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Source: Ardea, 98(1) : 3-12

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/078.098.0102

Assessing the role of multiple environmental factors on Eurasian Spoonbill departure decisions from stopover sites

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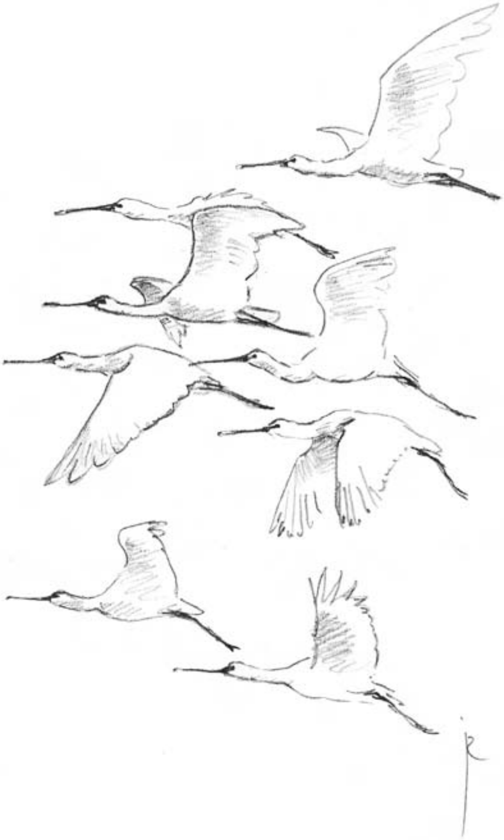

Navedo J.G., Masero J.A., Overdijk O., Orizaola G. & Sánchez-Guzmán J.M. 2010. Assessing the role of multiple environmental factors on Eurasian Spoonbill departure decisions from stopover sites. Ardea 98: 3–12.

Understanding the factors driving departure decisions from stopover sites is critical when predicting the dynamics of bird migration. We investigated the interactive effects of wind, tidal characteristics, and precipitation on the departure decisions of the Eurasian Spoonbill *Platalea l. leucorodia* from a major coastal stopover locality in northern Iberia. Most departing Spoonbills (>80%) crossed an adjacent mountain range to follow a direct route over inland Iberia, while the remainder made a detour following an indirect coastal route along the coast of the Iberian Peninsula. During four consecutive autumns, we daily monitored departing Spoonbills leaving along these two routes. The birds taking the inland route, crossing unsuitable habitats and needing therefore higher fuel-loads, departed preferentially under favourable tailwind conditions (TWC). This represented a significant increase in distance covered and/or a decrease in energy spent per unit time. Moreover, Spoonbills taking the inland route often departed during spring tides. For the indirect coastal route, TWC did not affect the onset of migration but bird departures increased with neap tides. Precipitation and date were negatively correlated with departures towards both routes, whereas Spoonbill density at the stopover had a positive effect. Our findings provide empirical support for the role that wind assistance may play for Spoonbills to resume migration.

Key words: departure decisions, ecological barriers, migratory strategies, Spoonbill, tides, waterbirds, wind assistance

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Once involved in migration, birds must decide how fast to fly, where to stop for refuelling, and how much fuel to accumulate before departing on the next flight (Alerstam et al. 2003). In order to be as fast, energy efficient, and safe as possible, optimal decisions at each stopover are thus necessary (Alerstam & Lindström 1990, Hedenström & Alerstam 1997, Purcell & Brodin 2007, Hedenström 2008). In most avian species, departure decisions are influenced by multiple environmental factors. Specifically, a body of theoretical and empirical work suggests that birds migrating with wind assistance obtain an important energetic benefit (Zwarts *et al.* 1990, Butler *et al.* 1997, Liechti & Bruderer 1998, Weber *et al.* 1998, Weber & Hedenström 2000, Shamoun-Baranes *et al.* 2007, Felicísimo *et al.* 2008). Nevertheless, except for nocturnal migratory songbirds (e.g. Åkesson & Hedenström 2000, Erni *et al.* 2002, Delingat *et al.* 2006, Tsvey *et al.* 2007), there is little empirical data on the role of wind assistance in departure decisions towards the next stopover site, specially for waterbird populations of tidal landscapes (Alerstam & Enckell 1979, Alonso *et al.* 1990a,b). Therefore, more detailed information on departure decisions will provide a further understanding about the dynamics of bird migration.

