Wind effects on habitat use by wintering waders in an inland lake of the Iberian Peninsula

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Abstract

Wind effects on habitat use by wintering waders in an inland lake of the Iberian Peninsula. We aimed to identify the effects of the direction and wind speed on feeding habitat selection of wintering dunlins and little stints in an inland lake of the Iberian Peninsula. Feeding habitat (muddy surface or shallow water) and location in the lake with respect to wind direction (windward and leeward) of feeding flocks of both species were assessed on days with different wind speed (light or strong). We also performed visual counts of potential prey items (zooplankton) in mud and water habitats. In light wind conditions, wader flocks mostly selected the shallow water on the lake's leeward shore. On the contrary, in strong wind conditions, the birds tended to forage on the windward shore, with a similar frequency in mud and shallow water habitats. The abundance of prey items in the mud and water column varied according to wind conditions, being higher in the sites preferred by waders. Our findings advance knowledge on how small–sized waders cope with environmental dynamics of wind in non–tidal lakes.

Key words: Abiotic factors, Foraging habitat, Saline lakes, Shorebirds, Wintering season

Resumen

Los efectos del viento en el uso del hábitat que hacen las aves limícolas invernantes en una laguna interior en la península ibérica. Nuestro objetivo fue determinar los efectos de la dirección y la velocidad del viento en el uso del hábitat de alimentación que hacen el correlimos común y el correlimos menudo en una laguna interior de la península ibérica. Se evaluaron el hábitat de alimentación (superficie fangosa o aguas poco profundas) y la ubicación en la laguna con respecto a la dirección del viento (barlovento y sotavento) de los grupos de limícolas en días con diferente velocidad del viento (suave y fuerte). También se realizaron recuentos visuales de posibles presas (zooplancton) en hábitats de lodo y agua. En condiciones de viento suave, el grupo de limícolas seleccionó principalmente la zona de aguas poco profundas ubicada a sotavento de la laguna. Por el contrario, en condiciones de viento fuerte, las aves tendieron a buscar comida en la orilla de barlovento, con una frecuencia similar en los hábitats de lodo y de aguas poco profundas. La abundancia de presas en las columnas de lodo y de agua varió según las condiciones del viento, y fue más alta en los sitios preferidos por los limícolas. Nuestros resultados se suman al conocimiento de cómo los limícolas de tamaño pequeño hacen frente a la dinámica ambiental del viento en lagunas no mareales.

Palabras claves: Factores abióticos, Hábitat de forrajeo, Lagunas salinas, Aves limícolas, Período invernal

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Introduction

Multiple environmental components act independently or in association with one another to influence habitat selection and use by birds (Jones, 2001). The choice of foraging sites by waders is fundamentally a consequence of the balance of costs and benefits of feeding in potential foraging habitats, defined mainly by depth of the water column and the quality and quantity of prey (e.g. Piersma, 2006; Granadeiro et al., 2007; Beerens et al., 2015a, 2015b). Other important factors, such as predation risk (Mikula et al., 2018), anthropic disturbances (Holm and Laursen, 2009), eco–physiological adaptations (Gutiérrez et al., 2012; Lourenço and Piersma, 2015), and roost location and landscape attributes (Dias et al., 2014; Santiago–Quesada et al., 2014) are associated with wader habitat selection outside the breeding season, but they have been poorly documented for inland natural wetlands.

Large numbers of small– and medium–sized waders rely on inland natural wetlands to replenish their energy stores during their migrations (Verkuil et al., 1993). In these non–tidal wetlands, wind significantly affects the predator–prey relationship by altering detection or locomotion, and consequently, the foraging habitat or microhabitat selection patterns (Verkuil et al., 1993; Cherry and Barton, 2017). The main food supply for waders is aquatic invertebrates, which can be detected and captured visually or using tactile sensibility (Piersma et al., 1996). Many waders, especially scolopacid species, are long–billed and may feed efficiently on small prey items suspended in water by using distal rhynchokinesis and a feeding mechanism termed surface tension transport (Estrella and Masero, 2007; Estrella et al., 2007).

