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Patrones espacio-temporales y ecología del comportamiento de aves limícolas en lagunas continentales

Spatial-temporal patterns and behavioral ecology
of waders in inland wetlands

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“En toda respuesta posible
debería haber otra
pregunta”

Wislawa Szymborska

Dedicado especialmente a mi hija,
Maria Isabel.

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Resumen

Esta tesis trata sobre las aves limícolas residentes y migratorias de los ecosistemas húmedos continentales en España. El área de estudio es el complejo de lagunas de la región central de España, insertadas en la Reserva de la Biosfera "La Mancha Húmeda". La base de datos que permitió la confección de los capítulos de este documento fue construida a lo largo de más de una década de monitoreo de lagunas salinas temporales y permanentes de la región de Castilla La Mancha, sumados a los recogidos entre 2014 y 2017 en el Complejo Lagunar de Manjavacas. La tesis se distribuye en 7 capítulos que tratan de la ecología y conservación de humedales continentales. Así, en el capítulo 1 se presenta un marco general introductorio; el capítulo 2 evalúa los patrones de riqueza de aves limícolas en los períodos de reproducción y estación invernal; el capítulo 3 observa un fenómeno ecológico conocido como sincronía espacial de poblaciones, teniendo como especies-modelo *Recurvirostra avosetta*, *Himantopus himantopus* y *Charadrius alenxandrinus* (limícolas residentes); el capítulo 4 trata de la distribución espacio-temporal de *Calidris alpina* (limícola invernante), con énfasis en los movimientos locales dentro del Complejo Lagunar de Manjavacas y; el capítulo 5, observa cómo el uso de hábitat por limícolas invernantes es influenciado por factores abióticos, particularmente las condiciones de dirección e intensidad del viento. Dentro de los muchos factores asociados a los principales resultados de estos capítulos, tanto en las preguntas a nivel de comunidades (capítulo 2), como en el nivel de poblaciones y comportamiento (capítulos 3, 4 y 5), el hidroperiodo de las lagunas, es decir, el tiempo con agua de un ciclo anual que puede estar motivado o no por la entrada de aguas residuales, fue un factor ambiental importante asociado de forma directa o indirecta a los resultados alcanzados.

Finalmente, los capítulos 6 y 7 presentan un resumen global y principales conclusiones de la tesis, reflexionando sobre la relevancia teórica y práctica de los resultados, así como destacando el bajo grado de conservación de las zonas húmedas continentales de España, sobre todo aquellas distribuidas en la Reserva de la Biosfera "La Mancha Húmeda".

Palabras-clave: Aves acuáticas, lagunas, fenología, riqueza de especies, sincronía espacial, ecología del forrajeo, hidroperíodo, actividades humanas, aguas residuales, conservación

Abstract

This thesis deals with resident and migratory wading birds of the inland lakes of Spain. The study area is the wetlands complex in central Spain, inserted in the "La Mancha Húmeda" Biosphere Reserve. The database that allowed the preparation of the chapters of this document was constructed over more than a decade of monitoring of temporary and permanent lakes in the La Mancha region, with the addition of data collected between 2014 and 2017 in the Manjavacas Lagoon Complex. The thesis is divided into seven chapters dealing with the ecology and conservation of continental wetlands and wader birds. Chapter 1 presents a general introdutction; chapter 2 assesses the richness patterns of waders in breeding and wintering seasons; chapter 3 observes an ecological phenomenon known as spatial synchrony of populations, analyzing the variations of abundance of three wader species – *Recurvirostra avosetta*, *Himantopus himantopus* and *Charadrius alexandrinus*; chapter 4 deals with the spatiotemporal distribution of *Calidris alpina*, with emphasis on local movements within the Manjavacas Lagoon Complex; chapter 5 observes how habitat use by waders is influenced by abiotic factors, particularly direction and wind intensity. Among the many factors associated with the results of these chapters, the hydroperiod of the lakes (time with water during an annual cycle influenced or not by wastewater input) was the most important environmental factor. Finally, chapters 6 and 7 present an overall summary and the main conclusions of the thesis, reflecting on the theoretical and practical relevance of the informations, as well as highlighting the low degree of conservation of the continental wetlands of Spain.

Keywords: waterbirds, lakes, phenology, species richness, spatial synchrony, foraging ecology, hydroperiod, human activities, effluents, conservation.

Listado de artículos

Tesis Doctoral ha sido escrita en la modalidad de compendio de artículos. Los artículos I, II y IV están publicados o aceptados. Consta de las siguientes publicaciones:

I. Gonçalves, M. S., Gil-Delgado, J. A., Gosalvez, R. U., López-Iborra, G. M., Ponz, A., & Velasco, A. (2018). Seasonal differences in drivers of species richness of waders in inland wetlands of the “La Mancha Húmeda” Biosphere Reserve. *Aquatic Conservation: Marine and Freshwater Ecosystems*. Doi:10.1002/aqc.2968.

II. Gonçalves, M. S. S., Gil-Delgado, J. A., Gosálvez, R. U., López-Iborra, G. M., Ponz, A., & Velasco, A. (2016). Spatial synchrony of wader populations in inland lakes of the Iberian Peninsula. *Ecological Research*, 31, 947–956. Doi: 10.1007/s11284-016-1407-2

III. Gonçalves, M. S. S., Gil-Delgado, J. A., Gosálvez, R. U., López-Iborra, G. M., Ponz, A., & Velasco, A. Spatiotemporal patterns of dunlin (*Calidris alpina*) in continental lakes of the Iberian Peninsula. *Biorxiv*. Doi: 10.1101/434886

IV. Gonçalves, M. S. S., Gil-Delgado, J. A., López-Iborra, G. M., & Pons, P. (in press). Wind effects on habitat use by wintering waders in an inland lake of the Iberian Peninsula. *Animal Biodiversity and Conservation*, vol 42.

Los artículos no se presentan en un orden cronológico de publicación sino en un orden lógico para una mejor comprensión del trabajo global. Los artículos forman los principales capítulos de la Tesis, dejando el formato original con los que han sido o van a ser publicados.

Capítulo 1

Introducción general

Las áreas húmedas en su estado natural son fuentes de beneficio sustancial para la sociedad: almacenamiento de agua, protección contra inundaciones, recarga y descarga de acuíferos, purificación del agua, recreación y producción de granos y energía son algunas de las muchas funciones y valores que estos ecosistemas proporcionan (Vuuren & Roy, 1993). Esto hace que las áreas húmedas estén entre los ecosistemas más productivos de la Tierra, con enorme importancia ecológica y social para la humanidad, siendo la disponibilidad de los recursos hídricos un aspecto extremadamente importante para la sostenibilidad de una región (Taylor et al. 1995).

Por otra parte, más del 50% de los humedales alrededor del mundo ya han sido destruidos o modificados (Davidson, 2014). Entre los diferentes tipos de ecosistemas húmedos, aquellos situados en el interior de los continentes están más amenazados que los situados en las áreas costeras (Mitsch & Gosselink, 2009). Esto es particularmente importante ya que los humedales continentales representan alrededor del 6% de la superficie de la tierra, con lo cual solo 11% están clasificadas como áreas prioritarias para la conservación (Reis et al., 2017).

Europa es una de las regiones más desarrolladas económicamente, pero solo 14,9% de los humedales continentales están protegidos legalmente (Reis et al., 2017). Este porcentaje es claramente inferior al que nos encontramos en América Central (20,3%), América del Sur (17,8%) y Oceania (15,4%) (Reis et al., 2017). Paradójicamente, entre los países europeos, los humedales de España central tienen uno de los mejores indicadores de la Unión Europea. Particularmente en la región central de España, en Castilla La Mancha, existe una constelación de al menos 1500 humedales distribuidos en miles de hectáreas, los cuales la gran mayoría están protegidos por un diverso número de figuras de protección internacional (Florín & Montes, 1999), tales como la Reserva de la Biosfera de la UNESCO “La Mancha Húmeda”, sítios Ramsar, Sitios y Hábitats de Importancia para la Unión Europea, Parques Nacionales, Parques Naturales, Reservas Naturales, Monumentos Naturales y Microrreservas.

Desafortunadamente, muchas de estas figuras de protección son llamadas 'parques de papel', porque su estatus legal solo está presente en el papel. Esta situación ha colaborado para la ausencia de manejo y protección física de los humedales, facilitando el avance de la frontera agrícola y la gradual fragmentación y destrucción de esos ambientes (Cubero-Rivera, 2015). Sin embargo, tan importante en cuanto a la alteración de la estructura física promovida por las actividades humanas adyacentes, se resalta la dramática situación de la dinámica hídrica de estos ecosistemas (Martinez-Santos et al., 2008). La sustracción y la canalización del agua para irrigación de los extensos cultivos en los últimos 30 años han cambiado la capacidad de aporte de agua en los períodos de lluvia, acortando el hidroperíodo de los humedales manchegos (Florín & Montes, 1999). Además, las lagunas cercanas a las zonas urbanas se utilizan como punto de descarga de aguas residuales, que ha influido no sólo en el cambio de la composición bioquímica del agua, como la potenciación de la aparición de brotes de botulismo, matando a miles de aves en las últimas décadas (Anza et al., 2014; 2016).

En este contexto, se sabe que a medida que los ecosistemas húmedos son fragmentados, el tamaño y la función de esos remanentes van siendo modificados, sin que haya un completo entendimiento sobre esos eventos en la biodiversidad (Sharpe et al., 1981; King et al., 2010). Además de la forma y la conectividad de las áreas, el área total de hábitats disponibles en la escala del paisaje también se reduce durante el proceso de alteración y destrucción (Fahrig 2002, Villard et al., 1999), y la nueva matriz modificada reduce la permeabilidad los movimientos de animales entre los sítios (Johnson et al., 1992, Johnson & Boeriijst, 2002).

Hay miles de especies amenazadas de extinción en el mundo, de las cuales más del 80% sufren con la destrucción y fragmentación de áreas naturales (Baillie et al., 2004). Interesantemente, las áreas alteradas pueden permanecer hospitalarias para una parte de la biodiversidad, complementando o suplementando sus necesidades de recursos (Brotons et al., 2003; Norton et al., 2000). Este es el caso de los humedales continentales ibéricos que aunque estén bajo fuerte presión humana, estos sistemas mantienen recursos y condiciones para una importante parcela de la biodiversidad ibérica (Gosálvez et al., 2012). Por ejemplo, ésta región sirve de escala para muchas aves acuáticas reproductoras y migratorias, incluyendo especies amenazadas como el avetoro-común (*Botaurus stellaris*), la garcita-real (*Ardeola ralloides*), la cigüeña-negra (*Ciconia nigra*), el porrón pardo (*Aythya nyroca*) y la malvasía cabeciblanca (*Oxyura leucocephala*) (Gosálvez et al., 2012; SEO/BirdLife, 2012).