Long-distance migratory waterbirds are suitable organisms to investigate the role of environmental factors on departure decisions from stopover sites, due to their energetically demanding life history (Pennycuick & Battley 2003, Battley *et al.* 2005, Gill *et al.* 2005, Piersma *et al.* 2005), and to their reliance on just a few patchily scattered stopover areas (van de Kam *et al.* 2004). Once loaded enough fuel to successfully reach the next stopover site (Ueta & Higuchi 2002, Warnock & Takekawa 2003, Hupp *et al.* 2006, Lee *et al.* 2008, Bobek *et al.* 2008), waterbirds must accurately choose the right environmental conditions to resume migration (Piersma *et al.* 1990). In addition to wind, precipitation is an important factor in the decision to depart, since it reduces migratory efficiency (Liechti & Bruderer 1998, Åkesson & Hedenström 2000, Erni *et al.* 2002, Schaub *et al.* 2004, Tsvey *et al.* 2007, Newton 2008). Tidal phase could affect departure decisions since the foraging period for waterbirds is mostly limited to low tide, which is of a different magnitude depending on the moon phase (tidal amplitude) (Piersma *et al.* 1990).

The existence of ecological barriers could also influence migratory decisions in birds (Alerstam 2009). Individuals confronted with a barrier may decide to travel around it, leading to the development of a detour in the migratory route, or even stop further migration (Alerstam 2001, Alerstam *et al.* 2003). Moreover, if the obstacle is a mountain range located immediately after the stopover area, the required rate of climb may make crossing it difficult, especially for large birds (Åkesson & Hedenström 2007). The use of thermal currents will be thus crucial for large birds trying to pass those mountain obstacles (Alonso *et al.* 1990b, Åkesson & Hedenström 2007). Environmental conditions may therefore differentially affect departure decisions in birds taking the direct route over the obstacle or the alternative around it (Alerstam *et al.* 2003, Åkesson & Hedenström 2007). Under these circumstances, wind conditions could become one of the major driving forces for the evolution of optimal migratory strategies (Weber *et al.* 1998, Purcell & Brodin 2007).

Here, we address the effects of wind, precipitation, and tidal phase in explaining two different routes followed by Eurasian Spoonbills *Platalea l. leucorodia* resuming autumn migration from a coastal stopover (Santoña marshes) in northern Iberia. This coastal stopover site is used as a refuelling area by a large percentage of the 'Atlantic' population of Eurasian Spoonbills (Navedo 2006a). Most Spoonbills departing from Santoña must cross an adjacent mountain range to follow a direct south western (SW) route through inland Iberia to winter in West Africa, while the remainder use an indirect western (W) coastal route without any obstacle to winter in Southern Iberia (Navedo 2006a). The former requires a long non-stop flight to the next available stopover site in SW Iberia, while the latter involves only short flights. The direct route thus presumably requires higher energy loads than the coastal route.

Our main prediction is that birds following the SW inland route across the Iberian Peninsula should take advantage of wind assistance to complete their migration flight, whereas wind should be not a crucial factor for birds following the W coastal route. We also predict that Spoonbills following the direct SW route, which needs a higher energy load compared to the W route, should take advantage of higher tidal amplitudes, since available foraging areas and/or resources are increased during spring tide periods. Finally, precipitation should negatively affect departures for both routes.

METHODS

The study was conducted in Santoña Marshes Natural Park (43°30'N 3°30'W, Fig. 1), an estuarine area located on the northern coast of the Iberian Peninsula (SW Europe), with semidiurnal tides exposing the intertidal zone (roughly 1200 ha) for 5.5–6.5 h and 3.5 metres of mean tidal amplitude (Navedo & Masero 2007). During autumn, migrating Eurasian Spoonbills of the 'North-Atlantic' population (estimated at 5000 individuals during the study period; O.O., unpubl. data) make a stopover for refuelling at Santoña (Navedo 2006a). Foraging habitat use is driven by the tides as birds feed in the intertidal channels at low tide, resting at high tide (Navedo 2006a). Autumn migration in the study area starts in mid-August and ends at the beginning of October, with >90% of the birds stopping during September (Navedo 2006a). Most birds (80%; Navedo 2006a) resume migration towards the southwest, crossing inland Iberia, to the potential next stopover sites located on the coast of SW Iberia (Fig. 1). The majority of these birds overwinter in wetlands of West Africa (data from PVC-ring recoveries; Triplet *et al.* 2008). The rest of the population (20%; Navedo 2006a) migrate towards the West, following the Iberian coastline until they reach their wintering areas located in the Southwest of the Iberian Peninsula (Lorenzo & de le Court 2007) (Fig. 1).