Wind can act in two different ways on aquatic invertebrate distribution. On one hand, it can centre on specific sites of the foraging grounds, concentrating prey and facilitating the visual strategy (Verkuil et al., 1993). On the other hand, it can expose the organisms on the mud surface, favoring both visual and tactile detection (Verkuil et al., 1993, 2003; Masero et al., 2000).

Most studies on wader habitat selection focus on coastal systems, where most migratory wader populations spend the wintering season (van de Kam et al., 2004). In the Iberian Peninsula, dunlin (*Calidris alpina*) and little stint (*C. minuta*) are two of the most abundant wintering waders and most of their populations winter in coastal areas (SEO/BirdLife, 2012). Specifically, the winter populations of dunlin and little stint in Spain are approximately 100,000 and 12,813 individuals, respectively, and for both species, less than 5 % of these individuals spend this season in continental wetlands (SEO/BirdLife, 2012; BirdLife International, 2018). Although several studies have been carried out on habitat selection by waders wintering in Iberia, they were performed on intertidal habitats or coastal areas (e.g. Masero et al., 2000; Masero and Pérez–Hurtado, 2001; Dias, 2009; Lourenço et al., 2013; Martins et al., 2016), and information on wader habitat use or selection during the winter period in continental Iberian wetlands is lacking.

In this study, we aimed to determine how wind conditions influenced microhabitat use by two small–medium wader species –dunlin and little stint– foraging in an inland wetland located in 'La Mancha Húmeda' Biosphere Reserve (Spain). We studied the relationship between wind direction and wind speed and the selection of two foraging habitats –mud and shallow water. In accordance with Verkuil et al. (1993), we expected to find that wind direction and speed had significant effects on the spatial distribution of aquatic invertebrates and, consequently, on the habitat use by foraging waders.

Material and methods

Study area

'La Mancha Húmeda' Biosphere Reserve in central Spain is formed by a constellation of temporary and permanent wetlands of international importance (SEO/BirdLife, 2012; BirdLife International, 2018). This study was conducted in Lake Alcahozo (N 39º 23' 26,7'' / W 2º 52' 35,7''), a temporary, natural wetland located in this reserve (fig. 1). The lake has a roughly circular shape and covers an area of approximately 88 ha, surrounded by 19 ha of natural halophile vegetation (Gonçalves et al., 2016). It has homogeneously flat shores and a maximum depth of approximately 45 cm. There are no sedimentary islands within the lake.

Data collection and sampling design

To evaluate the foraging habitat use, we applied a used sampling design versus a non–used sampling design (Jones, 2001). Habitat use was recorded between December and February (winters 2014–15 and 2015–16). Previous observations showed that dunlins and little stints often foraged in mixed flocks. Twice a week, we selected the largest foraging flock inside the lake and recorded its habitat use. Observations were separated by a minimum of seven hours and a maximum of 120 hours, with a maximum of two samplings per day. The size of the mixed flock varied between 145 and 530 individuals (mean = 258.9; SD = 130.7), usually with the dominance of dunlins (60–80 % of the individuals). The largest flock usually concentrated around 90% of the individuals of both species present at the lake at counting time. When waders were observed foraging for at least five minutes in a single habitat, the foraging habitat was assigned to one of the following types: mud (muddy surface at the lake's shore) or shallow water (< 2 cm) (fig. 2). We next identified their position in relation to the wind direction as windward or leeward (fig. 2). Following this identification, the wader flocks could be found in any of four situations: mud/leeward, mud/windward, water/leeward and water/windward. We also defined two wind speed classes, light (0–12 km/h) and strong (> 25 km/h) winds. Wind speed was measured using a handheld Brunton ADC Atmospheric Data Center (Brunton, Inc., USA). The lake was visited frequently during both winters until thirty observations were accumulated for each wind/habitat situation.