Entre los diversos grupos de animales que componen los ecosistemas húmedos, las aves acuáticas se sitúan en el grado máximo de alerta de conservación debido al declive de sus poblaciones (Mitsch & Gosselink, 2009). Las aves acuáticas necesitan utilizar múltiples hábitats diariamente y estacionalmente para satisfacer sus necesidades de alimentación, descanso y reproducción, siendo potencialmente vulnerable la fragmentación del paisaje y cambios en la estructura del hábitat (Conners et al., 1981; Gibbs, 1991; Warnock & Takekawa, 1996; Weaver & Charles, 2002). Además, muchas aves acuáticas vuelan en altitudes que les permiten evaluar el paisaje en escalas amplias, probablemente seleccionando hábitats de alimentación, refugio y reproducción, en un proceso jerárquico de aproximación (Johnson et al., 1992). Esto es particularmente importante ya que, como consecuencia de los movimientos entre los lugares de invernada, reproducción y alimentación, las aves acuáticas desempeñan un papel vital en el intercambio de nutrientes entre sistemas acuáticos y terrestres (Figuerola & Green, 2002).

Las aves acuáticas poseen una amplia diferenciación de nichos debido a la alta diversidad morfológica, taxonómica y ecológica, y por lo tanto, este grupo de especies constituyen excelentes indicadores ambientales (Green & Elmberg, 2014). Particularmente, dentro del grupo de aves acuáticas, las aves limícolas constituyen un grupo ecológico diferenciado. Las especies de este grupo son mayoritariamente representadas por la Orden Charadriiformes y aunque algunas pocas especies pueden observarse más frecuentemente en sistemas no definidos como zonas húmedas, en general están asociadas a los habitats con aguas poco profundas, dulces o saladas, notablemente en las zonas estuarinas y costeras. Una característica notable de la mayoría de las especies de este grupo son las largas y periódicas migraciones continentales e intercontinentales, en parte como consecuencia de las bajas temperaturas y el dominio de la nieve en las áreas de reproducción (Evans, 1976). Interesantemente, este patrón general tiene excepciones. Por ejemplo, algunas especies de limícolas migratorios pueden pasar la invernada en las frías costas noruegas (Greenwood, 1984), utilizando ambientes menos proclives a congelarse y sugiriendo adaptaciones locales para sobrevivir en condiciones de bajas temperaturas.

La Península Ibérica es una región geográfica muy importante para un gran número de aves limícolas migratorias, especialmente durante los meses de otoño, invierno y primavera, cuando las aves de Europa septentrional y central hacen sus migraciones de ida y vuelta hacia las zonas costeras del sur del continente europeo y las regiones costeras de África (Piersma et al., 2006). Por otra parte, las zonas húmedas continentales que se intercalan entre estos puntos de partida y de destino son muy importantes para reponer fuerzas antes de continuar con la migración hacia las áreas de invernada (Piersma et al., 2006). Este es el caso de los humedales en España central, que como pueden comprobarse en los mapas de distribución observados en el BirdLife International (2018), muestran que no solo se utilizan durante la época de reproducción, sino también como sitio de invernada anual de limícolas migratorios.

Sin embargo, en paisajes marcados por la actividad agrícola, como la región central de España, los efectos del hábitat y del paisaje en la estructura de las comunidades acuáticas son altamente significativos (Elphick 2008; Guadagnin 2005; Devictor & Jiguet, 2007). En particular, los patrones espaciales de aves limícolas se han asociado frecuentemente a la altura de la profundidad, la superficie de hábitat adecuado para el forrajeo y la cantidad de presas (Piersma, 2006; Granadeiro et al., 2007; Beerens et al., 2015a, b). En lo que se refiere a las variaciones temporales, éstas dependen no sólo de los cambios en las condiciones del hábitat, sino también de la estacionalidad de los movimientos migratorios y de los desplazamientos regionales (García et al., 1997).

En este contexto, estudios de biodiversidad se convierten en herramientas importantes para la elaboración de estrategias de conservación en paisajes fragmentados (Barbosa & Callisto, 2000). Aunque muchos patrones y procesos ecológicos son bien conocidos para las aves limícolas costeras, poco se conoce en zonas húmedas distribuidas en el interior de los continentes y, claramente, monitoreo de larga duración son esenciales para reconocer no sólo las distribuciones geográficas, pero también sus tamaños poblacionales y sus interacciones ecológicas. Además, conocer los patrones espacio-temporales de grupos indicadores y sus procesos asociados son piezas claves para identificar estrategias de manejo y conservación de estos ambientes, e indicar el estado actual de mantenimiento de los servicios ecológicos.

Justificación y objetivos

Las últimas décadas fueron marcadas por una revolución en cuanto al grado de preocupación con las aves de ambientes acuáticos, especialmente en virtud de sus descensos poblacionales a escala global. Se suma a ello, la intensa modificación y fragmentación de los humedales continentales cuando se compara con ambientes costeros y el bajo grado de conocimiento de muchos grupos biológicos que ocupan permanentemente o temporalmente estos ambientes. Esta tesis trata sobre la ecología de aves limícolas en lagunas interiores de España (Castilla La Mancha). Los factores ambientales en la escala local (hábitat) y/o paisaje, y sus efectos en los patrones espaciales y temporales de aves limícolas en diferentes niveles ecológicos (comunidad, poblaciones y comportamiento) constituyen el núcleo central de esta tesis. La tesis está distribuida en 7 capítulos, de los cuales el primero de ellos explora un marco general, abordando el contexto ambiental y conservacionista de los ecosistemas húmedos continentales de España y del objeto de estudio seleccionado para la investigación – aves limícolas. El capítulo 2 trata de los factores de hábitat y paisaje que condicionan la riqueza de especies de aves limícolas durante los períodos de reproducción e invernada. En consecuencia, el capítulo 3 buscó comprender si las curvas temporales de abundancia de poblaciones limícolas entre diferentes humedales están correlacionadas, es decir cuando dos o más áreas presentan curvas variando igualmente en la misma fase de tiempo, un fenómeno ecológico conocido como sincronía espacial. Para ello, los valores de abundancia mensual de tres limícolas reproductores se utilizaron como modelos. El capítulo 4 buscó describir los patrones espaciales de abundancia en dos períodos – invernal y no invernal – de una de las especies invernantes más abundantes en la Península Ibérica (correlimos común). En adición, dado que la vasta mayoría de los registros estuvo concentrada en apenas dos lagunas, ambas pertenecientes al Complejo Lagunar de Manjavacas, un análisis más detallado de las variaciones de abundancia de esa especie fue realizada, buscando comprender potenciales movimientos locales de los individuos y sus factores asociados. El capítulo 5 buscó comprender cómo el uso de hábitat local de limícolas invernantes es influenciado por factores bióticos (cantidad de presa) y abióticos (dirección e intensidad del viento) en la principal área de invernada del Complejo Lagunar de Manjavacas – laguna Alcahozo. Este documento se concluye con un resumen global (capítulo 6) y conclusiones (capítulo 7), donde se destacan una reflexión referente a la conservación de las zonas húmedas continentales de España, así como los hallazgos principales de las investigaciones de esta tesis.

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Capítulo 2

Seasonal differences in drivers of species richness of waders in inland wetlands of La Mancha Húmeda Biosphere Reserve

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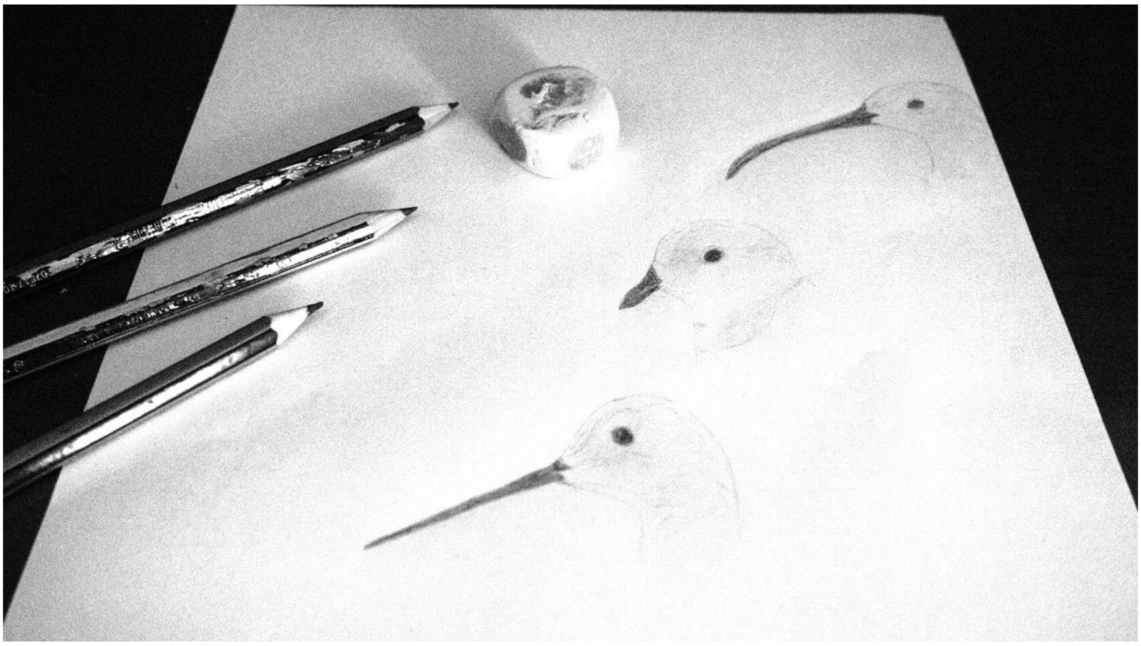

Géneros: ***Tringa, Charadrius*** **y** ***Limosa***

Aquatic Conservation: Marine and Freshwater Ecosystems, Doi:10.1002/aqc.2968.

SEASONAL DIFFERENCES IN DRIVERS OF SPECIES RICHNESS OF WADERS IN INLAND WETLANDS OF THE “LA MANCHA HÚMEDA” BIOSPHERE RESERVE

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Abstract

1. Temporary inland wetlands are among the most threatened ecosystems worldwide and recognition of the factors that determine species richness in different seasons is key for developing conservation plans for these systems. The "La Mancha Húmeda" Biosphere Reserve in central Spain has many inland wetlands of this type but driving ecological processes of species richness are poorly understood.
2. This study examines the association of landscape and local variables with species richness patterns of inland wetlands of the “La Mancha Húmeda” Biosphere Reserve during winter and the breeding season. The number of lakes in several increasing radii was a proxy of connectivity and maximum flooded surface and shoreline length were surrogates of the species-area relationship.
3. Other landscape and local habitat variables, such as hydroperiod (length of inundation period), distance from human settlements, shoreline development index, vegetation surface cover, average lake depth, number of existing islands and surface of islands were also analyzed. Hierarchical partitioning analysis was used to evaluate the contribution of the environmental variables to explain the species richness of waders.
4. Species richness (26 species, 4 threatened in Europe) had different associations with the variables during wintering and breeding seasons. The richness of breeding and wintering species was positively associated respectively with hydroperiod and maximum flooded surface. No variable measured was negatively associated with the species richness in any season.

