

Research Article

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Habitat selection and ontogeny of habitat use by juvenile Eurasian Spoonbill *Platalea leucorodia* revealed by GPS tracking

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Summary

Despite the widely recognized value of wetlands in providing vital ecosystem services, these are presently being degraded and ultimately destroyed, leading to a decrease in the biodiversity associated with these areas. Some species inextricably linked to wetlands, however, have been increasing and (re)colonizing areas across their range; a notable example being the Eurasian Spoonbill *Platalea leucorodia*. In this study we aimed to identify the most important habitats for juvenile spoonbills fledging from a traditional colony in Portugal, located in Ria Formosa, during the period of their life with the lowest survival rates: the first months after leaving the colony. We deployed 16 GPS/GSM tags on juveniles captured in different years (2016 to 2020) and tracked them during post-fledging dispersal and first winter (average 166.4 ± 29.2 SE days). Using Corine Land Cover data, we were able to identify which habitats were most important. Several habitats were used in variable proportions by individuals originating from the same colony, but there was a general trend towards using fewer habitats along the first months of life. Intertidal wetlands were the most used habitat, but anthropogenic habitats such as Wastewater Treatment Plants, saltpans and rice fields were identified as alternative habitats for young spoonbills, and may have contributed to the recent expansion of this species in Portugal.

Introduction

Wetlands are highly productive natural systems (Tiner 1989, Keddy 2010) that provide multiple ecosystem services such as climate regulation, nutrient cycling, and provisioning of food and freshwater (M.E.A. 2005, Nellemann and Corcoran 2010). However, some studies estimate that at least 50% of the world's wetlands have been destroyed (M.E.A. 2005, Davidson 2014), with Europe presenting the highest value: 75% of all wetlands disappeared over the last 100 years (Owen 2007). The main reason for such destruction is the conversion of wetlands into agricultural and industrial areas, but also water drainage, and indirect pollution from agricultural, industrial and urban effluents (Van Asselen *et al.* 2013, Dodman *et al.* 2018). Due to wetland degradation, many waterbird species declined and changed their distribution range (Luthin 1987, Boere *et al.* 2006, Okes *et al.* 2008). However, since the 1980s some of these species began to recover, showing positive population trends and recolonizing areas within their distribution range, despite only marginal restoration of wetlands (Wetlands International 2016). European wetlands received more protection in recent decades owing to the Water Framework Directive (2000/60/EC). Several waterbirds, however, began to recover long before the implementation of this directive, which suggests alternative causes for population recovery.

Understanding the habitat requirements of these species is fundamental for their conservation, particularly in critical phases of their lives, in order to establish sound management plans. Altricial birds that are fed by parents after hatching, experience the highest mortality following independence (Sullivan 1989, Daunt *et al.* 2007, Lok *et al.* 2013b). And one of the main factors for this high mortality during the first months after independence is low foraging efficiency and consequent starvation, either by inefficient searching and/or handling proficiency, competition with adults, or low ability to locate suitable feeding patches (Wunderle 1991, Kershner *et al.* 2004, Daunt *et al.* 2007). Juveniles often show a different spatial and temporal ecology from adults

(Goss-Custard *et al.* 1982, Wunderle 1991, Kershner *et al.* 2004), either by displaying preferences towards different habitats (Fayet *et al.* 2015), exploring wider areas (Zango *et al.* 2020) or by foraging for longer periods (Daunt *et al.* 2007). It is therefore important to better understand habitat use during this critical phase to better inform the conservation of waterbird species during such key life stage.

The population of Eurasian Spoonbill *Platalea leucorodia*, like other migratory waterbird species, decreased drastically in Europe in the early 20th century, and by 1950 only two breeding colonies were still active: one in Spain and other in the Netherlands (Triplet *et al.* 2008). After intense recovery programmes, the East Atlantic population (that breeds along the East Atlantic European coast and winters from France to coastal West Africa, as south as Senegal) is currently increasing (Overdijk 2013, Champagnon *et al.* 2019), and the species is now classified as 'Least Concern' (LC) in the European Red List (BirdLife International 2015). The (re)colonization of breeding areas is currently ongoing in Europe and, in most cases, this occurred following habitat conversion or restoration at traditional breeding locations (Tucakov 2004, Marion 2013, Ramo *et al.* 2013). In Portugal, despite the existence of few historical breeding records from the 17th century (Tait 1924), the species was classified as a non-breeder until 1988, when the first successful breeding event was registered in Paúl do Boquilobo (Pereira 1989). Since then, the breeding population of spoonbills increased from 43 pairs in 1996 (Farinha and Encarnação 1996, Equipa Atlas 2008) to 540 in 2014 (Farinha and Trindade 1994, Farinha and Encarnação 1996, Equipa Atlas 2008, Encarnação 2014) and expanded northwards. The number of breeding colonies also increased to 10, as recently as 2014 (Encarnação 2014), when the newest colony in the country was established.

