permutations, analyses we could deduct that the prevalence of Individual specialization was low overall (spoonbills were more generalist) but was lowest in late Summer (late Summer: IS= 0.60, p-value= 0.93; Autumn: IS= 0.56, p-value= 0.80).

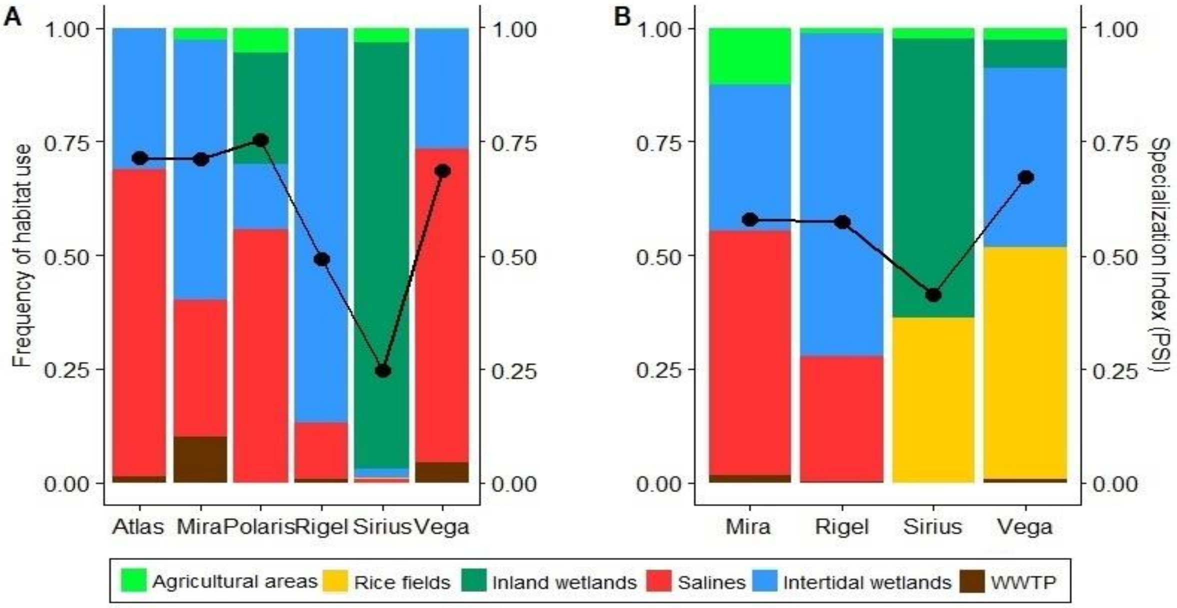

Figure 9: Variation on frequency of habitats used by juvenile Spoonbill in South Iberian Peninsula and associated Specialization Index (Psi, line with dots). A) Late summer; B) Autumn.

Movement study

NSD mean values for each spoonbill ranged between 3.01 km and 187.78 km, with maximum values varying between 6.44 km and 791.63 km. Based on visual examination of graphical representation of NSD (Fig 10) we can see that Polaris, Sirius and Vega performed a migration/dispersion, even though Polaris was of a higher scale. We can also see that Mira movements approximates of a dispersive and exploratory type of movement, and that Atlas and Rigel have more central place movements.