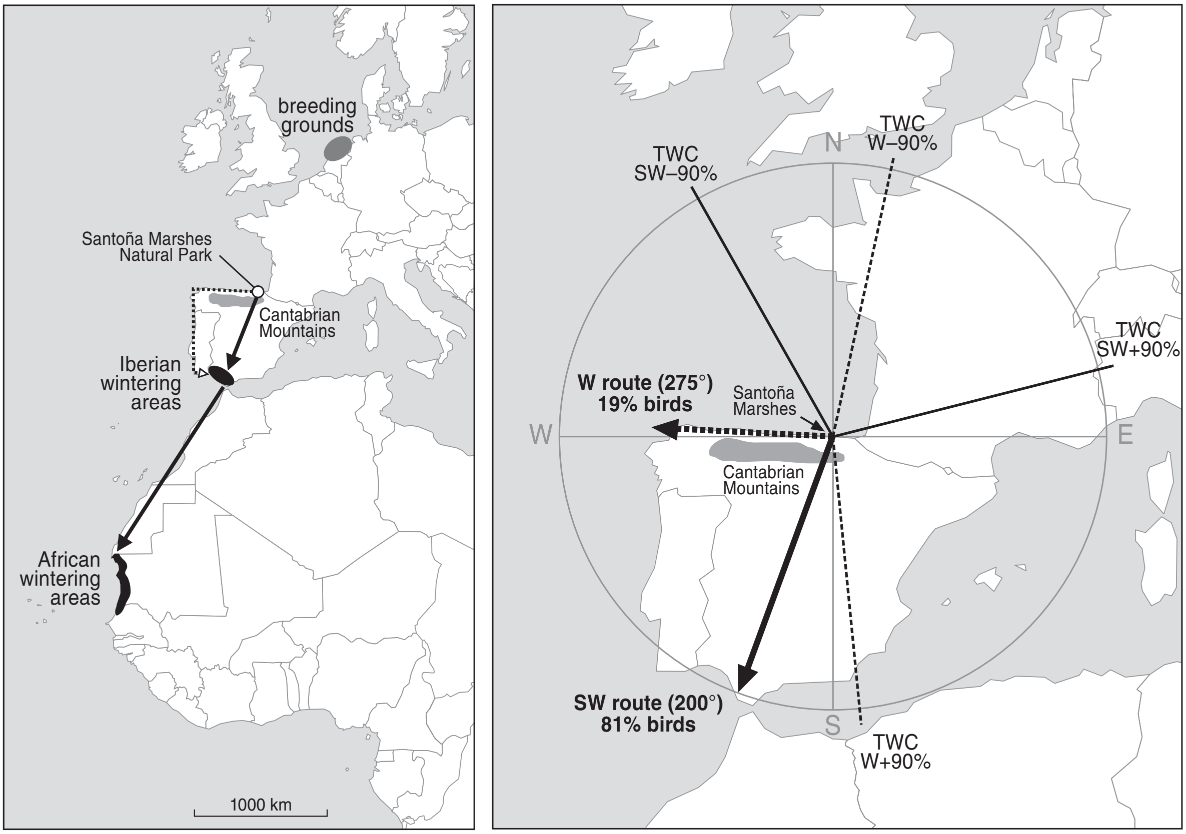

Figure 1. Location of the Santoña Marshes Natural Park and the Cantabrian Mountains in the Iberian Peninsula, indicating breeding grounds and main wintering areas for Spoonbills (SW Iberia and West Africa). Arrows indicate the direct inland (SW; solid) and the indirect coastal (W; dashed) routes followed by Spoonbills after their stopover at Santoña. The lines indicate the 90% confidence intervals of the tail wind component (TWC) corresponding to each route.

To follow the SW route, Spoonbills have to climb to over 1500 m a.s.l. to cross the Cantabrian Mountains, located just 20 km from the study area, and travel over about 800 km of unsuitable land to reach the next stopover sites on the SW Iberian coast. Spoonbills that follow the western route (W) do not encounter any relevant obstacle, and can stop for refuelling in several wetlands along the Iberian coast (Fig. 1).

The number of Spoonbills leaving Santoña was monitored by two experienced ornithologists, with the support of trained volunteers, from two small hills overlooking the entire estuary, constantly from 9:00 to 20:00, for 28 consecutive days in September in four consecutive years (2002–05).

Flocks leaving Santoña were noted as well as their migratory direction (SW or W). Flocks departing to the SW circled to gain altitude for 15–20 min, and then initiated a flapping flight in V-formation towards the Cantabrian Mountains. Flocks departing to the W followed the coastline without gaining altitude. Occasionally the numbers of Spoonbills were lower at sunrise than at the previous sunset, which indicates that we may have missed the departure of some flocks (16%).