Juvenile spoonbills fledge between 35 and 54 days (Cramp and Simmons 1977, Triplet *et al.* 2008), and during the post-fledging period perform exploratory movements in the vicinity of the colony, that can reach distances of more than 100 km (Hancock *et al.* 1992, Aguilera 1997, Volponi *et al.* 2008, Jelena *et al.* 2012). Following this period, juveniles either migrate to southern wintering areas or remain in the vicinity of the colony, particularly birds originating from southern Europe (Bauchau *et al.* 1998, Triplet *et al.* 2008, Volponi *et al.* 2008, Lok *et al.* 2013a). To understand the habitat requirements of juvenile spoonbills during a key phase of their life, (after leaving the breeding colony), we attached GPS/GSM tags to pre-fledglings from a Portuguese colony (Ria Formosa, Algarve) and tracked their movements and ontogeny of habitat use up to their first year of life. Our specific objective was to identify the most important habitats for juvenile spoonbills during their dispersal phase from the natal colony. This information is essential for the development of conservation strategies that may benefit this and other waterbird species with similar ecological requirements.

Methods

Fieldwork was carried out in the Ria Formosa Natural Park (36° 59'N, 7°55'W), a lagoon system separated from the Atlantic Ocean by a system of small islands and sandbanks composed by several habitats such as marshes, fresh and brackish lagoons, salt pans, dune banks and agricultural fields (Figure 1). The Ria Formosa Natural Park was established in 1987, later becoming a Special Protection Areas (SPA) for birds under the European Bird Directive (2009/147/EC), being thus part of Natura 2000 Network, and is also a Ramsar site since 1981. Even though Ria Formosa has historically been an important area for spoonbills, both as wintering

and as a stopover site, the species only started breeding locally in 1993, in a small marsh island within the lagoon (Farinha and Trindade 1994). This spoonbill breeding colony has its limits established by the water line around the island at low tide and during the study period the number of nests fluctuated between 66 and 116 (in 2018 and 2020, respectively; J. Silvério pers. comm.).

From 2016 to 2020 we captured 16 pre-fledglings (two in 2016, five in 2017, four in 2018, two in 2019 and three in 2020; Table 1) from the nests by hand (making sure such procedure was harmless to the bird) and tagged them with solar-powered GPS/accelerometer GSM tags (Movetech Telemetry, www.movetech-telemetry.com) attached using a backpack harness made of Teflon ribbon. We recorded biometric measurements (tarsus and head/bill length) to back-calculate hatch date based on Lok *et al.* (2014). Chicks were measured and selected for tagging based on their development stage (35 ± 2 SE days). The weight of the tags, harness and rings was 33 g, thus below the 3% threshold of the body mass of the tagged spoonbills (mean body mass $1,524 \pm 217.53$ g; $n = 16$) to avoid adverse effects (Phillips *et al.* 2003, Casper 2009). Tracked spoonbills were named instead of simply using a code (Table 1). Tags recorded a burst of 10 seconds of GPS fix (with an associated error of ≤ 3 m) and 3D accelerometer data at 1 Hz every 30 minutes. We kept only one GPS point per burst and removed GPS locations that used less than four satellites for geopositioning to avoid uncertainty. Accelerometer data were used to determine probable mortality events when inactivity was recorded, and to confirm flying fixes as indicated by the GPS metadata, that were removed from the present analysis. During most of the nocturnal period (between 21h00 and 05h00) only one GPS fix was collected at 01h00 to save battery. QGIS, version 3.10, combined with R software (R Core Team 2019), version 3.6, were used to perform all the spatial data analysis and visualization of geographical data.

Habitat selection and usage

All analyses of habitat use start when juvenile spoonbills left the colony for the last time, i.e. when no subsequent returns to the colony where recorded. We defined this period as After Leaving the Colony (ALC). The last position of each spoonbill considered for analysis was the last location of the bird (when it either died or the tag failed) or the last location in Europe (if the bird migrated to Africa), until the maximum period of one year since chick hatching.

To study habitat usage by juvenile spoonbills we used Corine Land Cover 2018 (CLC), with data accessible from Copernicus Land Cover monitoring services (Bossard *et al.* 2000). The CLC map was complemented with satellite images (Google 2020) to reclassify incorrectly classified points due to cell size. CLC identifies 44 land use types and those present in the study area were grouped into higher levels of organization resulting in six final habitat categories (Table 2). We excluded from the analysis a few fixes that occurred in urban areas ($n = 32$; 0.06%), considering those to be an error in GPS localization.