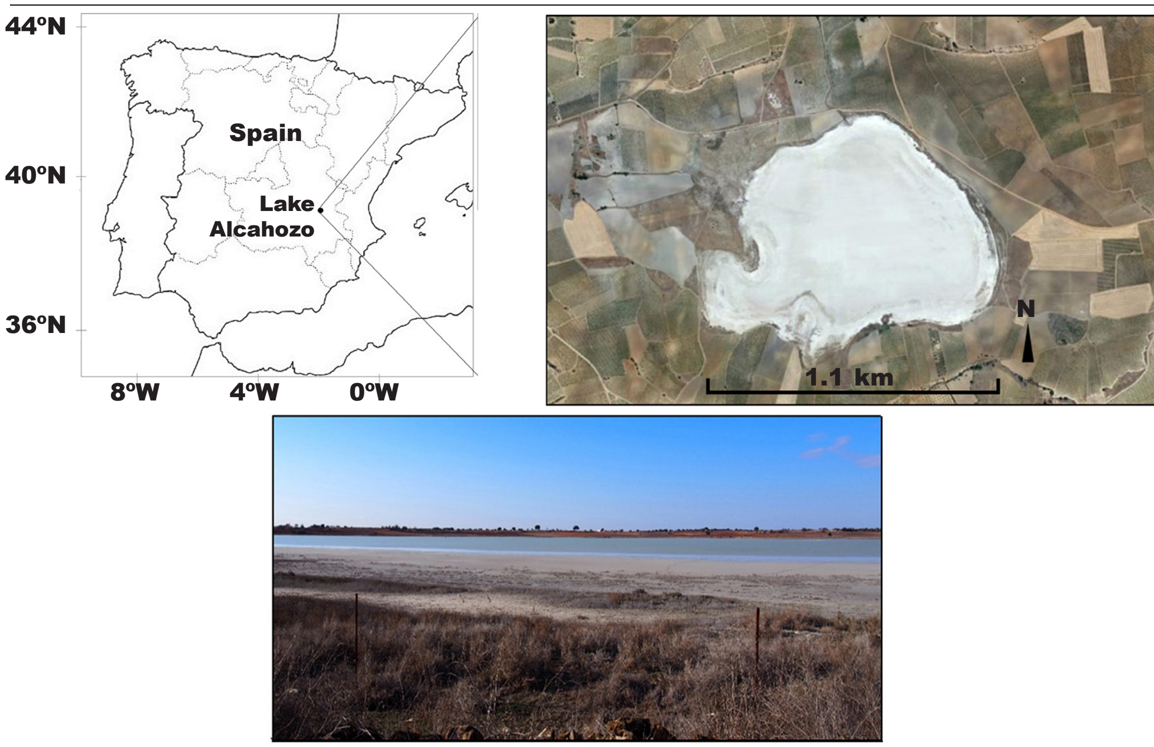

Fig. 1. Location (A) and view (B and C) of Lake Alcahozo in 'La Mancha Húmeda' Biosphere Reserve, Spain.

Fig. 1. Localización (A) y vista (B y C) de la laguna de Alcahozo en la Reserva de la Biosfera de La Mancha Húmeda, en España.

Anostracans and copepods are abundant in Lake Alcahozo and commonly distributed in the water column (Pons et al., 2018). Small–sized waders such as dunlins and little stints feed on these prey items (Verkuil et al., 1993). In December 2014, preliminary inspections noted that by approaching cautiously and remaining motionless, these and other groups, such as ostracods, could be observed at a close distance. Although the best method to quantify the abundance of invertebrates is the collection of water samples and identification in the laboratory (e.g. Pons et al., 2018), careful visual counts can also be good indicators of the quantity of prey in aquatic systems (e.g. McIntosh and Townsend, 1996). To observe whether prey abundance varied with wind conditions and influenced the habitat use of waders, we obtained an index of invertebrate abundance from visual counts in the four habitat/wind combinations (fig. 2). Samplings were performed between January and February 2016. Invertebrate counts were performed on six days for each wind speed class. Five plots of 40 cm x 40 cm distributed every 2 m along a line parallel to the shore were placed in mud and water, both in windward and leeward positions. Therefore, 20 plots were surveyed each counting day. The observer's visual distance to the water or mud surface was 40 cm. All invertebrates observed inside a plot for 30 seconds were counted. One set of plots was located at the habitat/wind direction combination where the flock was observed and the others were located at places representative of the other three categories not used at that moment. The location of the plots thus varied at each sampling occasion because it depended on the location of the waders and wind direction.