5. Hydroperiod and flooded surface are altered directly by human activities. Water extraction for irrigation reduces hydroperiod in some wetlands while wastewater input extends hydroperiod in others, promoting wader concentrations in lakes flooded in summer and potentially favoring botulism outbreaks. In addition, the lack of protection and management on most the lakes in “La Mancha Húmeda” Biosphere Reserve also favours encroachment of agriculture, destroying and degrading habitat for wintering and breeding waders.

Keywords: conservation, continental wetlands, flooded surface, Iberian Peninsula, human activities, hydroperiod, seasonal variation, temporary lakes, wader species richness

1. Introduction

Natural inland wetlands are among the most threatened ecosystems worldwide (Kingsford, Basset, & Jackson, 2016). Understanding drivers of ecological patterns and processes is critical to effective biodiversity conservation. In particular, inland wetlands form habitat patches or fragments across landscapes, allowing analysis of the mechanisms to be investigated. Two processes drive richness patterns in isolated habitat patches: increases with the size of the area and decreases with isolation (Cook, Lane, Foster, & Holt, 2002; Prugh, Hodges, Sinclair, & Brashares, 2008). Many other integrated processes can also drive species richness patterns (Skórka, Martyka, & Wójcik, 2006; Keil et al., 2012). Degradation or habitat fragmentation may alter the shape and connectivity of patches by reducing the total area available at the landscape scale (Fahrig, 2003) and decreasing species richness (Peintinger, Bergamini, & Schmid, 2003; Guadagnin & Maltchik, 2007; Guadagnin, Maltchik, & Fonseca, 2009). This problem may be accentuated for continental natural wetlands where habitat loss is more rapid than in coastal wetlands (Davidson, 2014).

La Mancha Húmeda Biosphere Reserve (hereafter referred to as MHBR) in the central Iberian Peninsula is characterized by inland wetlands of high conservation value in Europe. The reserve was established in 1980 and includes more than 25,000 ha of temporary and permanent wetlands (Crespo, García, & Bravo, 2011). Many inland wetland types occur in the reserve, varying significantly in shape, area, hydroperiod (length of inundation period), habitat characteristics, biodiversity and threats (Florín & Montes, 1999; Hera & Villarroya, 2013; Doña et al., 2016). Most of these wetlands are classified as Ramsar Sites and Important Bird Areas (Crespo et al., 2011; Infante, Fuente, & Atienza, 2011). In addition, most of the wetlands of the MHBR are also designated within two Natura 2000 sites. These share the same name – Humedales de la Mancha – one is a Special Protection Area (SPA) (code ES0000091) designated under the Birds Directive (Council of the European Communities, 2010) and the other is a Special Area of Conservation (SAC) (code ES4250010) designated under the Habitats Directive (Council of the European Communities, 1992) (Cubero-Rivera, 2015). At a national level, Spain has protected some of these wetlands as Natural Parks and Natural Reserves. However, despite their environmental importance, the landscape has been drastically transformed by agriculture (mainly vineyards, cereal crops and olive groves), and by forestry and pasture land (Crespo et al., 2011). Furthermore, the water regime of these wetlands has changed considerably owing to the overexploitation of aquifers for irrigated agriculture and wastewater inputs from adjacent urban areas (Martinez-Santos, De Stefano, Llamas, & Martínez-Alfaro, 2008; Gonçalves et al., 2016).

Waterbirds use multiple habitats seasonally, playing a vital role in the exchange of nutrients between ecosystems, and structuring ecological communities (Green & Elmberg, 2013). Seasonal variations in waterbird richness may reflect different processes, such as changes in environmental conditions, seasonality of migratory movements, and local displacement of resident species (Dalby, McGill, Fox, & Svenning, 2014; Guadagnin, Peter, Perello, & Maltchik, 2005; Sebastián-González, Sánchez-Zapata, & Botella, 2010; Tomankova, Boland, Reid, & Fox, 2013). In the MHBR region, the variability of rainfall during the breeding season affects the temporal abundance of resident species, which may be forced to move to other wetlands in the late summer, returning in the winter (Gonçalves et al., 2016). On the other hand, whereas most of the migratory populations use the region as a stopover site, species such as dunlin (*Calidris alpina*) and little stint (*C. minuta*) occupy the region all winter (Birdlife International, 2015). In addition to species' phenology, other factors commonly linked to species richness can also vary between seasons. For example, during the wintering period, species prioritize sites for foraging and resting, but are more selective during breeding, requiring safe environments for nesting and suitable habitats for foraging (Pino, Roda, Ribas, & Pons, 2000; Sebastián-González et al., 2010; Cherkaoui, Hanane, Magri, Agbani, & Dakki, 2015; Hamza, Hammouda, Selmi, 2015).

Effective conservation of wetlands depends on understanding how these factors affect species richness between different seasons (Ma, Cai, Li, & Chen, 2010). The aims of this study were to identify the effects of landscape and local factors on wader species richness during wintering and breeding seasons in inland wetlands of the MHBR. In addition, this article considers the conservation status of these wetlands, highlighting the degree of protection and the inefficiency of the management plans in maintaining this important ecosystem in the central Iberian Peninsula.

2. Methods

Study area

The MHBR is in Castilla-La Mancha, central Spain (Figure 1), an extensive semi-steppe landscape on slightly undulating and predominantly agricultural terrain (Crespo et al., 2011). In general, MHBR wetlands are shallow, saline and in closed drainage basins (endorheic), where water flows to a central point and is temporarily retained (Crespo et al., 2011; Castillo-Escrivà, Valls, Camacho, Rochera, & Mesquita Joanes, 2017). The region experiences an average temperature of 14.7 ºC, and average annual rainfall of 300-500 mm (Martinez-Santos et al., 2008), with low to no precipitation levels in summer (July-October). Thus, the wetlands are usually hydrologically stable between January and February after autumn and early winter rains, with some water usually remaining until mid-summer (Gonçalves et al., 2016). This is strongly altered in some sites by wastewater input, which prolongs the hydroperiod and changes physical-chemical conditions from hypersaline to fresh water (Castillo-Escrivà et al., 2017).

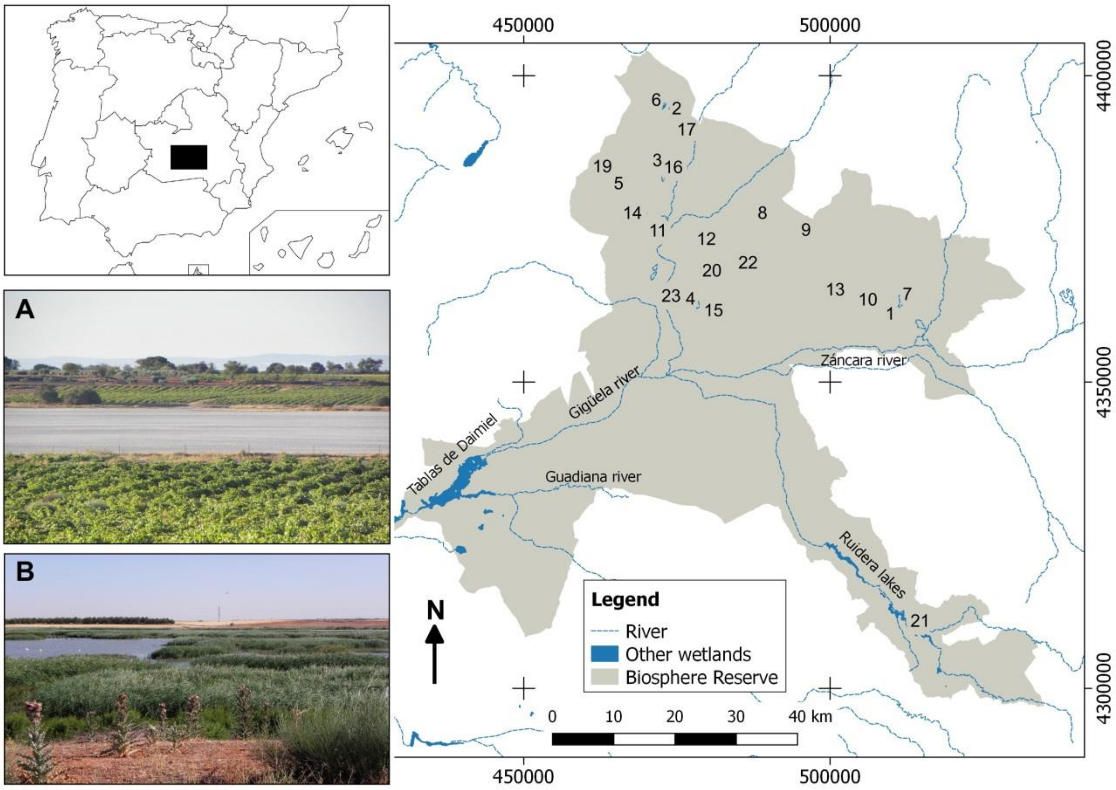


Figure 1. Location of the twenty-three lakes (identification codes are in Table 1) monitored in "La Mancha Húmeda" Biosphere Reserve, central Spain. Pictures: A: Alcahozo lake (Lake 1), a saline lake marked by a short annual hydroperiod, without influence of wastewater and surrounded by extensive vineyards. B: Pedro Muñoz lake (Lake 10), a typical lake with wastewater input, marked by long annual hydroperiod and dense aquatic vegetation at the edge.

Bird survey protocol and migration status

Twenty-three lakes formally included in national and/or international protection zones were selected for the study (Tables 1 and 2). The lakes were monitored monthly (October 2010-February 2014), with 10 lakes also monitored over a longer period, starting in October 2006. Counts were made in the last week of each month (08:00h - 12:00h), when climatic conditions were favourable (with little wind or no rain). In each lake, the same researcher counted birds (using telescopes of 20-60x65 and 20-60x80) from fixed observation points that provided the best views of the lake area. Following BirdLife International (2017), species were classified into three categories, reflecting their temporal pattern of habitat use in the Iberian Peninsula: resident (using a habitat throughout the year, including for breeding), breeding (species present only in the breeding season), and non-breeding (using a habitat, but not normally for breeding). For the breeding season, only breeding and resident waders with occurrences in May, June and July were included (comprising 21 monthly counts for the lakes monitored in the extended period and nine counts for the rest of the lakes). For the wintering period, all species with occurrences in December, January and February were analysed (comprising 24 counts for the lakes monitored in the extended period and 12 samples for the rest).

Environmental variables

Thirteen environmental variables were analysed per lake (Table 1). They were separated into two groups: i) landscape variables (distance from human settlements and number of lakes within three radii, 2 km, 5 km and 10 km), and ii) local variables – hydroperiod: length of inundation period calculated as the percentage of months with water (October 2010 – February 2014), shoreline length, shoreline development index, average lake depth, total lake surface area, maximum flooded surface area, surface area with natural vegetation surrounding the lake, number of sedimentary islands, and total surface area of sedimentary islands). Maximum flooded surface area was defined by the vegetation marking the edge of lakes. Similarly, shoreline length is the perimeter along a lake’s edge added to the perimeter of the sedimentary islands. The shoreline development index (D L) is the ratio between the total shoreline length (lake’s edge plus island edges) and its shoreline length if it were circular with the same area (Kent & Wong, 1982; $DL = \mathrm{L}/(2\sqrt{rA})$, where L is the lake shoreline length and A the lake area). The average depth is the difference between the average of the altitude above sea level at the four cardinal points on the lake’s edge and the altitude of the deepest point of the lake. Data for these variables were obtained by fieldwork and from the geographical viewer Iberpix (Spanish National Geographic Institute) and Google Earth Pro Version 2015.