To assess how the use of different habitats varied for each individual ALC we quantified the weekly frequency of usage of each habitat by dividing the number of locations in a given habitat in a week, by the total number of locations in that week. Because juveniles in their first year are likely to be exploratory, we did a revisitation analysis to identify the most important habitats for juvenile spoonbills, using the package 'Recurves' in R (Bracis *et al.* 2018). This package allows calculation of the number of times the trajectory of an individual enters a circular area centred in each position of the trajectory, that is, how many times one individual

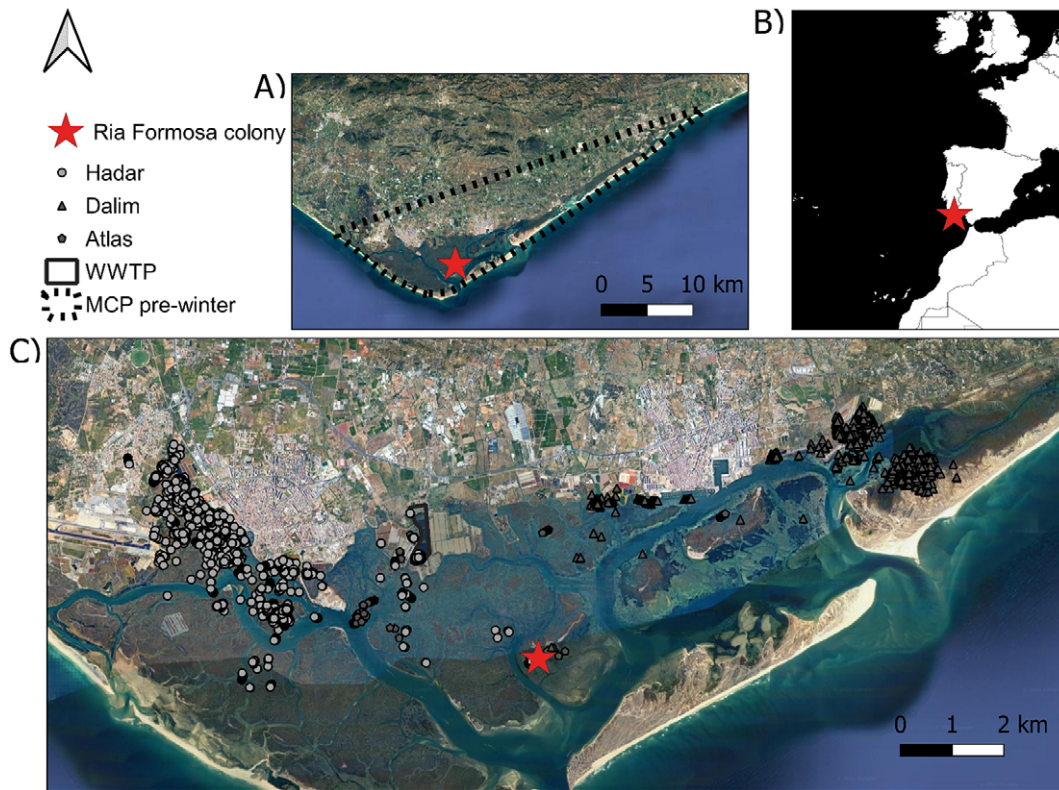


Figure 1. A) and B) Location of Ria Formosa colony in Portugal (star) and representation of the Minimum convex polygon (MCP – dashed black line) considering all locations attained from juvenile spoonbills in the vicinity of Ria Formosa during pre-winter (see text for details); C) Locations of three selected juvenile spoonbills tracked with GPS/GSM tags in Ria Formosa during pre-winter, and the location of the wastewater treatment plant (WWTP) most used by spoonbills.

revisits the same location. As we did not know which habitats were revisited the most, nor the activities performed in those areas by spoonbills, we did not have any *a priori* consideration of the size of the radii to use in order to define the area around locations. Hence, we did a preliminary analysis of radius size, testing radii ranging from 10 m to 1,000 m through a sensitivity analysis (see Appendix S1 in the online supplementary material) and established that 100 m was appropriate, as higher values did not produce different results. We defined a minimum threshold of 60 minutes (between two consecutive locations) to ensure that revisitations were independent (if the individual left the defined radius but returned within 60 minutes, for example during a bout of foraging movements, it was not considered a new revisitation, but as part of the prior visit). We selected the locations that had a ratio of relocations in the 75th percentile of total relocations of each individual, as an indication that those were chosen as suitable to feed or rest (Bracis *et al.* 2018) rather than only exploratory.

To evaluate if the most revisited habitats changed during the first year of life, we divided the study period into two, following the delimitation of yearly periods suggested for spoonbills from the nearest breeding colony in Odiel, Spain (Aguilera 1997): a) “pre-winter”, defined as the period between ALC and 30 September, encompassing the more exploratory phase of juveniles, when large migratory movements are more likely to occur; and b) “winter”, from 1 October to 31 January. As we collected virtually no information from nine spoonbills (Nembus, Polaris, Dalim, Ascella, Mizar, Azha, Australis, Tabit and Enif) in winter in Europe, these individuals were excluded from the analysis for this second period.