To explore effects of wind assistance on departure decisions, we obtained daily data of wind direction and speed at sea level at Santoña. We calculated a daily direction and speed as the mean value of the two records at 12:00 and 18:00. Daily wind conditions were characterised by the tailwind component (TWC, following Åkesson & Hedenström 2000) for the two main routes (TWC-SW and TWC-W). This parameter is measured in m/s, and was calculated as $V_w \times \cos(\phi_t – \phi_w)$, where V_w stands for wind speed, ϕ_t for the mean migratory direction of the Spoonbills, and ϕ_w for wind direction. Long-distance recoveries of ringed Spoonbills supported mean migratory directions of 200° and 275° for the SW and W routes, respectively (Spoonbill ringing database; O.O., unpubl. data). Positive TWC indicates wind conditions favouring flights. Negative values indicate winds opposing migration in the preferred direction.

A TWC equal to zero means still air or a wind exactly perpendicular to the migratory direction. Given these two possibilities, we manually checked the conditions for flocks departing at small TWC values (e.g. Tsvey *et al.* 2007). In seven situations a side wind for the SW route (mean wind speed 2.5 ± 0.3 m/s) resulted in a comparatively small TWC value (range: –0.5 to 0.5). Accordingly, for the SW route, we concluded that small TWC values corresponded to strong side winds, and extreme TWC values corresponded to rather strong tail or head winds. Only two situations like these occurred for the W route, thus we considered that small TWC values for this route corresponded to weak winds.

We examined whether the wind conditions registered at sea level were representative of conditions experienced by birds during flight at 1000 and 2000 m a.s.l., and whether the wind conditions at those altitudes were correlated. Wind direction and speed at those altitudes were calculated from values registered at 12:00 and 18:00 on a two-day basis during September 2005 (the year was chosen at random) using the HIRLAM HIR resolution model (Undén *et al.* 2002).

Daily rain conditions were registered as accumulated daily precipitation (mm). We also recorded daily tidal amplitude as a coefficient ranging from 20 to 120, a measure directly correlated with the height of the tide. It should be noted that in the study area the highest tidal amplitudes correspond to daytime low tides ranging from 10:00 to 12:00 (Navedo 2006b). As both variables were significantly correlated (linear-circular correlation (Fisher 1993; $r = 0.56$; $P < 0.01$), we used the residuals of this correlation into the model, thus avoiding collinearity (e.g. Müller *et al.* 2003). Meteorological data were provided by the official database of the Spanish Meteorological Agency of the former Spanish Ministry of the Environment.

Kruskal–Wallis tests were used to examine for differences between years in the number of birds departing daily to each route throughout the autumn migration in relation with TWC and precipitation. Potential correlations of wind direction at sea level with the values at higher altitudes were tested using circular correlation coefficients (CCC) (Fisher & Lee 1983) and linear correlation was used for wind speed. Effects of environmental factors on the number of birds departing daily for each route were analysed by fitting independent Generalized Nonlinear Models (GLZ) with Poisson distributions and log-link functions (best fit in all cases). We included in the model TWC (m/s), tide characteristics (standard residuals of the correlation between tidal amplitude and diurnal low tide hour), precipitation (accumulated daily rainfall), departure day (days after 1 September), and total Spoonbill numbers at the estuary as predictive variables. Most (66.5%) Spoonbills departed from Santoña with rising tides, with the biggest flocks departing just after the low tide hour (Fig. 2). Thus, we used the low tide count to control the potential effect of the daily number of birds at the stopover site on bird departure decisions (e.g. Alonso *et al.* 1990a). Departure day was included to account for potential differences as the migration period progresses (e.g. Alonso *et al.* 1990a).

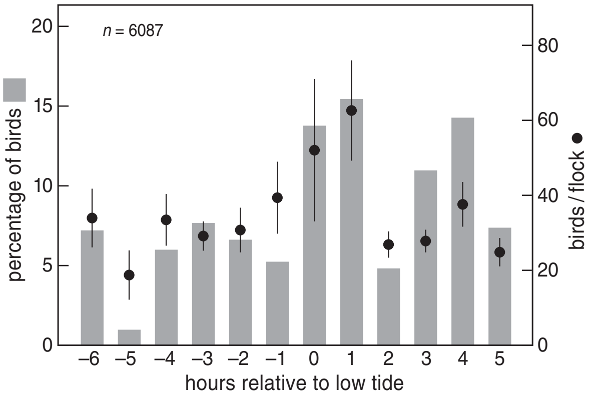

Figure 2. Percentage of departing birds (bars) and number of birds (mean ± SE) within a flock (dots), relative to the time of low tide at Santoña.