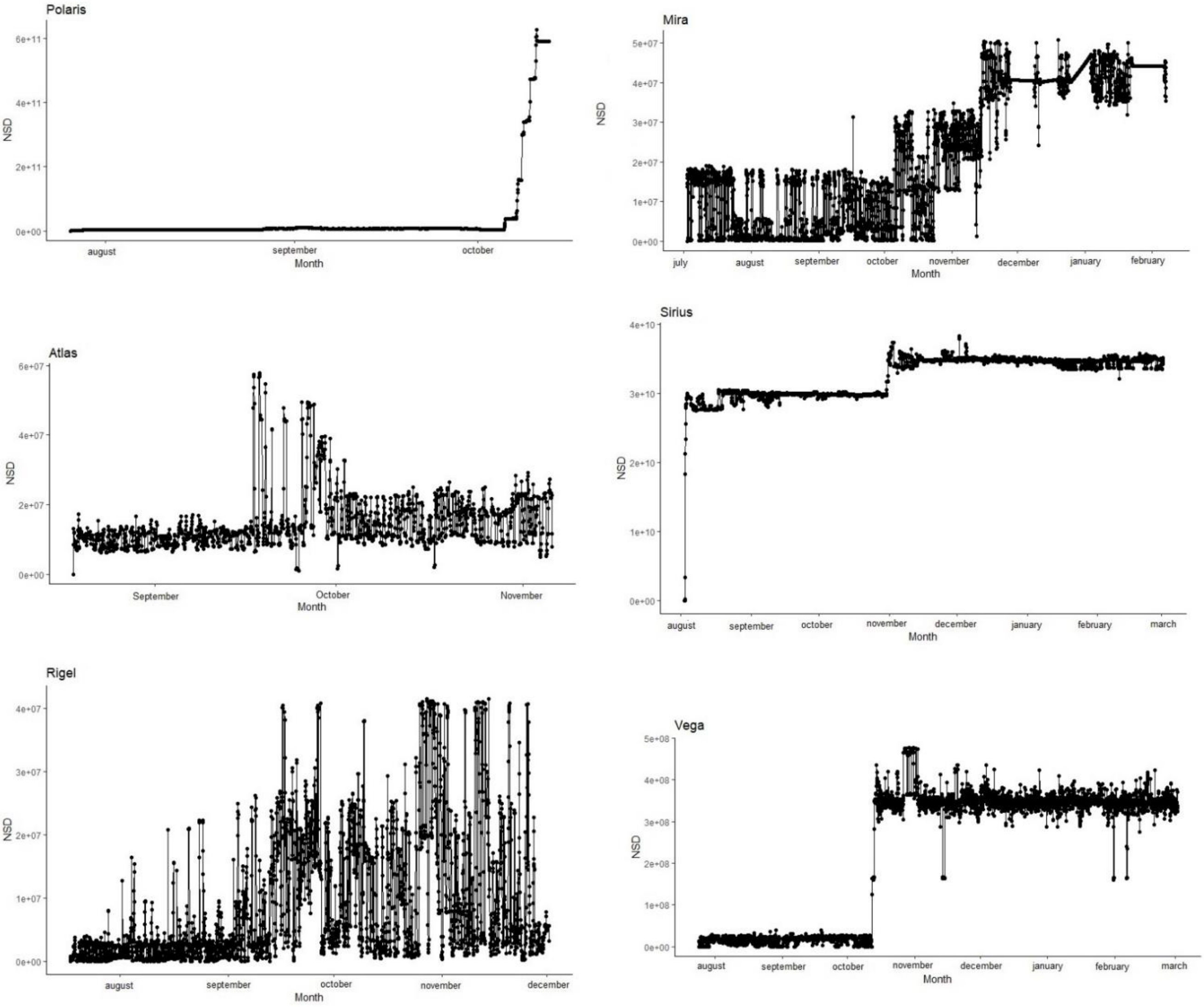

Figure 10: Net squared displacement (NSD) values of spoonbills tracked in Ria Formosa.

The PCA resulting from the five metrics calculated to evaluate movement syndromes, TAC, RT, TtoR, VI and MNSD (Table A3, Fig 11A). explained 82% of variance in two first axis: in axis 1 RT, VI and MNSD were the most important metrics, whereas in axis 2 it was TtoR, VI and MNSD. Overall, spoonbills showed mostly movement patterns influenced by MNSD (decreasing along the PC1 axis), TtoR (decreasing along PC2 axis) and VI (increasing both in PC1 and PC2 axis). The subsequent cluster analysis separated our juveniles in 2 groups (Fig. 11B). The first one (encompassed by Vega, Polaris and Sirius) is a group with high values of MNSD and low VI, and a second one (enclosing Atlas) more heterogeneous, with higher VI values and low MNSD, and, in general, less TtoR.