In order to assess if habitats in Ria Formosa were used in accordance with their availability, we performed a second order

selection of habitat (Johnson 1980). We estimated the availability of each habitat type comprised in the minimum convex polygon (MCP) of the positions of all spoonbills during “pre-winter”, when the majority of spoonbills remained in Ria Formosa, close to the breeding colony (excluding the positions of Polaris, Sirius Mizar, and Azha after they left the vicinity of Ria Formosa). We used the package ‘phuassess’ (Fattorini *et al.* 2017) in R, to test the probability of the null hypothesis being true, that is, habitats were used in the same proportion of their availability, thus being neither preferred or avoided (Aebischer *et al.* 1993, Fattorini *et al.* 2014).

Results

GPS/GSM tags recorded on average 166.4 ± 29.2 SE days of tracking, with the maximum period corresponding to 16 months, and the minimum to 55 days, in cases when the bird died or the tag failed (Table 1). Spoonbills left the colony for the first time on average at 50.6 ± 1.8 SE days of life, and their final visit to the colony occurred at the age of 67.6 ± 3.98 SE days (Table 1). Of all the spoonbills tracked, five migrated to North Africa: Polaris, Ascella, Sirius (only in its second winter), Australis and Tabit, while the remaining birds stayed in Iberia. Seven spoonbills died during the tracking period. Survival in early winter varied between 0.31 and 0.62 until December (considering tag failure as either death or alive), and in late winter varied between 0.8 and 1 until March (with only one tag failure during the coldest months of the year). Mortality was identified by multiple overlapping GPS fixes in the same location, and confirmed by the 3D accelerometer showing static readings. Based on the accelerometer data we were able to determine date, and approximate hour of death. Because the

Table 1. Tracking details of juvenile spoonbills from Ria Formosa equipped with GPS/GSM tags.

Name	Year	Date of GPS/GSM attachment	First GPS record date	Last GPS record date	Days of data recording	Weight when equipped (g)	First date out of colony	Last date on colony	Age at last date on colony (days)	Fate
Mira	2016	14/06/2016	21/06/2016	07/02/2017	232	1780	28/06/2016	02/07/2016	59	Unknown (tag failure)
Nimbus	2016	14/06/2016	20/06/2016	13/08/2016	55	1570	28/06/2016	09/07/2016	70	Unknown (tag failure)
Polaris	2017	23/06/2017	23/06/2017	12/10/2017	112	1550	05/07/2017	26/07/2017	67	Dead
Atlas	2017	23/06/2017	23/06/2017	05/11/2017	136	950	23/07/2017	18/08/2017	72	Dead
Rigel	2017	23/06/2017	23/06/2017	01/12/2017	162	1750	16/07/2017	17/07/2017	55	Dead
Sirius	2017	23/06/2017	23/06/2017	18/10/2018	483	1530	11/07/2017	02/08/2017	81	Unknown (tag failure)
Vega	2017	23/06/2017	23/06/2017	09/04/2018	291	1350	05/07/2017	24/07/2017	61	Unknown (tag failure)
Dalim	2018	11/07/2018	11/07/2018	24/09/2018	76	1640	02/08/2018	08/08/2018	61	Dead
Castor	2018	11/07/2018	11/07/2018	04/04/2019	268	1360	26/07/2018	01/08/2018	46	Dead
Hadar	2018	11/07/2018	11/07/2018	21/05/2019	315	1400	23/07/2018	28/07/2018	50	Unknown (tag failure)
Ascella	2018	11/07/2018	11/07/2018	02/10/2018	84	1360	26/07/2018	04/08/2018	53	Unknown (tag failure)
Mizar	2019	26/06/2019	26/06/2019	31/08/2019	67	1970	10/07/2019	12/08/2019	81	Dead
Azha	2019	26/06/2019	26/06/2019	01/09/2019	68	1700	05/07/2019	14/08/2019	83	Dead
Australis	2020	09/06/2020	09/06/2020	07/09/2020	90	1425	24/06/2020	01/07/2020	60	Unknown (tag failure)
Tabit	2020	09/06/2020	09/06/2020	03/11/2020	147	1600	21/06/2020	01/07/2020	73	Unknown (tag failure)
Enif	2020	09/06/2020	09/06/2020	23/08/2020	76	1422	20/06/2020	13/08/2020	110	Unknown (tag failure)

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
Saltpans	—
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	—

analysis only started when spoonbills left the colony (ALC) and ended when either the juvenile died, migrated to Africa, or completed one year of life, the number of days considered for analysis is smaller than the total tracking period (on average: 120.3 days \pm 25.83 SE, ranging from 10 to 297 days). Enif was thus excluded from the subsequent analysis as only 10 days of data were recorded after it left the colony (ALC). Each tag collected on average 23.23 ± 0.51 SE points per day, from which 20.88 ± 0.51 SE were collected during the day and 7.38 ± 0.42 SE during the night.