Statistical analyses were performed using STATISTICA v6.1 (StatSoft Inc. 2002), using a 0.05 level of significance. Values are presented as means ± SE.

RESULTS

Environmental conditions. Spoonbills departed under light to moderate wind conditions (mean wind speed experienced by flocks departing to SW: range 1.5–9.2 m/s, average 3.6 ± 0.2 m/s; mean wind speed experienced by flocks departing to W: range 1.8–9.2 m/s; average 4.1 ± 0.4 m/s). Wind directions at sea level were not correlated with wind direction at 1000 m a.s.l. or 2000 m a.s.l. (circular $r = –0.03$ and $r = 0.05$, $P > 0.05$). However, wind directions at 1000 m and 2000 m were significantly correlated (circular $r = 0.25$, $P < 0.01$). Wind speed at sea level was significantly correlated with the speed at 1000 m a.s.l. and 2000 m a.s.l. ($r = 0.\ 72$ and $r = 0.52$, $P < 0.001$). There were 13 days with more than 10 mm accumulated precipitation, and total precipitation showed no significant differences between years (Kruskal–Wallis $H_{3,112} = 2.70$; $P = 0.44$).

SW Route. Residuals of tidal characteristics, rain conditions, departure day, and wind assistance, as well as bird density, significantly affected the daily number of birds following the principal SW inland route (Table 1). These associations remained significant after removal of two outlying data points (see Fig. 3). TWC values and tidal amplitude had a positive effect on bird departures (Figs 3A,B), whereas diurnal low tide hour, departure day and accumulated daily rainfall were negatively correlated with the daily number of departing birds towards this route (Figs 3C,D,E). Bird density positively affected departures (Fig. 3F). Favourable wind conditions for the SW route (positive TWC) were present on 81% of days, showing a high tail direction component (Table 2; Fig. 1), and nearly all Spoonbills following the SW route departed on days with tailwind (89%). There were no differences in TWC between years (Kruskal–Wallis $H_{3,112} = 2.04$; $P = 0.56$). An average of 39.3 ± 7.2 birds departed daily (range: 0–528) in SW direction (Table 2), without differences between years (Kruskal–Wallis $H_{3,112} = 3.20$; $P = 0.36$).

W Route. As for the SW route, residuals of tidal characteristics, rain conditions, and departure day, as well as bird density, significantly affected the daily number of birds following the W route (Table 1). However, TWC had no significant effect (Table 1; Fig. 3A). Interestingly, tidal amplitude and diurnal low tide hour were both correlated with the number of departing birds to this route, but the relationships were of opposite sign compared to the SW route (Figs 3B,C). Favourable wind conditions for the W route occurred on 60% of days, with a high side direction component (Table 2; Fig. 1). Half (51%) of the birds following the W route departed on days with favourable winds. In contrast with the SW route, there were significant differences in TWC between years (Kruskal–Wallis $H_{3,112} = 10.98$; $P < 0.01$). We registered 8.1 ± 1.9 daily departing birds (range: 0–121) to the W route (Table 2), without significant differences between years (Kruskal–Wallis $H_{3,112} = 2.29$; $P = 0.51$).

DISCUSSION

As predicted, the majority of Spoonbills using the direct route over inland Iberia departed under favourable wind conditions (positive TWC), and crossed the nearby mountain obstacle using wind assistance. By contrast, wind conditions were less favourable and more variable between years for Spoonbills using the indirect

Table 1. Generalized nonlinear model (GLZ) showing the effects of Spoonbill density (number of birds at low tide), departure day, residuals of tide characteristics, precipitation, and tailwind component (TWC) on the daily number of Spoonbills departing for two migratory routes from Santoña. SW: direct inland route; W: indirect coastal route.

	SW			W		
GLZ	χ^2_1	*P*	Estimate	χ^2_1	*P*	Estimate
Total bird density	4074.55	0.001	0.1044	233.84	0.001	0.0068
Residuals of tide	195.41	0.001	0.1270	23.83	0.001	– 0.2490
Departure day	35.68	0.001	– 0.0284	390.06	0.001	– 0.1056
Precipitation	194.28	0.001	– 0.0014	86.90	0.001	– 0.0057
TWC	125.31	0.001	0.1044	0.36	0.55	0.0072

Table 2. Averages and SE of number of Spoonbills departing daily from Santoña, tailwind direction component ($\cos(\phi_t – \phi_w)$), and tailwind intensity (TWC) for the two migratory routes (SW: direct inland route; W: indirect coastal route.). Separately given are values of tailwind direction and TWC obtained on days with favourable wind conditions, indicated by [+].