Data analysis

As census effort differed among wetlands, sampled-based extrapolation curves (Colwell et al., 2012) calculated with program EstimateS 9.1.0 (Colwell, 2013) were used to estimate total comparable richness in the wetlands, sampled over the short time period. Curves were extrapolated to 21 and 24 samples (months), for the breeding and wintering periods respectively. This procedure made the most of the available information for each wetland but, to check if extrapolation was biased, the data were also analysed using the same surveys performed in the common census period for all the sites. The results of the latter analyses are presented as Supporting Information. To reduce the effects of collinearity among environmental variables, Pearson's correlation (r) were calculated; pairs of variables with r-value above 0.7 were identified, and only the variable of most biological importance was retained in the analysis (Table S1). Thus, the total lake area (correlated with the flooded surface area and vegetation cover surrounding the lake), the total area of sedimentary islands (correlated with the number of sedimentary islands), shoreline length (correlated with the flooded surface area) and the number of lakes within a 5-km radius (correlated with the lakes in 2 and 10 km radii) were removed from the analysis.

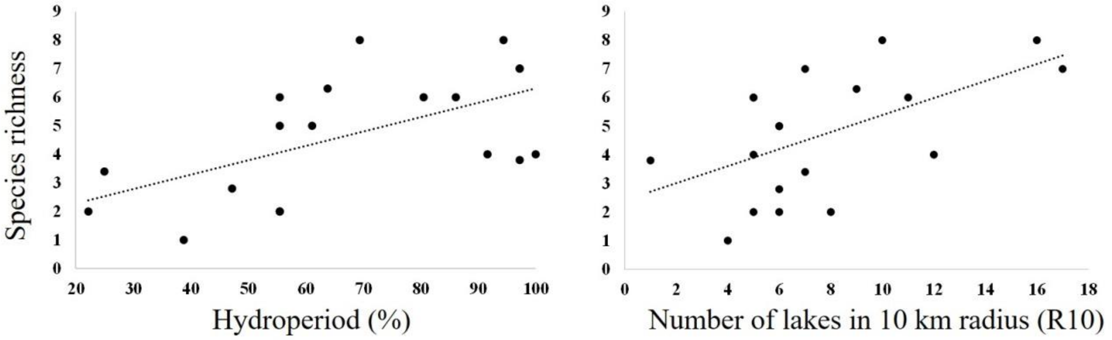
Hierarchical partitioning (HP) analysis, using R^2 as the goodness-of-fit measure, was used to estimate the independent contribution (I) of each environmental variable to explain species richness. The two groups of variables (local and landscape) were tested separately, and a final model with the significant variables of each group was run again using HP. In all the analyses, a spatial term was incorporated to control for spatial autocorrelation. The spatial term was defined from: $x + y + x^2 + xy + y^2 + x^3 + x^2 y + xy^2 + y^3$ (Legendre & Legendre, 1998), using the central UTM coordinates of each lake (López-Iborra, Limiñana, Pavón, & Martínez-Pérez, 2011; López-Pomares, López-Iborra, & Martín-Cantarino, 2015). The significance of the independent contribution of the environmental variables was evaluated by randomization tests based on 999 randomizations (Mac Nally, 2002). Hierarchical partitioning was conducted with the ‘hier.part’ package (Walsh & Mac Nally, 2003) in the R-Program (R Development Core Team, 2016) using the RStudio development environment (RStudio Team, 2015). The spatial association of the environmental variables was explored using the Mantel Test, by constructing a lakes dissimilarity matrix for each environmental variable using Euclidean distance for standardized data, and comparing these matrices with the matrix of distances between sites. The Monte Carlo method with 9999 permutations was used to evaluate significance ($P < 0.05$) (Zar, 2010), using the ade4 package (Thioulouse, Chessel, Dolédec, & Olivier, 1997) in the R-Program.

3. Results

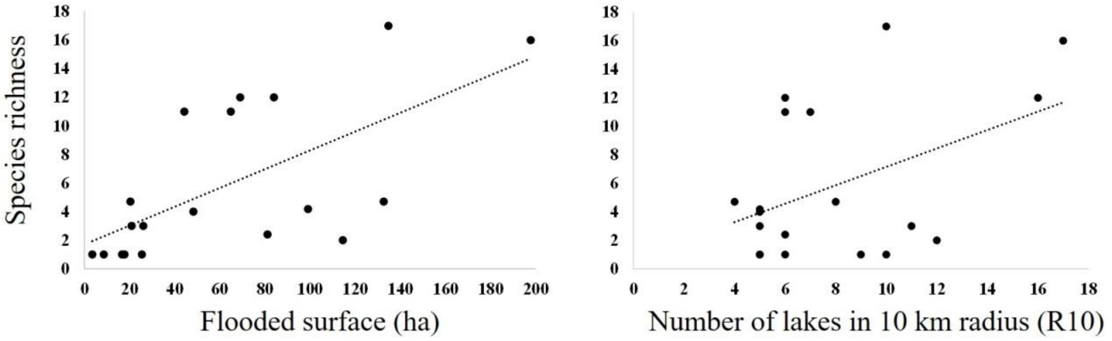
Twenty-six wader species were recorded (Table 3). For both seasons the higher richness values (observed and extrapolated richness) were detected in lakes Camino de Villafranca, Manjavacas, Quero and Veguilla (Table 4). Four of the species are threatened in Europe: curlew sandpiper (*Calidris ferruginea*), black-tailed godwit (*Limosa limosa*), Eurasian curlew (*Numenius arquata*) and northern lapwing (*Vanellus vanellus*). The species that occurred on most lakes were northern lapwing (resident species; 22 lakes), black-winged stilt (*Himantopus himantopus*) and pied avocet (*Recurvirostra avosetta*) (breeding species; 21 lakes), and black-tailed godwit (non-breeding species; 12 lakes) (Table 3).

Except for the number of lakes within a 2 km radius, no environmental variable showed spatial autocorrelation. In the breeding season, the lake hydroperiod and the number of lakes within the 10 km radius were the only significant variables (apart from spatial term), positively explaining the variability in species richness (Table 5; Figure 2). For the wintering season, maximum flooded surface area was the only significant variable, positively related to species richness, but the number of lakes within a 10 km radius was marginally significant ($P=0.08$; Table 5; Figure 2). In order to check if extrapolation could have introduced bias into the data, the analyses considering the same surveys for all the sites identified the same variables in the analyses based on extrapolation (Table S2).

For the breeding period, the final model explained 81% of the deviance, with only hydroperiod contributing significantly to explain species richness (Table 6). For the wintering period, the final model explained 82% of the deviance, with only maximum flooded surface area included as a significant predictor variable (Table 6). In both seasons spatial autocorrelation was important (I> 60%) (Table 6). Final models derived from surveys in the common census period added to the above variables the number of lakes within a 10 km radius (Table S3).



(a) Breeding season



(b) Wintering season

Figure 2. The most significant relationships, according to contribution (Tables 5 and 6), explaining species richness of waders, with lines of best fit.

3. Discussion

Different factors were related to patterns of wader richness in the inland natural lakes of the La Mancha Húmeda Biosphere Reserve, during wintering and breeding seasons. Local factors were more important than landscape variables for lakes in both periods. Breeding species richness was positively associated with hydroperiod, whereas maximum flooded surface area was associated with increased species richness during the wintering season. Both hydroperiod and flooded surface area were altered by human activities.

Waterbirds are vulnerable to changes in habitat structure during breeding (Hoover, 2009; O'Neal, Heske, & Stafford, 2008; Pino et al., 2000; Sebastián-González & Green, 2013). Variation in the water level of temporary wetlands alters habitat availability, structuring wader communities (Jenkins, Grissom, & Miller, 2003; Vanschoenwinkel et al. 2009). For the breeding period, lakes with extended hydroperiods were richer in wader species than those with shorter hydroperiods (Figure 2). This is particularly important because the hydroperiod of natural lakes in the MHBR region has changed due to anthropogenic causes. In wetlands receiving underground water, the hydroperiod contracts as a result of water extraction for agriculture overexploiting the aquifer (Florín & Montes, 1999). In contrast, some endorheic lakes now receive wastewater input (e.g Manjavacas, Quero, Veguilla, Pedro Muñoz, Miguel Esteban, Mermejuela, Larga de Villacañas and Longar) (Gonçalves et al., 2016), extending the hydroperiod in dry years and providing adequate habitat for foraging and breeding during summer months when the water deficit is high. This leads to some breeding wader populations moving from the wetlands with shortened hydroperiods to lakes receiving wastewater.

Wastewater input decreases salinity and increases organic matter in shallow lakes, but with high temperatures in summer it can increase the risk of botulism outbreaks (Vidal et al., 2013), a key factor reducing waterbird populations throughout the world. In the MHBR region, botulism outbreaks have been recorded since 1978 (Vidal et al., 2013), affecting many wader species (Anza, Vidal, Feliu, Crespo, & Mateo, 2016; Minias, Włodarczyk, & Janiszewski, 2016). Specifically, more than 2000 individuals from 19 species died between 1978 and 2008 (Vidal et al., 2013). For black winged stilt, occurring on many lakes in the study area, mortality rates of 1.8% and 85.3% were estimated in two botulism outbreaks in Navaseca Lake (MHBR region), with variation potentially caused by annual differences in turnover rates (Anza et al., 2016). Extended hydroperiod in summer can also attract other waterbird species (particularly moorhens, gulls and mallards), which may carry *Clostridium botulinum* (Anza et al., 2014; Vidal et al., 2013). Long-term monitoring is essential to assess the potential effects of these disturbances on wader species, especially breeding species in lakes with wastewater input and high contamination.

The hydroperiod was not associated with species richness of waders during the wintering season, possibly because water levels were stable. Maximum flooded surface area was the most important predictor in winter (Figure 2), probably because of increased habitat. Similarly, pond size was the factor most related to species richness in spring in a group of experimental ponds in Doñana (Sebastián-Gonzalez & Green, 2013). Guadagnin et al. (2009) also detected a positive relationship between wetland area and waterbird species richness over a year, partly owing to increased microhabitat diversity and individuals in large wetlands. The effect of increased area on waterbird richness is widespread (Brown & Dinsmore, 1986; Rosselli & Stiles, 2012) so it is surprising that in the present study it was only detected in winter. This may have resulted from the strong effect of hydroperiod variation in the lakes studied, overriding the effect of area.