Habitat selection and usage

Juvenile spoonbills selected a broad range of habitats, with large variation between weeks (Figure 3). The most revisited habitats were intertidal wetlands (30.7%) followed by rice fields (27.5%) and saltpans (18.4%; Table 3a). However, when considering only the pre-winter period, Wastewater treatment plant (WWTP) was the most revisited habitat (35.9%), despite accounting for only 0.2% of the habitats present in the vicinity of colony within the area comprised by the MCP. This was followed by saltpans (26.9%), present in 5.8%, and by intertidal wetlands (24.2%), one of the most common habitats in the area (36.0%). Agricultural areas are the most available habitat, and rice fields and inland waters were absent of the 242.4 km² (MCP) around the colony.

Overall, available habitats were thus not used in accordance with their availability (Table 3b). Intertidal wetlands ($P = 0.27$) and saltpans ($P = 0.09$) were used in proportion to their availability, whereas agricultural and other habitats (mostly urban areas) were avoided (both $P < 0.01$). WWTP was the only preferred habitat ($P < 0.01$). During winter, intertidal areas were the most important habitat (33.4%), followed by saltpans (27.8%) and rice fields (25.9%). In total, anthropogenic habitats available in the vicinity of the colony accounted for 64.0% of the area comprised within the

MCP, whereas this was only 36.0% for natural habitats. Anthropogenic areas (created and/or manipulated by humans, including saltpans, WWTP, rice fields and other agricultural areas), were used more than natural areas (56.9% vs 43.1%). In addition, during pre-winter, this difference was even larger, as 63.0% of the revisited habitats are classified as anthropogenic.

When considering annual tendencies (Figure 3), saltpans were used more in the first years of the study period (annual percentage in chronological order: 37.7%, 25.5%, 20.9%, 1.2%, 4.2%) and intertidal wetlands in the most recent years (annual percentage in chronological order: 42.1%, 25.9%, 66.0%, 56.4%, 83.5%). WWTP were used in all years but only until November whereas rice fields started to be used only in October.

Individual habitat usage fluctuated considerably during the first weeks following ALC (Figure 2). For individuals tracked more than 20 weeks, it appears that between week 12 (Castor) and 20 (Mira) two habitats became clearly dominant, with their usage being mirrored, and all other habitats becoming considerably reduced (Figure 2). This pattern was also apparent for some individuals from a much earlier stage (e.g. Atlas, Rigel and Hadar, from week 2).

Discussion

Habitat selection and usage

Juvenile spoonbills born in Ria Formosa rely not only on intertidal habitats but also on anthropogenic habitats, such as saltpans, rice fields and Wastewater treatment plants. The importance of intertidal wetlands, a category that encompasses several natural habitats (Table 2), was to be expected since it is well known that spoonbills use these for obtaining food. For example, in the Wadden Sea, spoonbills mainly feed their chicks with marine prey instead of freshwater prey (Jouta *et al.* 2018). Also in the German Wadden Sea, both adults and juveniles selected tidal creeks for foraging during breeding and post-breeding (Enners *et al.* 2020). In our study, we did not differentiate habitat usage by behaviour, and this may explain the utilization of a larger array of habitat types that fulfil other requirements, like roosting. Alternatively, the use of different habitats may be a function of their availability since anthropogenic habitats were very common in the study area (Table 3). Nevertheless, such habitats appeared to be a good substitute for natural ones, considering the survival found in our study, which did not differ substantially from the results from a well-studied population (early winter: 0.31–0.62 vs 0.33 \pm 0.03 CI and late winter: 0.8–1 vs 0.58 \pm 0.05 CI; Lok *et al.* 2013b). It should be noted that there are two WWTPs (the only preferred habitat) in the area: Faro-Olhão (the most used by spoonbills in this study) and Olhão-Poente; both with maturation ponds that are extensively used by several species of waterbirds all the year around (Matos *et al.* 2018, Rias 2019). This is a known alternative habitat for waterbirds, including spoonbills (Frederick and McGehee 1994, van Dijk and Bakker 1998, Newman and Lindsey 2011) that may be attracted by the constant water levels. Nonetheless, juveniles using these areas may be more exposed to pathogens and toxins such as those causing botulism outbreaks (Hamilton 2007, Murray and Hamilton 2010), not only due to the presence of these substances in the water but also because of the usual large congregation of birds in these sites that facilitates the propagation of diseases (Anza *et al.* 2014). Interestingly, this habitat was not used in winter which leads to the question of why this apparently suboptimal habitat was used by juveniles in pre-winter. It is possible that continued water availability in WWTP explains this since its usage