	SW			W		
	Mean	SE	*n*	Mean	SE	*n*
n birds departing daily	39.3	7.18	112	8.1	1.9	112
$\mathrm{Cos}(\Phi_t – \Phi_w)$	0.51	0.05	112	0.16	0.07	112
TWC (m/s)	1.87	0.18	112	0.57	0.29	112
$\mathrm{Cos}(\Phi_t – \Phi_w)$ [+]	0.71	0.02	91	0.74	0.03	67
TWC (m/s) [+]	2.60	0.12	91	2.76	0.17	67

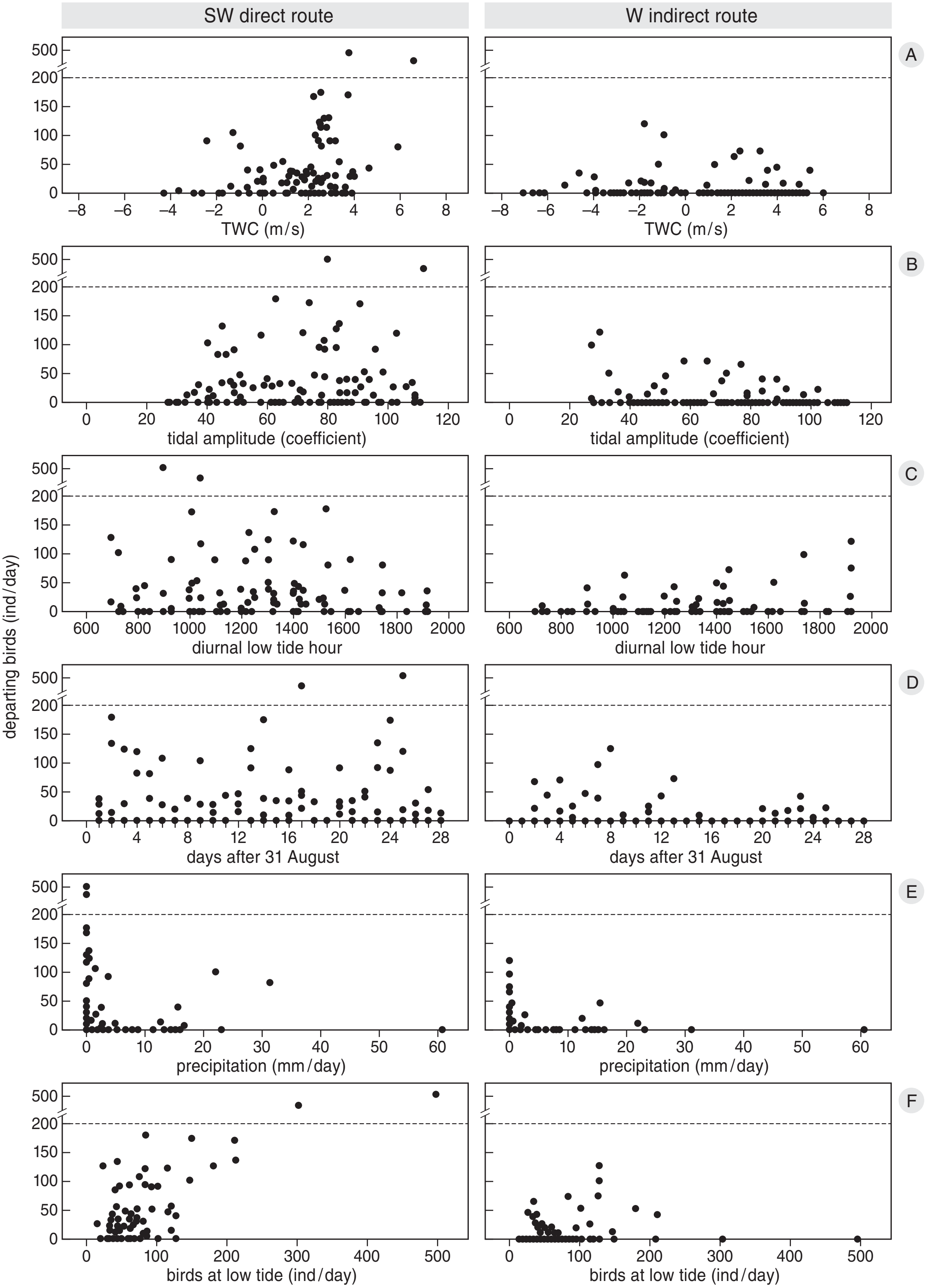

Figure 3. Relationships between the daily number of Spoonbills resuming migration towards the direct inland (SW) and indirect coastal (W) routes and (A) wind assistance (TWC), (B) tidal amplitude, (C) diurnal low tide hour, (D) departure day, (E) accumulated precipitation, and (F) bird density (number of birds at low tide).