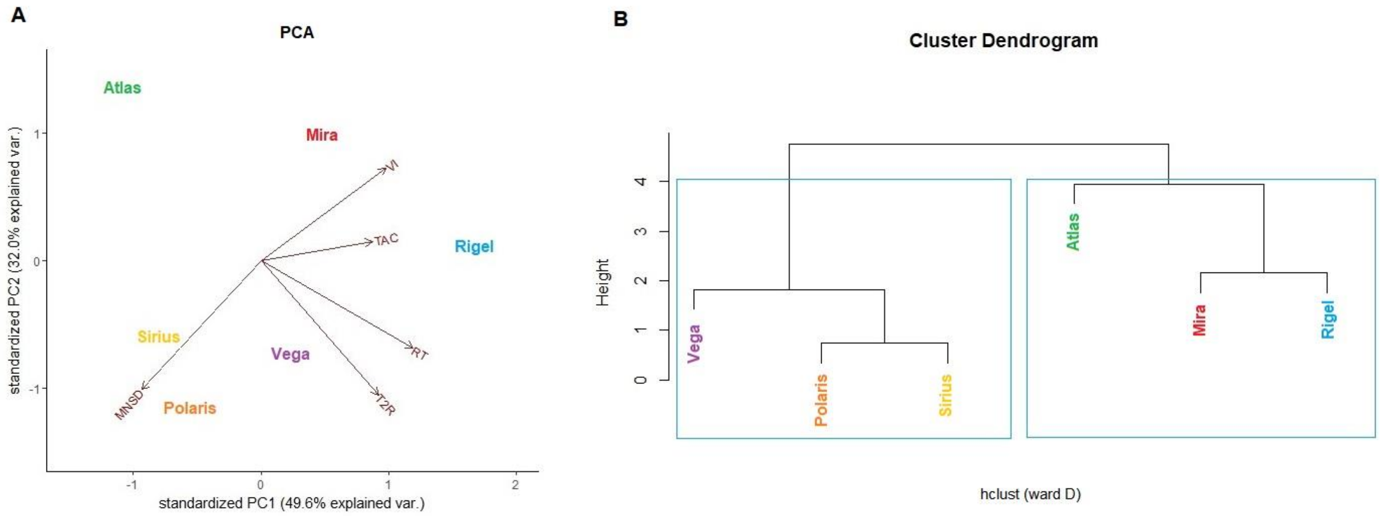

Figure 11: A) Principal Component Analysis of movement metrics separating juvenile spoonbill movements; B) Cluster dendrogram of juvenile spoonbills based in their trajectory parameters;

DISCUSSION

In this work we tried to unravel the factors constraining the distribution of spoonbills in Portugal, given the sharp increase in numbers of this species in the country, during wintering and breeding seasons. We explored three factors that can affect the ecology of this species and explain the recent expansion:

Immigration, dispersal and migratory connectivity

During winter, most re-sighted spoonbills from European countries were in the wetlands of Ria Formosa and Ria de Alvor, Southern Portugal, and in wetlands of the Tejo estuary. This confirms the importance of these areas for the maintenance of this species during winter (Farinha and Trindade 1994), and also the long recognized importance of the Tejo estuary for several waterbirds populations during winter, such as Dulin (*Calidris alpina*), Avocet (*Recurvirostra avosetta*) and Black-tailed Godwit (*Limosa limosa*) (Moreira 1997, Alves et al. 2010, Catry et al. 2011, Alves et al. 2012). Other areas include Paúl do Taipal, Paúl do Boquilobo and Beja wetlands. In our work, we classified birds as being wintering if they were sighted in the period from September to March, but Lok et al. (2011) considered only December and January to avoid possible stopover localizations. If we considered only these two months, spoonbills from Spain and Denmark would have no wintering re-sightings in Portugal (Table A4). This indicates that spoonbills from Spain may not winter in Portugal but only perform post-fledging and post-breeding dispersal, which is expected given the proximity of their breeding colonies. In relation to Denmark it could be a problem of the small number of re-sightings (N=4). In any case, re-sighting data is also influence by varying effort by observers which may not be constant throughout the entire period.

Regarding juveniles, most of the re-sightings were in the same areas where wintering birds were also observed (Ria Formosa, Ria de Alvor and Tejo estuary), which reinforces the importance of these areas for spoonbills. One interesting result was that all Spanish juvenile spoonbills were seen in Ria Formosa (which, in this work, includes Castro Marim), which is in accordance with the results of Aguilera (1997), who stated that Spanish juveniles rarely disperse more than 100km northwards.

Breeding birds re-sighted in Portugal originated mainly from Spain and the Netherlands (only one French spoonbill was observed in Ria Formosa during breeding season). This supports, at least in part, the idea that Portuguese breeding colonies originated from Spanish spoonbill colonisers (Farinha and Trindade 1994, Aguilera 1997). In fact, breeding birds from other countries (hereafter immigrants) were mainly from the oldest European colonies, meaning that these colonies may be acting as source populations, and their increasing population allows the species to colonise new areas across their range, supporting the theory of metapopulation (Hanski 1998). Indeed, density dependence factors increased the levels of juvenile dispersal (natal dispersion) in a Dutch colony (Lok et al. 2013b, Oudman et al. 2017). Moreover, immigrants are proved to have an important impact in colony growth, both in spoonbills colonies (Pigniczki 2017, Tenan et al. 2017), and in colonies of other waterbird species (MartInez-Abraín et al. 2001, Trakhtenbrot et al. 2005, Santoro et al. 2016).