Data analysis

We used log–linear models to evaluate whether observations of wader flocks were preferentially associated with particular habitat types as a response to wind. We created a three–dimensional contingency table with the factors habitat (mud/water), position relative to wind (windward/leeward) and wind speed (light/strong). The number of wader flocks found in each combination of the three factors was the response variable. The significance of the interactions between the factors considered was tested by removing interactions in turn from the most general model and comparing resulting models using the chi–square test (Bolker et al., 2009). Interactions were removed until a significant term was identified.

To assess invertebrate abundance, we tested the effects of abundance of the same factors cited above using Generalized Linear Mixed Models (GLMMs) with Poisson distribution. The response variable was the total number of invertebrates counted in each plot.

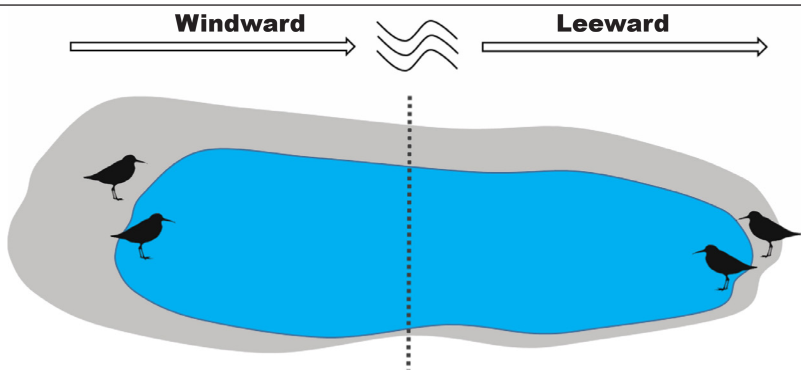

Fig. 2. Scheme showing the four possible distributions of the flocks (represented by a single bird) of waders during winter at Lake Alcahozo. At each observation, only one of four situations was possible: windward or leeward and mud (gray) or shallow water (blue).

Fig. 2. Esquema en el que se muestran las cuatro posibles distribuciones de los grupos de limícolas (representados por un único ave) durante el invierno en la laguna de Alcahozo. En cada observación, solo podía darse una de las cuatro situaciones: barlovento o sotavento y lodo (en gris) o aguas poco profundas (en azul).

Habitat type, position relative to wind and wind speed category were factors included as fixed effects. The sampling day was considered a random effect. As above, the he significance of interactions between fixed effects was tested by removing interactions in turn from the general model and comparing model deviances using the chi–square test (Bolker et al., 2009). All analyses were performed using the R–programming environment (R Development Core Team, 2016). The GLMMs were performed using the package 'lme4' (Bates et al., 2013).

Results

In light wind conditions, 74 % of the observations of foraging flocks were made on the leeward of the lake and were mainly of birds feeding in the water column (67 %) (fig. 3A). In strong wind conditions, 80 % of foraging flocks were found on the windward side, with 50 % and 30% of flocks using the mud and the water column, respectively (fig. 3A). All possible interactions were significant (table 1).

We identified three taxonomic groups of invertebrates during the visual counts: Anostraca, Copepoda, and Ostracoda. Under light wind conditions, invertebrate abundance was highest in shallow water, with the highest values located on the leeward side (fig. 3B). However, under strong wind conditions, invertebrate abundance was much higher in mud than in water on the windward side, while it was similar in both habitat types on the leeward side in both habitat types (fig. 3B). Interaction between the three factors (wind speed, direction and habitat type) was not significant ($\chi^2 = 0.95$; df = 1; $p = 0.32$), but the two–way interactions were all significant ($p < 0.01$, in all cases) (table 1).

Discussion

Wind speed had a strong effect on feeding habitat selection by overwintering dunlins and little stints. The circular shape and the homogeneous edge of the lake avoided local confounding variables potentially associated with the wind effects. Our results showed that under light wind conditions, birds foraged mainly in shallow water, on the leeward side of the lake, while under strong wind conditions, birds foraged on the windward shore and used both mud and shallow water microhabitats. Invertebrate abundance in mud and water microhabitats also varied with wind conditions, being higher in the sites preferred by waders.