coastal route, and wind seemed to play a less decisive role in determining the number of birds following this route. As was also expected (Alerstam *et al.* 2003), precipitation negatively affected overall departures.

It has been suggested that large birds may not have enough power to fly over high mountains if these are close to the point of departure (Åkesson & Hedenström 2007). Under such conditions the required rate of climb may make the crossing difficult. In our case, the majority of Spoonbills departing to the inland route circled to climb for 15–20 min before performing a flapping flight in V-formation towards the SW, directly surpassing the mountain range (~1500 m a.s.l.). Their take-off after low tide coincided with the period (around midday) when the probability of encountering thermal currents is greatest (Alonso *et al.* 1990b). Thermal currents helping the climb over a nearby mountain obstacle (i.e. reducing energy costs) could be viewed as a major factor explaining the evolution of diurnal instead of nocturnal migration in large waterbirds with restricted stopover sites (Alerstam 2009), such as Spoonbills.

As the migration period advanced there was a significant decrease in the number of departing Spoonbills, and the size of the local flock positively affected departures for both routes. These results suggest that Spoonbills migrating ahead of conspecifics could take advantage of this lead by reducing the potential negative effects of local competition at subsequent stopover areas as the season progresses (Gudmundsson *et al.* 1991, Prop *et al.* 2003, Newton 2004, Nolet *et al.* 2006), as well as by being able to outcompete conspecifics in the best foraging grounds at wintering areas (Alerstam *et al.* 2003).

Birds using the direct inland route departed with a mean wind assistance of 2.6 m/s, which should represent a significant increase in distance covered and/or decrease in energy spent per unit time for a migrating Spoonbill (Liechti & Bruderer 1998, Åkesson & Hedenström 2007), which has an air speed of about 15 m/s (Bruderer & Boldt 2001). Although wind assistance in this study was deduced from the wind conditions at sea level, this is indeed regarded as a reliable cue for birds indicating conditions at higher altitudes (Piersma & Jukema 1990). In our study, wind speed at sea level was significantly correlated with those at 1000 m a.s.l. and 2000 m a.s.l. However, wind direction calculated for higher altitudes was not correlated with wind direction at sea level. Data were derived only for one of the years (2005, see Methods), thus a more detailed study is needed to accurately assess this issue.

Spoonbills, as many other waterbird species, have evolved in a predictable tidal landscape (Alerstam & Enckell 1979, Alerstam *et al.* 2003). In the present case, this includes a significant delay of 2.0–2.3 h in the propagation of the tidal wave between the NE Iberian coast (Santoña) and SW Iberia (Dronkers 2005), and the low tide period at the intertidal SW Iberian stopover sites takes place 10.2–10.5 h after the low tide at Santoña. Similar to other migratory waterbirds, including shorebirds (Piersma *et al.* 1990), the majority of the Spoonbills taking the inland route departed with a rising tide. With a mean flight speed of ~70 km/h (data from satellite tracking; O.O., unpubl. data), which includes both air speed and wind assistance, they would take ~11 hours to travel the ~800 km nonstop migratory leg to SW Iberian intertidal stopover sites. Thus, only birds that used wind assistance (i.e. travelling at 70 km/h or more) would reach the next stopover sites on the SW Iberian coast during low tide, and therefore at a favourable feeding time. This underlines the role of wind assistance as a driving force for the development of Spoonbill migration strategies and supports the evolutionary benefit of a diurnal, fly-and-forage migratory pattern in a species with limited stopover sites (Alerstam 2009).