Migratory connectivity between European breeding populations and Portuguese wintering areas was very distinct for the different countries. Germany and France populations both showed strong migratory connectivity meaning that spoonbills wintering in Portugal and originating from these populations maintain the same relative distances during breeding and wintering periods, that is, they breed and winter close together. For spoonbills from the Netherlands the connectivity estimated for Dutch individuals wintering in Portugal was almost zero, indicating an absence of a spatial relationship between distances in breeding and wintering areas. Whereas for Spain, the migratory connectivity was negative, implying that these spoonbills winter much further apart of each other in Portugal, in relation to their proximity in the breeding colonies. Basically, the distance of these individuals between wintering areas is higher than the distances between breeding areas. For conservation issues, tough, these results could be summarized differently: Spanish and Dutch spoonbills use diverse and distant areas to winter within Portugal, whereas French and German populations maintain flock structure. These results suggest distinct levels of concern towards European populations, as Spanish and Dutch populations may, theoretically, be more resistant to stochastic events that can affect wintering populations in Portugal. This is because populations with a weak migratory connectivity occupy larger and diverse ranges of wintering areas and, therefore, are exposed to different environments and pressures, which make them less likely to decline. In contrast, strong connected populations are always facing equal pressures, and are less likely capable of adapting and resist to stochastic events that can promote the decline of populations (Webster et al. 2002, Jones et al. 2008, Gilroy et al. 2016). Even though these results are useful to estimate the connectivity between European spoonbills, they should be considered cautiously given the caveats of the method highlighted by Cohen et al. (2018). First of all, it is important to refer that this method perform better than the most recurrent method “Mantel test”, and is especially useful when dealing with incomplete data, and data with many possible source of errors, like our re-sighted data (Cohen et al. 2018). Despite of that, we used relative abundance of spoonbills in breeding areas, and we only take in consideration the colonies with re-sightings. This could not be true for the all breeding populations of the countries, because not all colonies have ringing and marking programmes and records outside Portugal are not considered. Furthermore, the transition probabilities matrixes were calculated only with information of the above-mentioned colonies and only based in our data, that is the re-sight data base of coloured ringing birds in Portugal, which should present large variation in re-sighting probabilities among sites (Perdeck 1977, Korner-Nievergelt et al. 2010, Thorup et al. 2014). Despite these problems, and according to Cohen et al. (2018) the estimations of MC method is more influenced by errors in transition probabilities that in relative abundance, so we suggest to use these results in an informative and indicative way, but not to rely in the true meaning of the numerical results.

Diet and trophic ecology analysis

The diet of spoonbill chicks in Ria Formosa was mostly constituted by crustaceans, even though fish was also a very common prey. We found no evidence of invasive prey species in the diet of spoonbills on Ria Formosa, which is in accordance with our study hypothesis that in traditional colonies spoonbills feed on native prey.

In Tejo estuary, we could only collect one regurgitation sample, that was entirely constituted of Louisiana crayfish (*Procambarus clarkii*), indicating that, at least, this invasive species is a consumed prey in this colony. In addition, all the faeces collected in Tejo (N=5), revealed red exoskeleton fragments, thus supporting the consumption of Louisiana crayfish by the spoonbills in this colony as frequent, again supporting our hypothesis of an increment of invasive species on the diet of spoonbills inhabiting recent colonies.

Contrary to other traditional European colonies, such as Odiel estuary in Spain and Dutch colonies in the Wadden Sea, where spoonbills preferred and consumed more small fish than crustaceans (Aguilera 1997, Jouta et al. 2018), in Ria Formosa spoonbills rely more on crustacean of genus *Palaemon*. This may be explained by the great availability of these shrimp species in the salt evaporation and aquaculture ponds, present in vast numbers near the colony. In fact, many other waterbird species, such as the Black Tailed Godwit and the Little Tern (*Sterna albifrons*), rely on this food source to supply their dietary requirements in several periods of the year (Rufino et al. 1984, Catry et al. 2006, Paiva et al. 2006b, Bluso-Demers et al. 2016). Nevertheless, and probably due to the small biomass and low energy content of shrimps (Paiva et al. 2006a), spoonbills in ria Formosa fed also on fish, a more profitable prey (van Wetten and Wintermans 1986, Aguilera 1997, Jouta et al. 2018). Fish from the genus *Atherinidae* and *Gobbidae* were the most consumed and these are common in Ria Formosa, both in the lagoons, and in salt evaporation ponds (Erzini et al. 2002, Catry et al. 2006, Ribeiro et al. 2008), suggesting that these prey were consumed in proportion with their availability.

The presence of Louisiana crayfish on the regurgitation and faecal samples of spoonbills chicks in the Tejo estuary, follows the recent trend in Europe of waterbirds starting to feed on the invasive Louisiana crayfish (Correia 2001, Poulin et al. 2007, Tablado et al. 2010). That we are aware of, only two studies had confirmed the ingestion of Louisiana crayfish by spoonbills, both in Southwestern Spain. The crayfish was found in 1.7% of spoonbill chick regurgitations and stomach contents in the Odiel estuary (Aguilera 1997), and in the Guadalquivir marshes spoonbills also included Louisiana crayfish on their diet (more than 40%) both during the breeding and non-breeding seasons (Tablado et al. 2010). With the information collected in the Tejo estuary, we are not able to confirm if the Louisiana crayfish is relevant to explain the establishment and expansion of this colony. Although, other waterbird species, such as the Eurasian bittern and the Grey Heron, increased their numbers in parallel with an increased consumption of Louisiana crayfish (Poulin et al. 2007, Tablado et al. 2010). This does not seem to be the case in a close relative species of the spoonbill, the glossy ibis (*Plegadis falcinellus*). In Donãna (Spain), glossy ibis feed on the Louisiana crayfish but their colonization on this area does not seem to be solely related with the increasing abundance of this invasive prey since it was not a very common prey, especially during the breeding season (Macías et al. 2004).