In shallow lakes, such as our study area, strong wind movements rapidly affect the water column, altering the spatial distribution of zooplankton (Cardoso and Marques, 2009) and increasing turbidity due to sediments in suspension (G–Tóth et al., 2011). In these ecosystems, therefore, wind potentially affects wader prey abundance and detectability. Our results agree with the general patterns that Verkuil et al. (1993, 2003) observed in shallow lagoons in the Ukraine region. Under light wind conditions, most feeding wader flocks used the water habitat on the leeward coast. This pattern was possibly a response to the gentle displacement of prey items towards the leeward shore. In addition, the light wind keeps water turbidity low, facilitating visual detection and predation on invertebrates. In this situation, the distribution of feeding waders flocks mirrors the variations in invertebrate abundance almost perfectly.

In contrast, under strong wind conditions, wader flocks mainly used the windward side of the lake for foraging activities. This may be due to two causes. First, the area of exposed mud is greatly reduced on

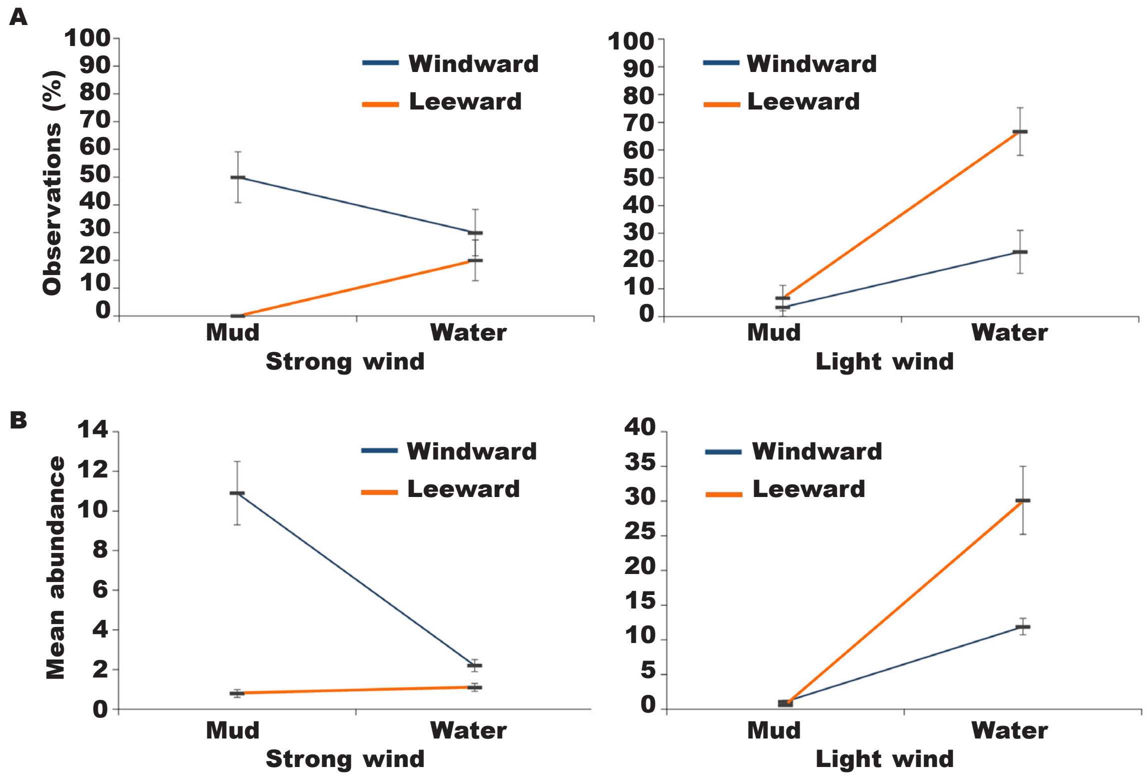

Fig. 3. A, percentage of observations of the wader flock based on 30 flocks observed under each wind speed category (± SE calculated using binomial distribution); B, invertebrates abundance (± SE) between mud and water habitats in relation to the direction (windward or leeward) and wind category (strong or light).