Energy demands and associated travel costs may differ between migratory strategies (Lundberg & Alerstam 1986, Alerstam *et al.* 2003, Drent *et al.* 2003, Schmidt-Wellenburg 2007, Hedenström 2008). Spoonbills taking the more predictable coastal route might increase their survival by lower travel costs during migration; the other side of the coin is that they winter at less profitable localities (Lundberg & Alerstam 1986). On the other hand, birds taking the direct inland route might improve their fitness by wintering at highly profitable sites in West Africa (Lundberg & Alerstam 1986), but incurring higher travel costs associated with the higher energy-load needed to make a longer non-stop flight (Drent *et al.* 2003). This suggests that Spoonbills are facing an evolutionary trade-off that affects their migratory decisions (Lundberg & Alerstam 1986, Schekkerman *et al.* 2003). Our results support the view that wind assistance plays an important role for Spoonbills migrating along the route that requires largest energy stores, as had been suggested by theoretical studies (Weber & Hedenström 2000, Purcell & Brodin 2007, Åkesson & Hedenström 2007, Alerstam 2009) and demonstrated for a trans-saharan migratory songbird (e.g. Dierschke & Delingat 2001, Delingat *et al.* 2006, Delingat *et al.* 2008).

In conclusion, wind conditions experienced at a major coastal stopover locality have been revealed as a crucial factor in migratory patterns in the Spoonbill. Wind appears to help the birds to take the direct route with higher associated travel costs, and, in conjunction with thermal currents, to cross a nearby mountain obstacle. It may even allow them to arrive at the next stopover site at the optimal time to fulfil their energy demands.

ACKNOWLEDGEMENTS

We are very grateful to Alejandro G. Herrera, Álvaro Bustamante, Máximo Sánchez, Manuel A. Alcántara, Juan José Aja, Virginia Iturriaga, Ana Casero, and the volunteers, especially Ludovico de Vega, for field assistance. Dra. Ana J. Abascal, Dr. Manuel Mota, Dr. Heiko Schmaljohann, Dr. Ken Kraaijeveld, Dr. Shogo Kato and Joaquín Bedia, made invaluable comments on an earlier draft. Jorge S. Gutiérrez, José Mª Abad and Óscar Uceda helped with graphics. We also thank the staff of the Centro Meteorológico Territorial de Cantabria y Asturias (Agencia Española de Meteorología-AEMet) for their invaluable help in supplying meteorological data. JGN was financially supported to carry out the field work by SEO/BirdLife and O.A. Parques Nacionales (belonging to the former Spanish Ministry of the Environment).

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SAMENVATTING

Een groot deel van de in Nederland broedende Lepelaars *Platalea leucorodia* maakt op de herfsttrek een tussenstop in Santoña, een getijdengebied langs de noordkust van Spanje. Van hieruit kunnen de vogels twee kanten op. De meeste Lepelaars (>80%) vliegen over land richting de volgende tussenstop in het zuidwesten van het Iberisch Schiereiland. Deze route is snel, maar vergt een lange non-stop vlucht en een oversteek over de bergen van Noord-Spanje. De rest van de vogels vertrekt in westelijke richting en volgt de kustlijn. Deze route kent geen lange non-stop vluchten of obstakels en is dus waarschijnlijk minder inspannend. Vanaf een strategisch punt konden de auteurs gedurende vier jaar noteren wanneer en in welke richting de Lepelaars vanuit Santoña vertrokken. Deze gegevens werden gekoppeld aan gegevens over het weer en

getij om te onderzoeken welke factoren van belang zijn voor de twee routes. Het bleek dat windrichting en windsterkte een significante invloed hadden op de aantallen Lepelaars die richting het zuidwesten vlogen. De vogels die deze route kozen, vertrokken bij voorkeur met een relatief sterke rugwind. Voor Lepelaars die richting het westen vertrokken, maakte de wind weinig uit. Voor beide routes gold dat de vogels liever niet in de regen vertrokken en dat het aantal vertrekkende vogels groter was als er meer vogels aanwezig waren in het gebied. Het getijverschil was ook van invloed op het aantal vogels dat vertrok, maar op verschillende manier voor de twee routes. Vogels die naar het zuidwesten vlogen, vertrokken bij voorkeur bij springtij (groot getijverschil tussen hoog- en laagwater). Mogelijk zijn de voedselcondities extra goed bij een zeer laag laagwater, waardoor ze weldoorvoed aan hun reis kunnen beginnen. De Lepelaars die voor de kustroute kozen, vertrokken juist rond doodtij (klein getijverschil tussen hoog- en laagwater), maar waarom was onduidelijk. In ieder geval leken meerdere omgevingsfactoren een rol te spelen bij het bepalen van het moment van vertrek. De rol van deze factoren verschilde al naar gelang de route die de vogels volgden. (KK)

Corresponding editor: Ken Kraaijeveld
Received 17 July 2009; accepted 23 November 2009