Even though the identification of prey remains in regurgitations and faeces is harmless and non-invasive for birds and allows direct identification of prey (Jordan 2005, Barrett et al. 2007), it has two majors disadvantages, the uncertainly of obtaining regurgitations and faeces in the field, and that prey could not represent all the diet ingested due to different digestive rates of prey (Jobling and Breiby 1986, Cottrell et al. 1996, Jordan 2005, Barrett et al. 2007). Therefore, is possible that parts of diet of spoonbill in both colonies could not be detected in this dietary analysis. With the purpose of filling these gaps, we complemented the diet study with stable isotopes analysis. This method does not permit a taxonomic identification of prey consumed (Hobson and Clark 1992), but it allows obtaining dietary information reflecting different temporal periods, depending on the isotopic turnover rates of different tissues (Hobson and Clark 1992, Hobson et al. 1994, Bearhop et al. 2002). Blood stable isotope values reflect diet in recent months (Hobson 2005), whereas in feathers, stable isotope values represent the period when feather was grown (Mizutani et al. 1990, Thompson and Furness 1995) and therefore, analysing different subsamples of the tip and the base of feather allows the discrimination of dietary changes along time (Thompson and Furness 1995, Bearhop et al. 1999, Knoff et al. 2002, El-Hacen et al. 2014).

Trophic niche of earlier and late development of chicks (assessed by sampling distinct parts of the feathers) showed no differences on both colonies suggesting a constant diet since feathers start to be developed. These results contrast with those found in Netherlands, where El-Hacen et al. (2014) reported a shift from freshwater diet to marine diet in the middle of the season, suggesting that, rather than being a species specific pattern, it is related with environmental and ecological factors driving prey availability in the vicinity of colonies. However, a difference was found between the feather base and the blood Carbon values in both colonies. Given that blood reflects the diet of the chick since birth, this result could indicate a recent shift on diet, towards more freshwater prey, that because of being so recent could not be detected between the size of feather parts that we analysed. In a future work, to answer this question the best approach should be measuring the feathers and compare it with the growth curve (like did by El-Hacen et al. (2014)) to estimate the temporal time of this changes. Nevertheless, we cannot exclude the possibility of $\delta^{13}C$ changes being caused by the use of a general discriminant factor for birds (Caut et al. 2009) between isotopic signal from different tissues and not a specific factor calculated for spoonbills, even though several authors suggest that the use of general discriminant factor improves the reliability of the stable isotopic analysis (Caut et al. 2009, Cherel et al. 2014).

Isotope analysis revealed that spoonbill chicks from both colonies fed on similar trophic level as there were no differences in $\delta^{15}N$ signatures between colonies. Similar results were found for spoonbills in Netherlands, where no differences in trophic position were detected throughout the season (El-Hacen et al. 2014). The values of $\delta^{15}N$ for chicks from Dutch colonies were overall higher than those from our study (El-Hacen et al. 2014, Jouta et al. 2018), indicating consumption of higher trophic level prey such as fish, contrasting with Portuguese spoonbills that relied more on invertebrates, which is in accordance with the regurgitation and faecal sample analyses.

On the contrary, differences in $\delta^{13}C$ signatures were evident between spoonbill colonies. The lower values of $\delta^{13}C$ in samples of spoonbills from the Tejo estuary reveals that they were feeding on freshwater prey, easily found in the surroundings of the colony in the rice-fields and other brackish habitats (e.g. reedbeds). A similar pattern likely occurs at Ria Formosa, where the higher levels of $\delta^{13}C$ indicates a more marine diet, present in the saline waters of the lagoon that surrounds the colony. Although these results were expected, it is important to highlight the apparent avoidance of salt evaporation ponds in Tejo, where the ditch shrimp (*Palaemonetes varians*) is highly abundant (one of the most common dietary items found in diet of spoonbills in Ria Formosa), as well as intertidal wetlands. This can be explained by the high availability of freshwater prey in the vicinity.