Fig. 3. A, porcentaje de observaciones del grupo de limícolas basado en 30 grupos observados en cada categoría de velocidad del viento (± DE calculada utilizando la distribución binomial); B, abundancia de invertebrados (± DE) entre los hábitats de lodo y de agua en relación con la dirección (barlovento o sotavento) y la categoría del viento (fuerte o ligero).

the leeward shore and the water column moves so rapidly that prey are exposed on the muddy surface on the windward shore (Verkuil et al., 1993), facilitating predation. Second, in addition, under strong wind conditions, the prey abundance index is relatively low at the water column in both positions relative to the wind, while the frequency of waders feeding in water does not vary so much on leeward and windward sides. This suggests that the prey abundance index may be affected by turbidity and tends to underestimate prey abundance under these conditions, while waders may overcome this problem, at least partially, using tactile senses to forage (Estrella and Masero, 2007).

The visual counts of invertebrates identified Anostraca, Copepoda, and Ostracoda as the main groups. At Lake Alcahozo, these groups are represented by *Branchinectella media* (Anostraca), *Arctodiaptomus salinus* (Copepoda) (Pons et al., 2018) and *Heterocypris barbara* (Ostracoda) (Castillo–Escrivà et al., 2015). Information about spatial distribution and habitat selection is available only for *B. media*. Pons et al. (2018) investigated the spatial distribution of *B. media* on days without wind and observed that adult individuals tend to occur on the central region of the lake, while juveniles are most commonly observed on the shore. Although our visual counts were only a proxy of prey abundance and availability, they showed the direction and wind speed are important factors influencing the spatial distribution of potential prey items, including *B. media*.

For both wind speed categories (smooth and strong), our results provide evidence that feeding flocks of dunlin and little stint seek to select sites with the highest abundance of prey. They therefore change their spatial distribution according to the wind conditions. However, we did not take into account the potential influence of predators or other birds that could influence habitat choice irrespectively of wind. Although we did not observe any predation attempts, the approximation of some species such as the lesser black–backed gull (*Larus fuscus*), the black–headed gull (*L. ridibundus*) and the Eurasian marsh harrier (*Circus aeruginosus*) often forced the flocks to change their foraging behavior. Specifically,

Table 1. Tests of interactions of factors in habitat use models of waders (log–linear models) and invertebrate abundance (GLMM). Interaction terms were tested by removing each interaction in turn and comparing resulting models using the χ^2–test: Ws, wind speed; P, position; H, habitat.

Tabla 1. Prueba de interacciones de factores en los modelos de uso del hábitat de los limícolas (modelo log–lineal) y abundancia de invertebrados (modelo mixto lineal generalizado). Los términos de la interacción se pusieron a prueba eliminando todas las interacciones por turnos y comparando los modelos resultantes con el uso de la χ^2: Ws, velocidad del viento; P, posición; H, hábitat.

Interaction	χ^2	df	*p*–value
Wader flock habitat			
Ws x P x H	3,95	1	0,0468
Invertebrate abundance			
Ws x P x H	0,95	1	0,3288
Ws x P	82,79	1	< 0,001
Ws x H	588,27	1	< 0,001
P x H	69,59	1	< 0,001

the waders presented three responses: short distance displacement before their immediate return to the same site; long distance displacement without return to the foraging site; and interruption of feeding. In addition, during the winter, we observed more than 1,500 gulls (*Larus* spp.) gathered to roost at the lake, and depending on the location chosen to settle, their arrival could have been a physical barrier to the habitat use of the waders. However, the gulls always roosted 50–60 m from the shoreline and therefore did not directly influence the habitat use of waders. Such effects on waders using these inland wetlands should be considered in research on the habitat selection by waders.

Findings in this study add to our understanding of factors influencing the foraging patterns of small–sized waders in inland (non–tidal) lakes. Wetlands in central Spain, especially in the region of the 'La Mancha Húmeda' Biosphere Reserve, are generally surrounded by plantations and most of the lakes have no physical protection limiting the advance of the agricultural frontier (Gonçalves et al., 2018b). The shore topography of some of these lakes has been modified in the past by agricultural and infrastructure works, including transformations for receiving wastewater from nearby towns (Gonçalves et al., 2018a). Thus, artificial modifications of the topography of inland lakes that limit availability of some preferred habitats under some wind conditions could reduce the suitability of these wetlands for wintering waders.

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