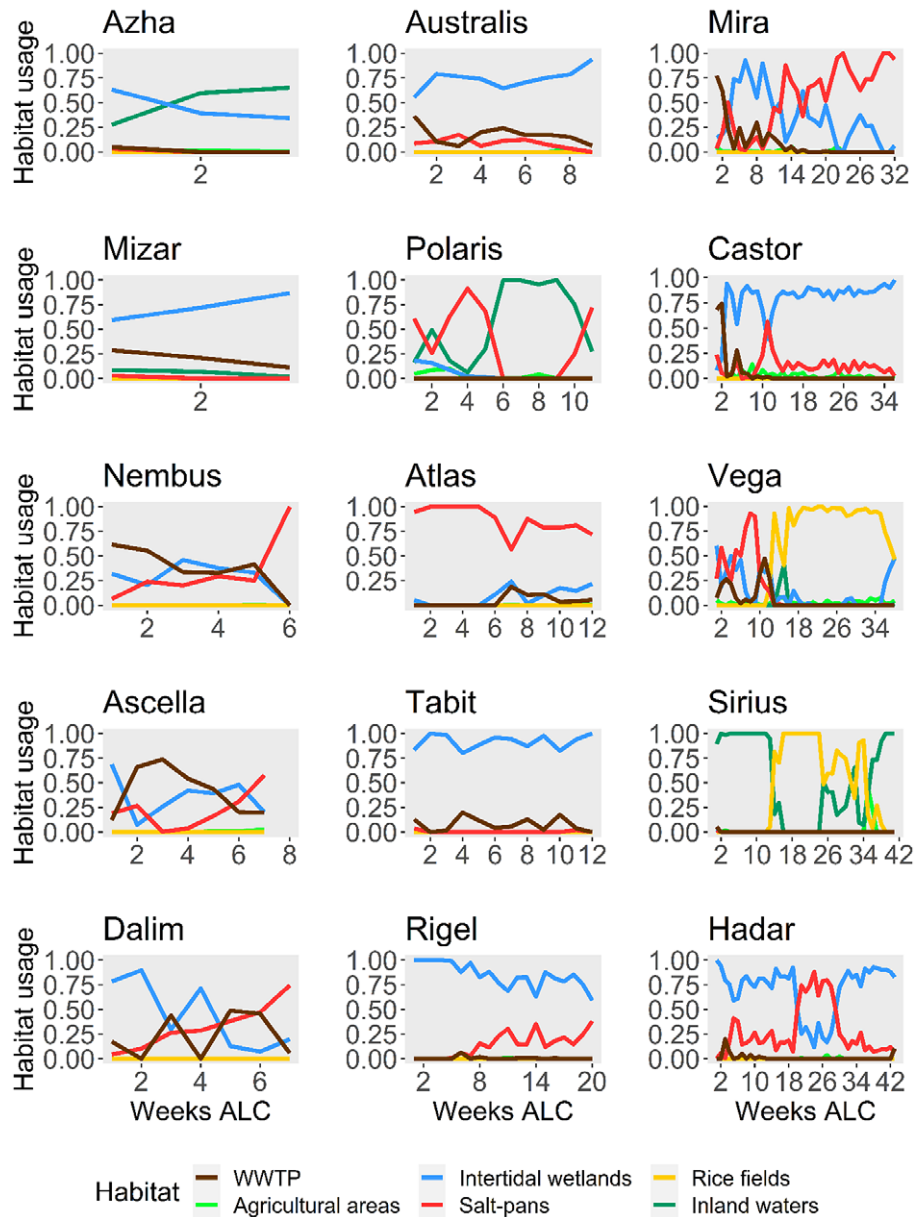


Figure 2. Frequency of habitat usage by tracked spoonbill juveniles from Ria Formosa per week, starting after leaving the colony (ALC) for the last time.

Table 3. Habitat use by juvenile spoonbills from a colony in Ria Formosa, Portugal: a) Percentage of juvenile spoonbills revisitation of each habitat type for the study periods (see text for details). Only locations with a ratio of relocations in the 75th percentile of total relocations of each individual were considered. b) Result of the second order habitat selection proposed by Fattorini *et al.* (2014). Habitat type availability in Ria Formosa (restricted to the minimum convex polygon, see text for details) by juvenile spoonbills.

	WWTP	Agricultural areas	Rice fields	Intertidal wetlands	Salt-pans	Inland wetlands	Others
a)							
Pre-winter	35.9	0.1	0.00	24.2	26.9	12.8	0.0
Winter	0.00	0.2	25.9	33.4	27.8	12.8	0.0
Entire study	10.9	0.1	27.5	30.7	18.4	12.3	0.0
b)							
Available	0.2	48.6	n.a.	36.0	5.8	n.a.	9.3
Outcome	preferred	avoided	n.a.	proportionally used	proportionally used	n.a.	avoided
P value	<0.01	<0.01	n.a.	0.27	0.09	n.a.	<0.01