Even though in Tejo the only diet remains found were from Louisiana crayfish, the isotopic niche size of blood was significantly larger than in Ria Formosa, suggesting a more diverse diet in this colony (Bearhop et al. 2004, Newsome et al. 2007). On the other hand, the reason for this difference could be the variability of $\delta^{13}C$ values caused by salinity gradients (Fry and Sherr 1989, Peterson 1999, Fry 2002). In estuaries, the variable inputs of fresh and marine water creates gradients of salinity, whereas in Ria Formosa, at least in the core area where spoonbills breed, the freshwater impute is almost zero (Falcão et al. 1992). Yet, to further understand this, more diet samples should be analysed, together with isotopic mixing models SIAR (Inger et al. 2006, Parnell et al. 2010), using the isotopic values of prey to estimate the percentage of each prey in the diet of spoonbill chicks.

Home range, habitat use and specialization

Home range sizes calculated for juvenile spoonbills from Ria Formosa varied greatly, both for core (50% UD) and foraging/exploratory areas (95% UD), and for before (BLC) and after leaving the colony (ALC). Also, no relationship between home range size and period of tracking was found which suggest interspecific differences in the range of exploratory movements (Fig. A1). This is in accordance with the work of El-Hacen et al. (2014) on adult Mauritanian spoonbills (*Platalea leucorodia balsaci*), which also presented marked differences in home range sizes between individuals. Home range was smaller during BLC than ALC. This was expected as in the post-fledging period but BLC young spoonbills are still dependent on their parents and may return to the nest areas often. ALC foraging/exploratory home range sizes of juvenile spoonbills were considerably larger than home range calculated for adult Mauritanian spoonbills (El-Hacen et al. 2014). This difference may be attributed to their exploratory phase (Cadahía et al. 2010) and could also be due to the fact that we used dBBMM (dynamic brownian bridge movement model) and not the traditional kernels (Horne et al. 2007, Kranstauber et al. 2012). Given that traditional kernels overestimate home range sizes this could be an even more relevant difference. Core home range sizes were smaller than those of adults in Mauritania, which can be justified by differences in the method used or to reliance on food resources that are abundant in a given area where spoonbills return after exploratory trips.

Juvenile spoonbills also presented diverse patterns of movements and migratory strategies. Based, both in the NSD (net squared displacement) values and on the results of the PCA/cluster analysis, we can infer that Vega, Polaris and Sirius did migratory or dispersive movements. The difference between these two types of movements could not be detected because we would need to continue the tracking of each individual to know whether it stayed in the settled area, performing a dispersal (Börger and Fryxell 2012), or returned to the natal area after a relatively long period (i.e. migration) (Bunnefeld et al. 2011). Nevertheless, we assume that Polaris started a migration since it was recorded in Africa, a known wintering area for European spoonbill (Hancock et al. 1992, Lok et al. 2011). Atlas, Rigel and Mira showed more fidelity to a central place, even though they also made exploratory movements. We observed that, of the six spoonbills tracked, one started a migration (Polaris) and another one made a dispersion of more than 100 km

(Sirius, 195km), which could potentially be a migratory movement as is beyond the values found for spoonbills post fledging distances studied by Aguilera (1997), that rarely exceeded 100 km.

Although post-fledging dispersal may not be correlated with natal dispersal (dispersing to breed in a different area) (Kershner et al. 2004), this could indicate which individuals are more prone to disperse, especially if it is related with a bolder personality, as suggested in the literature (Fraser et al. 2001, Dingemanse et al. 2003, Cote et al. 2010). Other possible explanation for this different exploratory range of movements is that spoonbills may make exploratory post-fledging dispersal in order to collect information of possible breeding sites and of habitat quality (Doligez et al. 2002, Morales et al. 2010). It was also suggested that exploratory movements are usually performed in order to avoid competition with adults and birds in better conditions, search for food opportunities and resting/shelter sites (Kershner et al. 2004). Independent of the reason leading to such a diversity in exploratory movements and strategies, the variance on movements between juveniles of the same species is not rare (e.g. (De Grissac et al. 2016)).