The lakes in the MHBR region have high structural diversity, varying in size, shape and proximity to other wetlands (Doña et al., 2016; Gosálvez, Gil-Delgado, Vives-Ferrándiz, Sánchez, & Florín, 2012; Hera & Villarroya, 2013). Apart from hydroperiod and flooded surface area, lakes within 10 km were related to richness of waders, more intensely during the breeding season and most significantly over the common census period (Table S2). Groups of more than 10 other lakes within this radius had more wader species than lakes that were more isolated. This may reflect daily movements of waders between neighbouring lakes, tracking variation in resource abundance (Sanzenbacher & Haig, 2002). This effect of isolation on species richness is uncommon (Guadagnin et al., 2009; Sebastián-Gonzalez & Green, 2013), and perhaps reflects less isolation of wetlands elsewhere. Other variables related to wader species richness in other studies include average depth (Colwell & Taft, 2000), vegetation cover (Froneman, Mangnall, Little, & Crowe, 2001) and settlement distance (Tavares, Guadagnin, de Moura, Siciliano, & Merico, 2015), but no relationships of these variables were detected, suggesting that their importance may depend on other factors. Other processes, apart from proximity of wetlands, might also explain the importance of spatial dependency.

Conservations implications

The record of 26 species, approximately 40% of the wader species of Spain (SEO/Birdlife, 2012), reinforces the importance of the MHBR lakes for aquatic biodiversity in the Iberian Peninsula. Wader richness in the wintering and breeding periods was related to flood surface area and hydroperiod, respectively, directly influenced by human activities. Bird conservation strategies in MHBR have been focused traditionally on waterfowl affected by similar factors, but other wetland characteristics that benefit waterfowl adversely affect waders. The use and management of water resources in this region is affecting the dynamics of the water level in the MHBR wetlands (Fornés et al., 2000) and consequently the richness of the wader assemblage. In addition, climate change is likely to aggravate these problems, given projections of decreasing rainfall (Estrela, Pérez-Martin, & Vargas, 2012; Ministerio de Medio Ambiente, 2005). Irrigated agriculture strongly drives the economic development of the region; however, calls to reduce the extraction of underground water have been resisted, severely affecting the wetlands (Esteban & Albiac, 2012). Wastewater has restored flooding in some lakes (Florín & Montes, 1999), but changed the chemical composition of water (García-Ferrer, Camacho, Armengol, Miracle, & Vicente, 2003), invertebrate community (Castillo-Escrivà et al., 2017) and vegetation structure and helophyte cover in the shoreline (Florín & Montes, 1999), with impacts on wader habitat.

Only four of the 23 lakes studied (Alcahozo, Camino de Villafranca, Miguel Esteban and Pedro Muñoz lakes) are protected by fences. As a consequence, the wetlands are affected by fire, car trails, dogs and garbage, which have often modified the flooded surface and the slope of the lakes, rendering these areas unsuitable for waders. In addition, despite warnings of the negative consequences of using wastewater for wetland restoration (Florin and Montes 1999), there is no recovery of the original hydroperiod or monitoring of water quality. According to the management plan for the conservation of the Natura 2000 site Humedales de la Mancha (Cubero-Rivera, 2015), the quality of effluent from the sewage treatment systems should be improved by removing mud that has accumulated in wetlands as a consequence of wastewater input. These actions have not been implemented.

In addition to the international designations for site protection, at a national level most of the wetlands studied are classified as Natural Protected Sites, such as Natural Reserves (ecosystems of high singularity and fragility) and, to a lesser extent, as Natural Parks (sites as important as Natural Reserves, but with higher geomorphological and aesthetic values) (Table 2) (Gobierno de España, 2007). These designations should promote the maintenance of environmental quality, but there are few environmental management projects. In addition, the wetlands of the MHBR region are part of private properties or public entities (Table 2). Until recently there was little difference in the legal responsibility between private owners and public entities, but wetlands in private ownership are subject to greater over-exploitation owing to the lack of local or regional management measures (Camacho, 2008).

Bird conservation strategies in MHBR have been traditionally focused on waterfowl affected by similar pressures but other wetland characteristics that benefit waterfowl have adverse effects on waders. The focus of this study on waders has identified factors which could be managed for wader conservation, although much still needs to be learned about their complex population dynamics. There are already a range of management strategies prepared that would improve habitats for waders and meet national and international conservation obligations, but they need to be implemented.

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Table 1. Twenty-three lakes monitored (2006-2014 (*), 2010-2014) in “La Mancha Húmeda” Biosphere Reserve (see Figure 1). Six landscape variables: UTM – Datum ETRS89; “R” – number of lakes present in radii of 2 (R2), 5 (R5) and 10 (R10) km; DH – distance from human settlement (meters). Nine local habitat variables: Area (ha); Flooded surface (ha); Veg – area covered by natural vegetation (ha); Ni – number of sedimentary islands; IsA – total area of existing sedimentary islands (ha); AD – average depth (meters); Hyd – hydroperiod (% of months with water); Leng – shoreline length (meters) and; SDI – Shoreline Development Index.

				Landscape variables				Local variables								
Code	Lake	UTM X	UTM Y	R2	R5	R10	DH	Area	Flooded	Veg	Ni	IsA	AD	Hyd	Leng	SDI
1	Alcahozo*	510620	4360164	1	2	6	5509	88.6	69	19.5	0	0	1.75	58.5	4805	1,63
2	Altillo Grande	474187	4393670	2	3	4	2649	32.9	20.4	12.4	0	0	4.25	43.9	2932	1,82
3	Artevi	472611	4385210	1	1	9	965	27.9	16.7	11.2	0	0	4.75	68.2	3102	2,14
4	Camino de Villafranca*	478055	4362616	0	2	10	2263	159.9	134.7	23.7	2	1.7	2.25	95.1	9181	2,23
5	Campo de Mula	464695	4381452	0	1	6	5483	50.9	25.5	25.3	0	0	3.25	21.9	4038	2,25
6	Longar	472448	4395066	2	3	5	1757	259.5	99.1	160.3	0	0	4	92.6	5895	1,67
7	Manjavacas*	511840	4363360	1	7	17	6639	262.8	197.8	64.0	3	9	2.75	97.5	9872	1,98
8	Mermejuela*	488191	4376617	0	2	5	4834	9.9	8.6	1.2	0	0	6.5	82.9	1374	1,31
9	Miguel Esteban	495294	4373855	0	1	1	1376	92.2	23.4	68.8	0	0	2.5	97.5	3966	2,31
10	Pedro Muñoz*	504589	4362479	2	3	11	362	41.3	26.1	15.2	0	0	3.25	87.8	5936	3,27
11	Peña Hueca	470426	4373729	0	2	8	8880	158.8	132.6	19.6	4	6.6	3.75	58.5	11146	2,73

12	Quero*	478215	4372367	1	6	16	787	95.7	84.0	11.6	0	0	2	70.7	4991	1,53
13	Retamar	502427	4364111	0	3	7	2503	79.1	62.7	16.4	1	4	3.5	21.9	5217	2,21
14	Tírez	469331	4376605	0	2	6	8546	131.8	81.1	50.6	1	0.04	4.25	51.2	6112	1,91
15	Veguilla*	479389	4360715	0	2	7	886	89.0	44.3	44.7	0	0	4.25	97.5	9607	4,06
16	Larga de Villacañas	472815	4384080	2	3	12	1458	167.3	114.5	52.7	0	0	3.25	100	9648	2,54
17	Albardiosa	474994	4390229	0	3	5	5085	71.8	39.5	32.3	0	0	2.5	8.3	3557	1,59
18	Altillo Chica	473975	4394727	2	3	5	1436	24.6	17.8	6.8	0	0	3	55.5	2200	1,47
19	Camino de Turleque	464403	4384224	0	1	4	4082	48.6	39.4	9.2	0	0	5.25	5.5	3097	1,39
20	Pajares*	482321	4367206	0	1	5	4669	23.5	20.9	2.6	0	0	2.75	39	2360	1,45
21	Redondilla	513136	4310021	5	9	10	171	5.7	3.5	2.2	0	0	11	26.8	981	1,47
22	Salicor*	485033	4368502	1	2	5	7161	81.4	48.3	23.7	3	9.2	5.75	55.5	5159	2,09
23	Yeguas*	475657	4363078	1	3	6	4683	96.2	64.9	31.3	0	0	2	61.1	4593	1,6

Table 2. List of studied wetlands distributed in “La Mancha Húmeda” Biosphere Reserve and their respective conservation status. International scale: Biosphere Reserve (CA=Core Area; BZ=Buffer Zone); Ramsar sites (RS); Natura 2000 network (SPA= Special Protection Area and SAC=Special Areas of Conservation). National scale: Protected Area (NR=Natural Reserve; NP= Natural Park).

Lake	Property	Biosphere Reserve	Ramsar	Natura 2000	Protected Area
Albardiosa	Private	CA		SAC/SPA	NR
Alcahozo	Private/Public	CA		SAC/SPA	NR
Altillo Chica	Private/Public	CA		SAC/SPA	NR
Altillo Grande	Public	CA		SAC/SPA	NR
Artevi	Private	BZ		SAC/SPA	
Camino de Turleque	Private			SPA	
Camino de Villafranca	Public	CA	RS	SAC/SPA	NR
Campo de Mula	Private			SPA	
Larga de Villacañas	Private/Public	CA		SAC/SPA	
Longar	Public	CA		SAC/SPA	NR
Manjavacas	Public	CA	RS	SAC/SPA	NR
Mermejuela	Private	CA		SAC/SPA	
Miguel Esteban	Public	BZ			

Pajares	Public	CA		SAC/SPA	
Pedro Muñoz	Public	CA	RS	SAC/SPA	NR
Peña Hueca	Private	CA		SAC/SPA	NR
Quero	Private/Public	CA		SAC/SPA	
Redondilla	Public	CA	RS	SAC	NP
Retamar	Public/Private	CA		SAC/SPA	NR
Salicor	Private	CA		SAC/SPA	NR
Tírez	Private	CA		SAC/SPA	NR
Veguilla	Private/Public	CA	RS	SAC/SPA	NR
Yeguas	Public	CA	RS	SAC/SPA	NR

Table 3. List, migration status (Birdlife International 2017) and conservation status of native wader species in the "La Mancha Húmeda" Biosphere Reserve in decreasing order of relative occurrence.

Species	**Common name**	**Migratory status**	**Lakes**	**Conserv ‡**
Vanellus vanellus	Northern lapwing	resident	22	VU
Himantopus himantopus	Black-winged stilt	breeding	21	LC
Recurvirostra avosetta	Pied avocet	breeding	21	LC
Tringa totanus	Common redshank	resident	14	LC
Charadrius alexandrinus	Kentish plover	resident	13	LC
Limosa limosa †	Black-tailed godwit	non breeding	12	VU
Tringa nebularia †	Common greenshank	non breeding	11	LC
Actitis hypoleucos	Common gandpiper	breeding	10	LC
Calidris alpina	Dunlin	non breeding	10	LC
Calidris canutus †	Red knot	non breeding	8	LC
Calidris minuta	Little stint	non breeding	8	LC
Calidris pugnax	Ruff	non breeding	8	LC
Charadrius hiaticula †	Common ringed plover	non breeding	8	LC
Tringa erythropus	Spotted redshank	non breeding	8	LC
Calidris alba †	Sanderling	non breeding	7	LC
Charadrius dubius	Little ringed plover	breeding	7	LC
Tringa ochropus	Green sandpiper	non breeding	7	LC
Numenius arquata †	Eurasian curlew	non breeding	6	VU
Calidris ferruginea	Curlew sandpiper	non breeding	5	VU
Gallinago gallinago	Common snipe	non breeding	5	LC

Glareola pratincola	Collared pranticole	breeding	4	LC
Pluvialis squatarola †	Grey plover	non breeding	4	LC
Tringa glareola	Wood sandpiper	non breeding	3	LC
Numenius phaeopus †	Whimbrel	non breeding	2	LC
Pluvialis apricaria	Eurasian golden	non breeding	2	LC
Tringa stagnatilis †	Marsh sandpiper	non breeding	1	LC

† Species that according to the maps provided by BirdLife International (2017) are not present in MHBR.