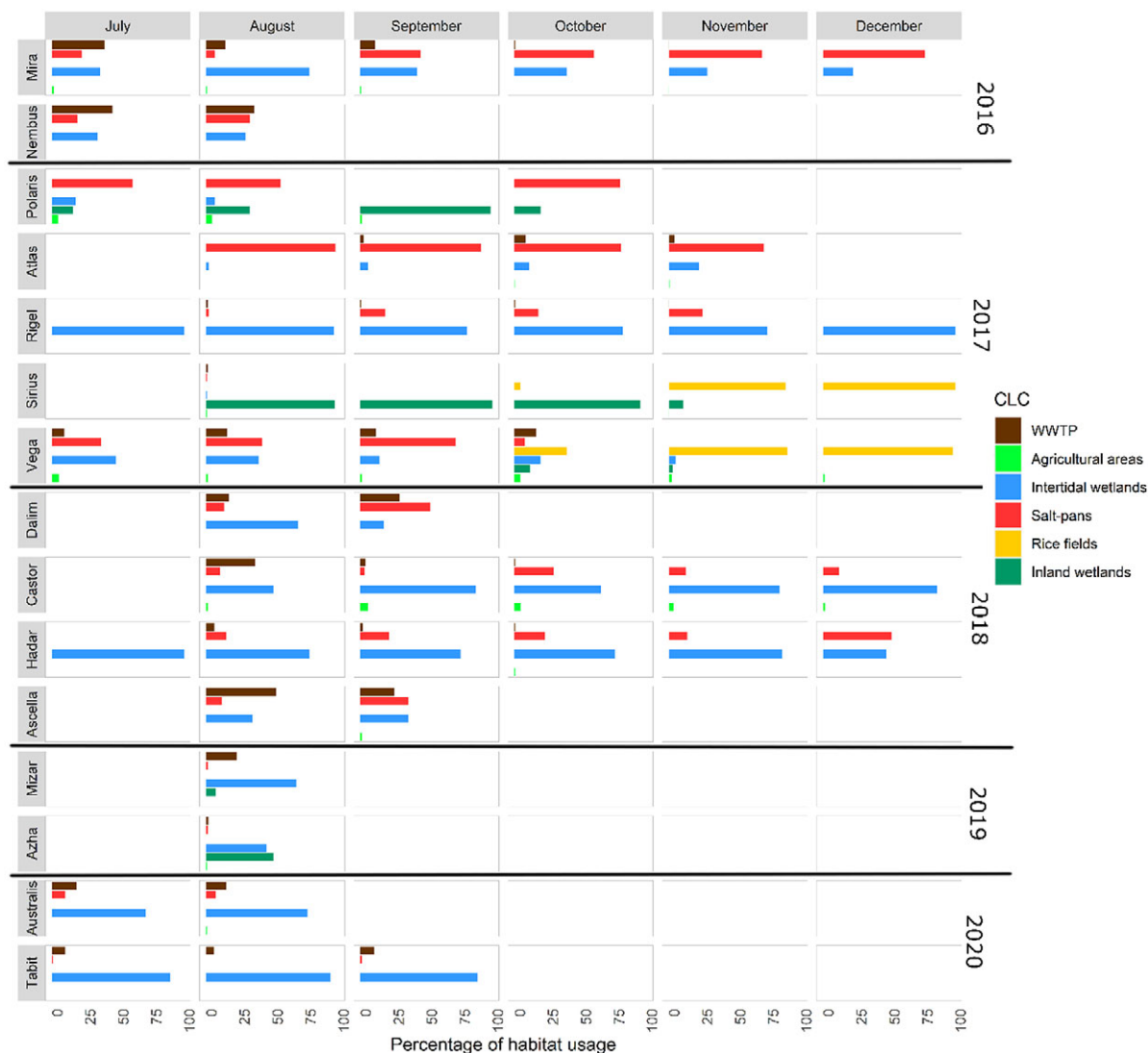


Figure 3. Percentage of habitat usage of each spoonbill in each month. Years are referenced to aid comparisons.

coincides with the driest season, when water levels are lowest in more natural habitats, or it may be related to density-dependence factors. The period when WWTP was most used (pre-winter) coincided with the period of highest abundance of spoonbills in the south of Portugal (Alves *et al.* 2012), potentially also reflecting the lower capacity of juveniles to compete for the most favourable natural habitats (Goss-Custard *et al.* 1982, Cresswell 1994, Durell 2000).

Salt-pans were often revisited in pre-winter, but also in winter, and are a common habitat in Ria Formosa. These habitats may be suitable for juveniles since they also have managed water levels, with some being used to produce salt and others converted to aquaculture. In fact, salt-pans replaced coastal wetlands in many areas throughout the world, and constitute an important habitat for many waterbird species (Rufino *et al.* 1984, Velasquez 1992, Warnock *et al.* 2002), including spoonbills (Aguilera *et al.* 1996, Fonseca *et al.* 2004, Pigniczki and Végvári 2015).