In the beginning of the post-fledging period juvenile spoonbills from Ria Formosa relied mostly on salt marshes within the intertidal lagoon wetland, the habitat where the nests are located. Salt marshes provide cover and are known nursery areas for several species of fish (Pihl and Rosenberg 1982, Yáñez-Arancibia et al. 1994), that young and inexperienced juveniles may be able to catch. Gradually, juveniles began to use different habitats, including salt evaporation ponds, rice fields and inland waters. This gradual change might be caused by the variable prey availability in salt marshes, as the abundance of fish in these areas decreases in autumn and winter months, due to recruitment and emigration of the young fish (Hyndes et al. 1999, Thiel and Potter 2001, Ribeiro et al. 2006, Ribeiro et al. 2012). After leaving the salt marshes, post-fledging spoonbills explored mostly salt evaporation ponds and rice fields. Salt evaporation ponds are widely used by waterbirds, specially outside the breeding season, where food is highly abundant (Rufino et al. 1984, Warnock et al. 2002, Ackerman et al. 2009) even if of lower quality (Paiva et al. 2006a). Rice fields have been indicated as good substitute habitat for waterbirds (Fasola and Ruiz 1996, Navedo et al. 2015). Spoonbills were already reported in rice fields in the Mediterranean, but in small proportion (less than 40% of times compared with times in natural areas), and only during winter and migration periods (Longoni 2010, Toral and Figuerola 2010). The use of rice fields may indicate that juveniles are choosing sub-optimal habitats, where prey may be easier to capture and the competition with adult birds lower. On the other hand, the use of these habitats indicates that anthropogenic habitats can be used by spoonbills, as already suggested by studies in the Central Europe, where spoonbills are increasing relying on artificial habitats (Tucakov 2004, Pigniczki and Végvári 2015).

Specialization was overall low in the population, meaning that most juveniles showed a generalist behaviour and used different habitats in a similar way across the population (Bolnick et al. 2002b, Ceia and Ramos 2015). Sirius, however was the individual that presented a more specialist behaviour using a narrow proportion of the total habitat used by the population. Specialization increased from late summer to autumn, suggesting a higher exploratory behaviour in the first weeks after fledging and a progressive increase in settlement along the season. Our results are not contradictory with the idea that spoonbills are specialist birds (Swennen and Yu 2005, Pigniczki 2017) because we analysed juveniles in a post-fledging phase when birds are naturally more prone to use and explore different areas (Bolnick et al. 2002a).

Overall, we can conclude that a set of factors may be acting to promote spoonbill population expansion. First off all, immigration birds from European older core colonies, probably experiencing density dependence (Lok et al. 2013b, Oudman et al. 2017), dispersing to breed in Portugal which increase Portuguese breeding numbers. This may promote conspecific-attraction to increase the numbers of local breeders (Stamps 1988, Hénaux et al. 2007, Tenan et al. 2017). Also, the increasing numbers of spoonbills wintering in Portugal (and juveniles during post fledging dispersal) may be related with the increase in quality of Portuguese wetlands, due to higher levels of protection (Donald et al. 2007) and increase of temperature (Sutherland 1998, Klein Tank et al. 2002, Parmesan and Yohe 2003). The use of these areas may influence birds to choose where to breed there, especially if they cannot find a place in traditional colonies, either because they are overpopulated or due to competition factors (McCarthy 1997, Matthysen 2005). Secondly, new prey may be contributing to the success and increase of Portuguese breeding colonies. The fact that spoonbills from Tejo fed their chicks with Louisiana crayfish suggest that recent colonies may be relying on invasive species. Thirdly, juveniles of a traditional colony showed a large heterogeneity of movements and strategies that may be useful to cope with density dependence factors and with environmental and habitat changes. Also, these different exploratory movements may indicate differences in the future propensity to natal dispersing (Fraser et al. 2001, Dingemanse et al. 2003, Cote et al. 2010). The selection of anthropogenic habitats by juvenile spoonbills also imply the capacity of these habitats to supply the necessities of such specialized waterbirds.

Conclusion and conservation considerations

Our work contributed to the mostly unknown ecology of spoonbills in Portugal providing new insights in their feeding and trophic ecology and spatial movements. We could also identify important Portuguese wetlands for European spoonbills during the wintering and breeding seasons. Some important facts should be taken from this work: 1) the need to protect and preserve anthropogenic habitats, such rice fields and salt evaporation ponds, that are fundamental during some life phases of spoonbills, including the post-fledging phase, when mortality is higher (Lok et al. 2011, Lok et al. 2013b); 2) These habitats play a role as substitute habitats and could became even more important owing to increasing levels of natural habitat destruction and climate change (that may decrease the availability of natural wetlands); 3) It is important to identify and conserve the wintering areas of European spoonbills: As the number of spoonbills selecting Portugal to spend the winter increases, there is a need to preserve those wintering areas since their quality may have consequences in the fitness of spoonbills in the breeding season via carry-over effects (Myers 1981, Marra et al. 1998, Alves et al. 2013, Flack et al. 2016). In general, this work highlights the importance of considering and studying populations as a whole across their range, recolonizations events may happen when the populations increase and with a larger variability of suitable areas, populations are more resilient and more likely to respond to stochastic and anthropogenic events, taking refuge in safe areas. Moreover, it is fundamental to study the suitability of anthropogenic habitats for birds to, at least, manage them in a way that can favours both human and wild life populations.