‡ Conserv: Conservation status according to European Red List, available in BirdLife International (2015). Least Concern (LC); Vulnerable (VU).

Table 4. Richness observed (*Obs*) and richness extrapolated (*Ext*) for the breeding and wintering species for each lake, listed in decreasing order of observed breeding species. NW code refers to lakes without waders.

	Species richness			
	Breeding		**Wintering**	
Lake	**Obs**	**Ext**	**Obs**	**Ext**
Quero	8	8	12	12
Camino de Villafranca	8	8	17	17
Manjavacas	7	7	16	16
Veguilla	7	7	11	11
Salicor	6	6	4	4
Pedro Muñoz	6	6	3	3
Mermejuela	6	6	1	1
Alcahozo	5	5	12	12
Yeguas	5	5	11	11
Artevi	5	6.3	1	1
Longar	4	4	3	4.18
Larga de Villacañas	4	4	2	2
Miguel Esteban	3	3.8	NW	NW
Retamar	3	3.4	NW	NW
Peña Hueca	2	2	3	4.7
Tírez	2	2.8	2	2.4
Altillo Chica	2	2	1	1
Campo de Mula	2	2	1	1
Altillo Grande	1	1	3	4.7
Redondilla	NW	NW	1	1

Pajares	NW	NW	3	3
Camino de Turleque	NW	NW	NW	NW
Albardiosa	NW	NW	NW	NW

Table 5. Hierarchical partitioning analyses performed to identify the most important variables within each variable group related to the wader species richness during breeding and wintering seasons. %Dev is the percentage deviation explained by the regression model, including all the analysed variables of each group, with sign indicating significant variables, showing independent variable (I and %I total), joint (J) and spatial variables contributions. P-value: significance of the independent contribution of the environmental variables, evaluated by randomization tests (z-score) based on 999 randomizations.

	Breeding season					Wintering season				
	%Dev/Sign	I	%I	J	p-value	%Dev/Sign	I	%I	J	p-value
Local variables	83%					85%				
Flooded surface		0.02	3.40	0.03	0.63	+	0.15	18.5	0.25	0.03
Vegetation surface		0.02	3.05	-0.02	0.66		0.01	1.99	0.0007	0.69
Shoreline Development Index		0.01	2.24	0.009	0.68		0.005	0.61	0.004	0.75
Hydroperiod	+	0.18	21.9	0.16	0.02		0.06	7.43	0.14	0.46
Number of islands		0.009	1.09	-0.004	0.73		0.03	4.14	0.05	0.60
Average depth		0.002	0.32	0.002	0.77		0.08	9.73	0.17	0.34
Spatial term	+	0.56	67.8	0.21	< 0.001	+	0.48	57.4	0.32	< 0.001
Landscape variables	82%					85%				
Distance from settlement		0.04	5.54	0.02	0.50		0.009	1.11	-0.006	0.69
Number of lakes in 2 km radius		0.02	2.87	-0.008	0.64		0.04	5.39	0.02	0.55
Number of lakes in 10 km radius	+	0.16	20.6	0.14	0.03		0.12	14.6	0.08	0.08
Spatial term	+	0.57	70.9	0.20	< 0.001	+	0.66	78.8	0.13	< 0.001

Table 6. Final model of the Hierarchical partitioning analyses with the variables of the greatest independent contribution of the two groups of species. %Dev is the percentage deviation explained by the regression model, including all the analysed variables of each group, with sign indicating significant variables, showing independent variable (I, %I total), joint (J) and spatial variables contributions. P-value: significance of the independent contribution of the environmental variables, evaluated by randomization tests (z-score) based on 999 randomizations.

	Breeding season					**Wintering season**				
	%Dev/Sign	*I*	*J*	*%I*	p-value	%Dev/Sign	*I*	*J*	*%I*	p-value
Final Model	81%					82%				
Hydroperiod	+	0.15	0.18	19	0.04		-	-	-	-
Flooded surface		-	-	-	-	+	0.21	0.20	26.2	< 0.001
Number of lakes in 10 km radius		0.13	0.17	16.9	0.07		-	-	-	-
Spatial term	+	0.52	0.25	64.0	< 0.001	+	0.60	0.20	73.7	< 0.001

Supporting Information

Table S1. Pearson correlation matrix (r) between all variables. Values in bold highlight Pearson correlations equal or greater than 0.7. In these cases, the variables with lower biological value were excluded from the Hierarchical Partitioning analysis. Variable codes: "R" – number of lakes present in radii of 2, 5 and 10 km; DH – distance from human settlement (meters), Area – total lake surface (ha); Flooded – maximum flooded area (ha); Veg – area covered by natural vegetation (ha); Ni – number of sedimentary islands; IsA – total area of existing sedimentary islands (ha); AD – average depth (meters); Hyd – hydroperiod; Leng – shoreline length (meters) and; SDI – Shoreline Development Index.

	R2	**R5**	**R10**	**DH**	**Area**	**Flooded**	**Veg**	**Ni**	**IsA**	**AD**	**Hyd**	**Leng**	**SDI**
R2	-												
R5	**0,70**	-											
R10	0,27	0,65	-										
DH	-0,47	-0,23	-0,15	-									
Area	-0,10	0,17	0,38	0,24	-								
Flooded	-0,16	0,25	0,59	0,35	**0,90**	-							
Veg	0,03	0,01	-0,05	-0,03	**0,77**	0,43	-						
Ni	-0,21	0,08	0,27	0,61	0,49	0,65	0,03	-					
IsA	-0,13	0,19	0,29	0,53	0,43	0,56	0,04	**0,91**	-				
AD	0,55	0,38	-0,06	-0,12	-0,35	-0,38	-0,19	-0,02	0,02	-			
Hyd	0,04	0,03	0,35	-0,26	0,51	0,42	0,45	0,13	0,09	-0,24	-		
Leng	-0,24	0,01	0,47	0,22	**0,76**	**0,82**	0,36	0,61	0,47	-0,37	0,53	-	
SDI	-0,16	-0,19	0,17	-0,18	0,16	0,14	0,13	0,19	0,14	-0,13	0,44	0,65	-

Table S2. Hierarchical partitioning analyses performed with the common census period for all the sites to identify the most important variables within each variable group related to the wader species richness during breeding and wintering seasons. %Dev is the percentage deviation explained by the regression model, including all the analysed variables of each group, with sign indicating significant variables, showing independent variable (I and %I total), joint (J) and spatial variables contributions. P-value: significance of the independent contribution of the environmental variables, evaluated by randomization tests (z-score) based on 999 randomizations.

	Breeding season					**Wintering season**				
	%Dev/Sign	I	%I	J	p-value	%Dev	I	%I	J	p-value
Local Habitat	71%					71%				
Flooded surface		0.09	13.9	0.08	0.23	+	0.17	25.4	0.25	0.02
Vegetation surface		0.01	2.8	-0.002	0.67		0.03	4.4	-0.02	0.57
Shoreline Development Index		0.03	4.5	0.18	0.63		0.006	0.8	0.005	0.74
Hydroperiod	+	0.18	26.4	-0.03	0.01		0.09	12.7	0.14	0.24
Number of islands		0.03	4.4	0.04	0.61		0.04	6.5	0.08	0.54
Average depth		0.05	7.8	0.07	0.48		0.05	7.5	0.12	0.52
Spatial term	+	0.28	39.9	0.24	< 0.01	+	0.29	42.3	0.28	< 0.01
Landscape	75%					69%				
Distance from settlement		0.12	16.5	0.03	0.12		0.02	3	-0.02	0.34
R2 km		0.02	2.6	-0.01	0.62		0.05	8.5	0.01	0.46
R10 km	+	0.27	36.2	0.16	< 0.01	+	0.17	25.4	0.10	0.02
Spatial term	+	0.33	44.5	0.19	< 0.01	+	0.43	62.9	0.14	< 0.01

Richness species of waders

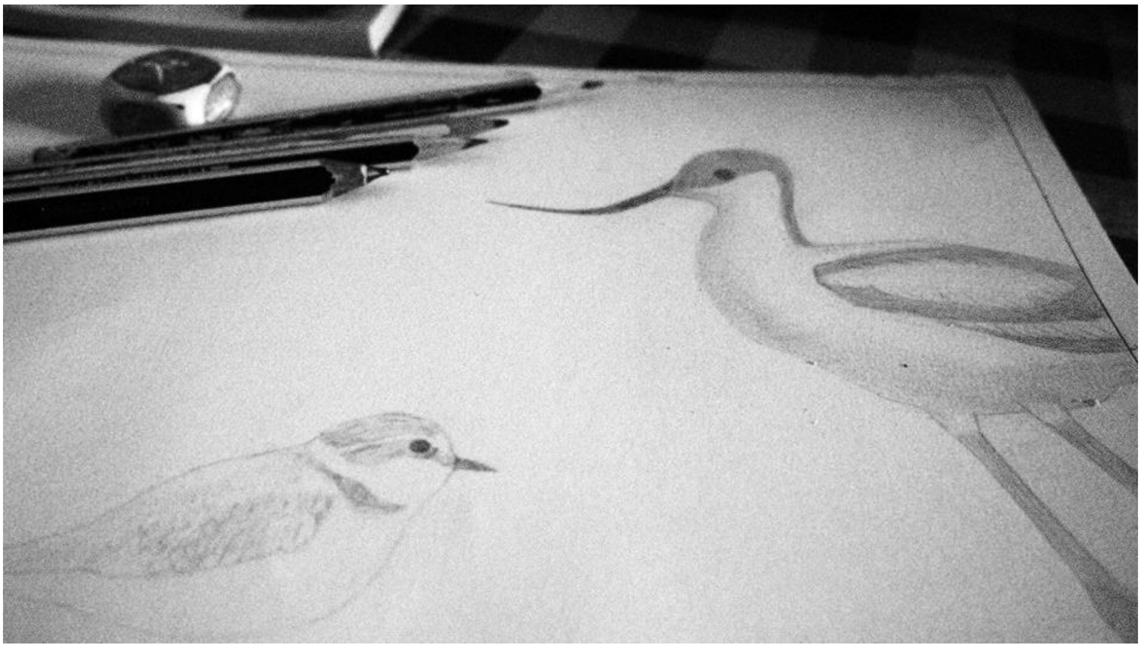
Table S3. Final model of the Hierarchical partitioning analyses performed with the common census period for all the sites with the variables of the greatest independent contribution of the two groups of species. %Dev is the percentage deviation explained by the regression model, including all the analysed variables of each group, with sign indicating significant variables, showing independent variable (I and %I total), joint (J) and spatial variables contributions. P-value: significance of the independent contribution of the environmental variables, evaluated by randomization tests (z-score) based on 999 randomizations.