Rice fields were only used in winter, and even though this was one of the most revisited habitats, it was only used by two individuals, Vega and Sirius, which dispersed beyond Ria Formosa lagoon system, where rice fields are absent. Vega dispersed to the west of Ria

Formosa and Sirius to Spain. During pre-winter they were not used, likely due to the hot and dry autumn in the Iberia peninsula which often leaves rice paddies totally dry in autumn and completely dependent on precipitation patterns. Rice fields have been widely identified as substitute foraging habitat for waterbirds (Fasola and Ruiz 1996, Czech and Parsons 2002), mostly when flooded, which in the Iberian peninsula occurs especially during winter and migratory periods (Elphick 2000, Alves *et al.* 2010, Toral and Figuerola 2010). Despite rice fields being an alternative habitat for waterbirds, usually most species prefer natural areas when available (Campos and Lekuona 2001, Tourenq *et al.* 2001). However, the fact that rice fields had a lot of revisitations only by two individuals, and was the main habitat revisited by Vega, may indicate that it can also be a good substitute habitat for juvenile spoonbills, at least in winter.

Ontogeny of habitat use

In the first weeks after leaving the colony, the proportion in which each habitat was used varied among weeks and individuals. Still, considering over 20 weeks of tracking, a clear pattern of habitat selection emerges, showing a tendency towards each individual

using only two habitat types. The decrease in the number of different habitats used during the weeks after leaving the colony may result from the start of a more specialized phase and the end of the most exploratory phase of the juvenile spoonbills, which occurs at the beginning of the post-fledging period. Alternatively, the use of a higher number of habitats in the initial months may be the result of higher competition with adults at the beginning of the post-fledging period, when more northerly breeders arrive in the area to spend the non-breeding season or to refuel on their way to Africa, potentially leading juveniles to spread over several habitats (Goss-Custard *et al.* 1982, Wunderle 1991, Cresswell 1994). Juvenile spoonbills' patterns of habitat use were very diverse across the entire study period but also within each study year. The fact that some juveniles were able to use habitats less used by others may suggest competition avoidance (Bolnick *et al.* 2003, Araújo *et al.* 2011). On the other hand, given that they were able to exploit several different habitat types, it suggests that this species may cope relatively well with habitat change and even habitat loss (Durell 2000), at least in areas where alternative anthropogenic habitats can buffer the loss of natural areas. In fact, other studies already suggested an opportunistic foraging behaviour by spoonbills (El-Hacen *et al.* 2014, Enners *et al.* 2020) and our study also seems to corroborate that. The fact that saltpans were mostly used by juveniles born in 2016–2018 and less used by juveniles born in 2019–2020 may indicate that in those early years, saltpans had more attractive conditions. Unfortunately, we do not have information on water levels on those habitats to be able to assess this. It may also be a consequence of the small sample size in each year, which limits the variation between individuals. Another result that suggests opportunistic habitat use by juvenile spoonbills is the difference between the three spoonbills that remained in Ria Formosa (Castor, Hadar and Mira) and the two that remained in the Iberian Peninsula but left the vicinity of the colony (Vega and Sirius). The first group used the same two habitats in different proportions (Figure 2): saltpans and intertidal wetlands (two available habitats in Ria Formosa), while the second group used other two different habitats: inland waters and rice fields (not available in Ria Formosa). In fact, rice fields only started being used by tracked spoonbills in October, most likely when these start being flooded, once Sirius had already dispersed to areas with rice fields by August, but only started using them in October. Polaris went to the same area as Sirius but migrated to Africa in September, which likely explain why it did not use rice fields.

One limitation of our work was the absence of extended nocturnal tracking, especially when studying the use of intertidal wetlands, but the use of those areas may be more limited by tidal movements than by daylight hours, and since the study spanned several months, the results should present little tidal bias. In order to better understand drivers of differences in habitat usage along the first year of independence, it would be important to obtain information relative to the use and habitat selection of adult spoonbills, to test if competition may be forcing juveniles into poorer habitats. Moreover, it will be important to quantify water availability in several habitat types and its variability throughout the year, to ascertain if juveniles are using anthropogenic habitats due to water scarcity in natural habitats. Furthermore, determining which activities are performed in different habitats will likely provide a better interpretation of the current patterns of habitat usage, particularly in assessing if anthropogenic habitats are used for foraging or mostly for other activities (e.g. roosting, preening, etc.)

In summary, we show that juveniles are able to use several habitat types, including anthropogenic habitats, which supports

the idea that the development of spoonbill colonies in Portugal is driven, at least partially, by the capacity of individuals of this species to explore new habitat types (Shultz *et al.* 2005), which was also the case in Serbia, where spoonbills are now using fish farms (Tucakov 2004). This work highlights the need to further protect and restore natural intertidal wetlands but also to identify and manage anthropogenic habitats important to spoonbills. The fact that anthropogenic habitats were used by spoonbills, which is considered a specialist species (Swennen and Yu 2005, Pigniczki 2017), highlights their opportunistic behaviour on habitat selection and may indicate that these habitats can also be favourable to other waterbird species with similar ecology.

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