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Appendix

Table A1: Population trends of European waterbirds (adapted from Wetlands International (2016)): Inc (Increase), STA (Stable), DEC (Decrease); Poor (Some international monitoring in either breeding or wintering periods although inadequate in quality or scope. Trends assumed through partial information); Reasonable (International monitoring in either breeding or non-breeding/wintering periods that is adequate in quality or scope to track direction of population changes); Good (International monitoring in either breeding or non-breeding/wintering periods that is adequate in quality or scope to track direction of population changes with defined statistical precision);

Specie	**Population**	**Trend**	**Trend Quality**	**Start and End Year**
Ardea cinerea	cinerea, Northern & Western Europe	INC	Reasonable	1997-2007
	cinerea, Central & Eastern Europe	INC	Poor	1995-2005
Ardea alba	alba, W, C & SE Europe/Black Sea & Mediterranean	INC	Reasonable	1996-2006
Ardea purpurea	purpurea, West Europe & West Mediterranean/West Africa	INC	Reasonable	1990-2008
Bubulcus ibis	ibis, South-west Europe	INC	Poor	1995-2005
Ardeola ralloides	ralloides, SW Europe, NW Africa (bre)	INC	Poor	1995-2005
	ralloides, C & E Europe, Black Sea & E Mediterranean (bre)	DEC	Poor	1995-2005
Egretta garzetta	garzetta, Western Europe, NW Africa	INC	Good	1997-2007
	garzetta, Central & E Europe, Black Sea, E Mediterranean	STA	Poor	1988-1998
Nycticorax nycticorax	nycticorax, W Europe, NW Africa (bre)	INC	Poor	1990-2000
	nycticorax, C & E Europe/Black Sea & E Mediterranean (bre)	INC	Poor	1990-2000
Botaurus stellaris	stellaris, W Europe, NW Africa (bre)	DEC	Reasonable	1995-2005
	stellaris, C & E Europe, Black Sea & E Mediterranean (bre)	DEC	Poor	1995-2005
Ixobrychus minutus	minutus, W Europe, NW Africa/Sub-Saharan Africa	STA	Poor	1995-2005
	minutus, C & E Europe, Black Sea & E Mediterranean/Sub-Saharan Africa	DEC	Poor	1995-2005
Ciconia ciconia	ciconia, W Europe & North-west Africa/Sub-Saharan Africa	INC	Reasonable	1985-1995
	ciconia, Central & Eastern Europe/Sub-Saharan Africa	INC	Reasonable	1985-1995
Platalea leucorodia	leucorodia, West Europe/West Mediterranean & West Africa	INC	Reasonable	1996-2006
	leucorodia, C & SE Europe/Mediterranean & Tropical Africa	DEC	Reasonable	1996-2006
Phoenicopterus roseus	West Mediterranean	INC	Reasonable	1994-2004
	East Mediterranean	STA	Poor	1995-2005

Table A2: Models fitted to the use of intertidal wetlands along weeks ALC. AIC (Akaike information criteria), R^2 (Multiple R-squared).

Model	AIC	R^2	p value	equation
lm(formula = y ~ x)	62.1	0.32	7.24E-14	Y=-0.219X+0.621
lm(formula = y ~ I(x^2) + x)	55.8	0.357	1.32E-14	$Y=0.000819X^2-0.0487X+0.768$
lm(formula = y ~ log(x))	47.2	0.384	<2e-16	Y=-0.251ln(X)+0.904
nlm(formula: y = a*exp(b*x) + c)	51.4	0.375	1.01E-25	Y=0.874exp(0.127X)+0.0657

Table A3: Movement metrics results for each Spoonbill. Median Return Time (RT), Maximum Net Squared Displacement (MNSD), Median Monthly Volume of Intersection of home ranges (VI), Median Turn angle correlation (TAC) and Median Time to Return (TtoR).

Platalea	RT	MNSD	VI	TAC	TtoR
Mira	49.45	1.37E+08	0.35	0.60	102.77
Polaris	61.87	6.27E+11	0.14	0.59	162.70
Atlas	25.41	8.63E+08	0.26	0.58	55.81
Rigel	147.18	25789006	0.47	0.60	204.32
Sirius	44.31	3.84E+10	0.06	0.60	118.81
Vega	107.00	8.03E+09	0.27	0.58	185.76

Table A4: Monthly numbers of re-sights of Spoonbill from European populations.

	January	February	March	April	May	June	July	August	September	October	November	December
Germany	6	1	1	0	0	0	1	0	1	6	1	2
Denmark	0	0	0	1	0	0	0	0	0	3	0	0
Spain	0	2	3	3	14	7	3	15	8	2	1	0
France	2	0	0	2	1	0	0	1	3	1	0	3
Belgium	0	0	0	0	0	0	0	0	1	0	0	0
Netherlands	18	22	17	7	17	0	1	3	17	30	21	31
Total	26	25	21	13	32	7	5	19	30	42	23	36