	Breeding season					**Wintering season**				
	%Dev/Sign	I	%I	J	p-value	%Dev/Sign	I	%I	J	p-value
Final Model	71%					66%				
Hydroperiod	+	0.19	27.7	0.17	< 0.01		-	-	-	-
Flooded surface		-	-	-	-	+	0.19	28.9	0.23	< 0.01
R10 km	+	0.23	32.3	0.20	< 0.01		0.11	17.6	0.16	0.16
Spatial term	+	0.28	39.9	0.24	< 0.01	+	0.35	73.7	0.22	< 0.01

Capítulo 3

Spatial synchrony of wader populations in inland lakes of the Iberian Peninsula

M. S. S. Gonçalves, J. A. Gil-Delgado, R. U. Gosálvez, G. M. López-Iborra, A. Ponz, & A. Velasco



Chorlitejo patinegro (*Charadrius alexandrinus*) y avoceta común (*Recurvirostra avosetta*)

Ecological Research, 31, 947–956

SPATIAL SYNCHRONY OF WADER POPULATIONS IN INLAND LAKES OF THE IBERIAN PENINSULA

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Abstract

Spatial synchronization refers to similarity in temporal variations between spatially separated populations. Three mechanisms have been associated with the spatial synchrony of populations: Moran effect, dispersal and trophic interactions. In this study, we explored the degree of spatial synchrony of three wader species populations (Pied Avocet, Black-winged Stilt and Kentish Plover) using monthly estimates of their abundance in inland lakes of the Iberian Peninsula. The effect of several types of wetland variables (structural, hydroperiod and landscape) on spatial synchronization was explored. Groups of lakes with significant synchronization were identified for all three species. The lakes with wastewater input presented longer hydroperiods than those that did not receive these effluents, and this factor was positively related to the spatial synchrony of the Pied Avocet and Kentish Plover populations. The distance between lakes (used as an indicator of the dispersal effect on synchronization) was significant only in Pied Avocet. No structural or landscape variables were related to spatial synchronization in any species. It was impossible to identify any variable related to the spatial synchronization of Black-winged Stilt abundance as a possible result of the high ecological plasticity of this species. Our data provides the first evidence for mechanisms that act on the spatial synchronizing of wader populations in temporary continental lakes in central Spain, and show that the hydroperiod of lakes acts as an important factor in the spatial synchronization of aquatic species and that its effect is mediated by the reception of urban wastewater.

Keywords: temporal similarity, spatial dynamic, wetlands, hydroperiod, wastewater

1. Introduction

Understanding variations of abundance in space and time has been one of the major goals in ecology (Cazelles and Stone 2003; Liebhold et al. 2004). Notably, population dynamics has received plenty of attention since the models presented by Patrick Moran in 1953. Moran (1953) described statistical methods to observe the temporal patterns of the Canadian lynx, and proposed a formal ecological mechanism to analyze spatial population synchrony on large geographic scales. Conceptually, spatial synchrony of populations refers to the temporal similarity of abundance (or any other characteristic of a population) between sites separated spatially (Liebhold et al. 2004). In other words, regardless of the size of the local population, two or more sites are synchronized if the curves of abundance of both sites are coupled. Spatial synchrony is one of the most important patterns in metapopulations dynamics, being observed at different scales (local, regional and global), as well as in many species groups (Holyoak and Lawler 1996; Thrall et al. 2001; Post and Forchhammer 2002; Trenham et al. 2003; Liu et al. 2009; Batchelder et al. 2012; Kvasnes et al. 2013).

In general, spatial synchrony of abundance has been associated to three ecological processes, which can act independently or in combination: dispersal of individuals, environmental conditions and trophic interactions (Ranta et al. 1995; Bjørnstad et al. 1999). Regarding dispersal mechanism, the populations tend to fluctuate synchronously since the increase abundance in a specific site raises the migration rate into adjacent areas, forcing the spatial synchrony. As the dispersion is distant-dependent, the level of synchrony tends to be higher between closer areas, decreasing as the distance between areas increases (Ranta et al. 1995). On the other hand, some distant sites may show high spatial synchrony of populations as a response to correlated environmental conditions, a process known as Moran effect (Koenig 2002). Haynes et al. (2013), for instance, noted that precipitation acted as synchronizer factor of populations of moths due to the similar effect on the survival and reproduction of individuals. In this case, as in many others, the Moran effect is mainly associated with environmental conditions extrinsic (or exogenous), which are common over large spatial scales (e.g. temperature and precipitation). Finally, trophic interactions between predator-prey populations may also force the spatial synchronization of populations, as shown by Ims and Steen (1990).

Although long-term monitoring has been conducted in many world regions, little is known about the synchronicity of bird populations in continental wetlands. In addition, most animal ecology studies have sought to identify synchronization patterns of annual periodicity (e.g. Koenig 2001; Bellamy et al. 2003; Williams et al. 2003; Eberhart-Phillips et al. 2015; Mortelliti et al. 2015). This temporal scale prevents closer relations between the intra-annual variability of ecosystems and spatial population dynamics from being detected. For example, many inland lakes in the Iberian Peninsula have a naturally short hydroperiod due to the small expanse of their basin and poor annual precipitations, while others have larger basins or receive some inputs from groundwater or rivers, and hold water for most of the year. To this natural variability, the contribution of urban wastewater has been added in recent decades (Martinez-Santos 2008). In these environments, where hydric changes are rapid, it is likely that annual sampling programs would not reveal the processes behind population fluctuations, even if they have been performed for many years.

In this paper we explored the degree of spatial synchrony of the populations in this type of Mediterranean wetlands using monthly estimates of abundance. We employed three wader species distributed in a set of saline lakes of central Spain as a model system: Black-winged Stilt (*Himantopus himantopus*), Pied Avocet (*Recurvirostra avosetta*) and the Kentish Plover (*Charadrius alexandrinus*). These are species with a good dispersion ability between wetlands and are good study subjects to observe the patterns and processes associated with spatial synchrony. Specifically, we explored whether habitat and landscape factors were related to the spatial synchrony of populations and we expected to find high levels of synchronization as a possible result of: *i*) hydrodynamics, including the potential effect of wastewater inputs; *ii*) distance between lakes, as an indicator of a dispersal limitations effect and; iii) variability in the structural and landscape features of the lakes.

2. Methods

Study area

The study area is located in the "La Mancha Húmeda" Biosphere Reserve (hereafter MHBR), in the Castilla-La Mancha region, central Spain (Fig. 1). The MHBR is one of the most important wetland complexes of the Iberian Peninsula (Florín et al. 1993), with a network of over 190 wetlands spread over three geographical areas - Campo de San Juan, Campo de Montiel and the Serrania de Cuenca (Gosálvez et al. 2012), of which 50 are temporary lakes (Florín and Montes, 1999). The average temperature in the region is 14ºC, and the minimum temperature in extreme years can reach -20°C in winter and the maximum can rise to 42°C in July. The seasons with the highest rainfall are winter and spring, and annual precipitation varies between 300-400 mm (Martinez-Santos et al. 2008). The landscape is predominantly agricultural, characterized by vineyards, cereal crops, olive groves, forestry and pastures. There are many types of wetlands in the MHBR, which range from temporary lakes to floodplains and permanent or episodically flooded. There are also natural or artificial lakes, some of which receive wastewater from adjacent urban centers (Florín et al. 1993; Florín and Montes 1999). In our study, most wetlands were temporary lakes, either with or without wastewater input. In general, the vegetation surrounding lakes was predominantly halophilous and some lakes were characterized by vegetation islands dominated by Reed (*Phragmites australis*), Cattail (*Typha dominguensis*), Common Club-rush (*Schoenoplectus lacustris*) and Alkali-bulrush (*Bolboschoenus maritimus*) (Gosálvez et al. 2012).

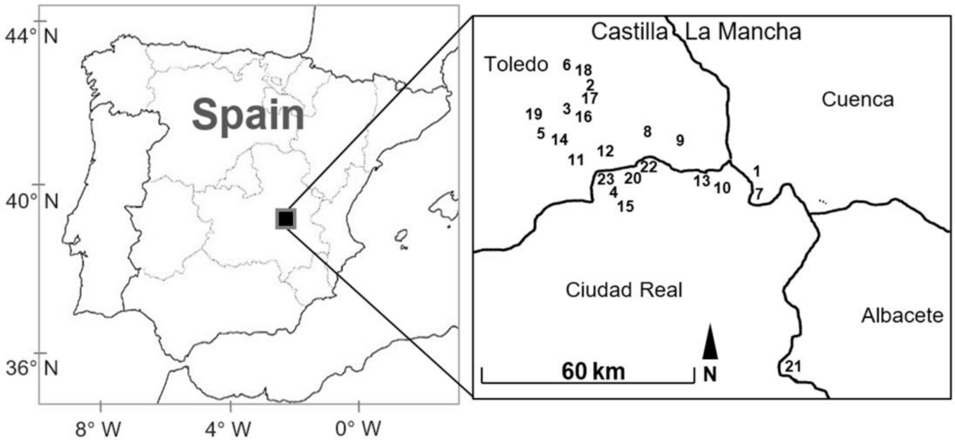


Fig. 1 Location of the 23 lakes (identified by numbers) monitored monthly between October 2010 and February 2014. The codes of each lake are available in Table 1

Bird counts and environmental variables

Monthly counts of Pied Avocet, Black-winged Stilt and Kentish Plover were conducted in 23 wetlands between October 2010 and February 2014. The study wetlands were selected as a representative sample of the types and conditions of lakes in the region within the framework of a previous project on the ecology of inland lakes in Central Spain (Gosálvez et al. 2012). They cover a wide range of sizes, depths, extent of vegetation in the edges (Table 1), as well as salinity (Florín et al. 1993). Counts were performed at fixed observation points and always by the same researchers. These points were selected to obtain the best view of the complementary sectors in the lagoon area in order to avoid loss of the individuals near or behind emergent plants. Counts were made in the last week of each month and conducted between 08:00h to about 12:00h, after ensuring favourable climatic conditions (little wind and no rain). Telescopes and binoculars were utilized in samples.

Twelve environmental variables were analyzed per lake (Table 1). These variables can be classified into four groups: (1) hydroperiod, i.e. percentage of months with water; (2) anthropogenic, i.e. distance from human settlements; (3) landscape, i.e. distance between lakes and number of lakes within three radii (2 km, 5 km and 10 km); and (4) structural, i.e. average depth, total lake surface, flooded surface, surface with natural vegetation surrounding the lake, number of islands and total surface of islands. The average depth was obtained by the difference between the average of the altitude at the four cardinal points on the lake border, obtained from a geographical viewer (see below), and the altitude of the deepest point of the lake. Structural variables were obtained by fieldwork and from the geographical viewer Iberpix (Spanish National Geographic Institute) and Google Earth Pro Version 2015.

Data analysis

The analysis to detect the spatial synchrony of abundance and its associations with the habitat and landscape features was performed for each species separately. For each studied species we selected the lakes where it occurred in at least 5% of the months (Pied Avocet, 13 lakes; Black-winged Stilt, 12 lakes; Kentish Plover, 6 lakes). To avoid the effect of the daily variability of censuses and to focus on the main temporal pattern of each lagoon, the series of monthly abundances were smoothed by calculating the central moving average for each month, with the exception of the first and last month in the series, using a window size of 3 months. Therefore the smoothed abundance in each month was obtained by averaging the census for that month and the censuses of the previous and subsequent months.

The degree of spatial synchrony between lakes was evaluated using Pearson's correlation coefficient (r), calculated from the time series of smoothed monthly abundance in each lake. For each species, a dendrogram, showing the resemblance of lakes in temporal pattern, was generated using the correlations of smoothed abundances between all pairs of lakes as a measure of similarity. Dendrograms were built with the PAST software (Hammer et al. 2001) following the UPGMA method. To identify groups of lakes with similar temporal patterns, we used the significant value of correlation for 37 degrees of freedom (number of values in the smoothed time series minus 2) and p-value < 0.01 (r = 0.408) as a threshold.

The matrix of correlations between wetlands calculated for each species was transformed to a dissimilarity matrix using the formula (1 – r)/2, where r is Pearson's correlation coefficient, to generate values that ranged between 0 and 1. A dissimilarity matrix was also built for each environmental variable after standardization using Euclidean distance. The relation between these two dissimilarity matrices (bird temporal patterns and a matrix for each environmental variable) was assessed by the Mantel Test, a statistical procedure that evaluates the correlation between two matrices (Anderson and Walsh 2013). The Monte Carlo method with 9999 random permutations was used to assess the significance of the Mantel Test (Zar 2010). Significant p-values were considered to be < 0.05. These analyses were performed with the “ade4” package (Thioulouse et al. 1997) in the R-Program, v. 3.1.3 (R Development Core Team 2014). Finally, we used the Mann-Whitney U-test to compare the average hydroperiod between the lakes with and without wastewater input.

3. Results

Groups of lakes with significant synchronization were identified for the three species. A few lakes showed temporal patterns which did not correlate to the others (Fig. 2). The groups of lakes also presented a coincident pattern of fluctuation between years - the groups with previous and later peaks of abundance maintained the same periodicity in years 1 and 3, but with distinct variation in study year 2 (Fig. 3).

Pied Avocet. Three groups of lakes with significant temporal similarity were identified (Figs. 2 and 3). Group 1 (Quero, Mermejuela, Artevi, Altillo Grande and Tírez) showed earlier peaks of abundance, which occurred in late winter and early spring (Figs. 3 and 4a). Group 2 presented later and more long-lasting periods of high abundance, which extended from late spring to late summer. In this group, Manjavacas lake had large numbers of Pied Avocets during the 2012 breeding season (year 2), when the abundance in the rest of the lakes sharply dropped. Group 3 (Veguilla and Pedro Muñoz) presented abundance peaks later (late summer-early fall).

Black-winged Stilt. Two groups which included all the analyzed lakes were identified (Figs. 2 and 3). Group 1 (Veguilla and Pedro Muñoz) showed later peaks, which occurred in late summer-early fall (Fig. 3). The lakes in Group 2 presented abundance peaks between late spring and midsummer (Figs. 3 and 4b).

Kentish Plover. Two groups with two lakes each were formed, but the similarity between lakes in the same group was relatively low (Figs. 3 and 4c). Lakes Alcahozo and Quero showed particular temporal patterns (Fig. 4c).

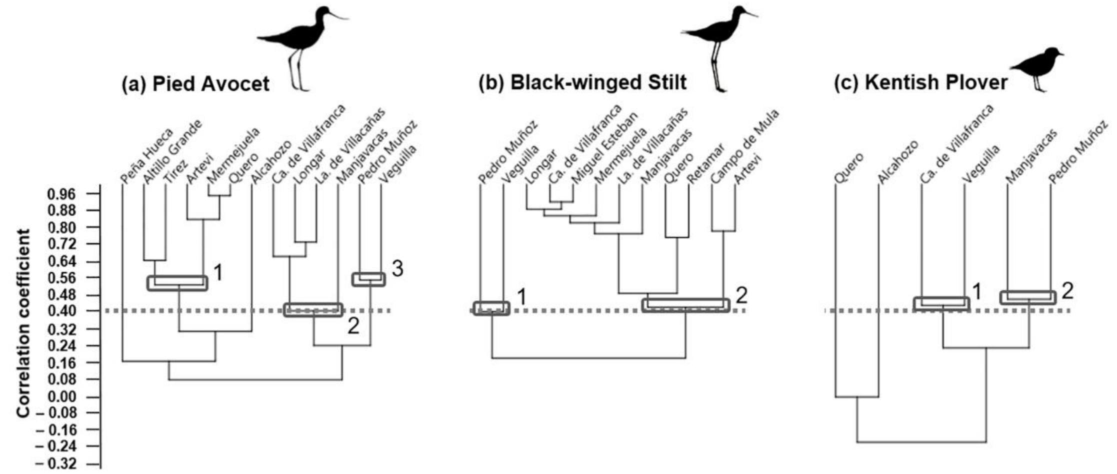


Fig. 2 Dendrogram showing the similarity of the seasonal patterns of the abundance of Pied Avocet, Black-winged Stilt and Kentish Plover in inland lakes of Central Spain. The horizontal line marks the significant correlation coefficient for a P value <0.01, used as a threshold to define groups, identified by numbered frames at the base of the branching shared within each group. The names of the lakes are located over the dendrogram branches.

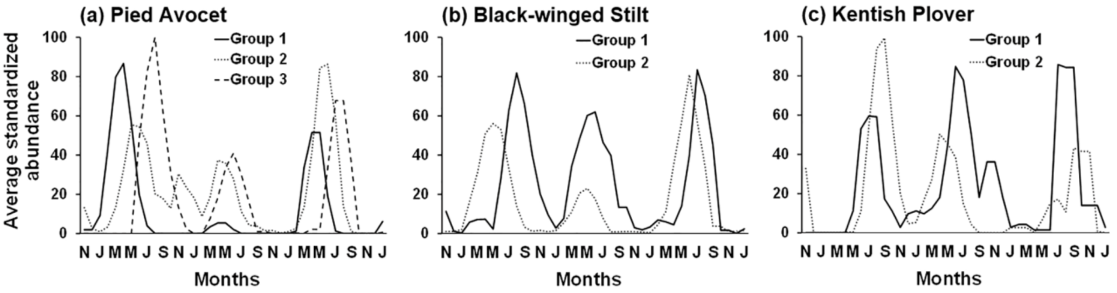


Fig. 3 Average temporal pattern of each group of lakes identified by the dendrograms of each species (Fig. 2). To generate these graphs we standardized the monthly abundance values of each lake by dividing them by the maximum abundance observed in that lake and then multiplying by 100. In this way, we obtained a series that ranged between 0 and 100 for each lake, and we then averaged the series of all the lakes of the group. Months are labelled alternately starting in November (N) 2010.

Environmental correlates of temporal similarity

Of the 12 environmental variables explored, only hydroperiod and distance between the lakes were related to the spatial synchrony of some species (Tab. 2). No correlation was observed between these environmental variables (Mantel Test, r = 0.048; *P* = 0.260).

For Pied Avocet, the environmental variables that correlated to spatial synchrony were hydroperiod (Mantel Test, r = 0.380; *P* = 0.004) and distance between lakes (Mantel Test, r = 0.250; *P* = 0.046). In Kentish Plover, the hydroperiod was the only variable that was related to the temporal patterns of the lakes (Mantel Test, r = 0.710; *P* = 0.043). None of the environmental variables was related to the high spatial synchrony levels observed for Black-winged Stilt (Table 2).

The lakes that received wastewater presented longer hydroperiods than those that did not receive such effluents (*U* = 4.00; *P* < 0.001) (Fig. 5). Seven of the eight lakes with no input of wastewater had marked seasonality of presence of water and were flooded between 22% and 68% of the months (except lake Camino de Villafranca) (Fig. 5). The eight lakes that received wastewater presented water for most of the study period (71%-100%).

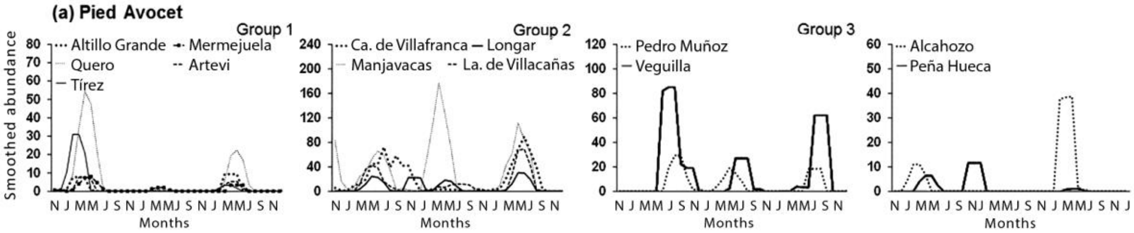
4. Discussion

Our results show that the degree of spatial synchrony of the populations of Pied Avocet, Black-winged Stilt and Kentish Plover in inland lakes of Iberian Peninsula is significant. However, the patterns of synchrony of the three species showed different levels of responses to the set of variables explored. The spatial synchrony of Pied Avocet and Kentish Plover is affected by the hydroperiod of lakes, which in turn is altered by wastewater input.

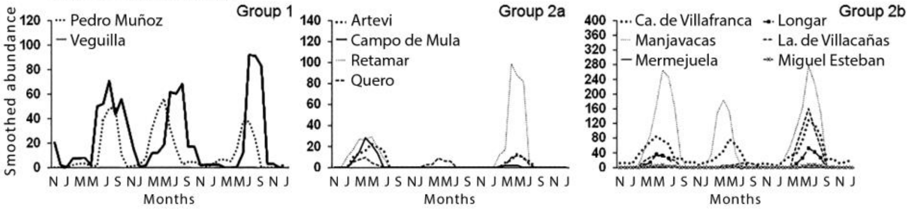
Spatial synchrony and hydroperiod effect

In partial agreement to our first hypothesis, the hydroperiod effect was important on temporal patterns of two of the three species: Pied Avocet and Kentish Plover. For Pied Avocet, we observed the formation of three groups of spatially synchronized lakes: groups with earlier peaks of abundance, intermediate peaks and later peaks. The group of lakes with earlier peaks (beginning of spring) were also characterized by shorter hydroperiods (flooded between 22% and 68% of the months) and they did not receive wastewater (except Lake Quero). Unlike the lakes that received wastewater, unaltered lakes tend to rapidly dry in the spring and summer. Temporal variation of abundance depends not only on movements for tracking the spatial changes in resources availability (Borkhataria et al. 2012), but also on large-scale migratory movements and reproduction output (Sirot and Touzalin 2014). Therefore, the passing of migrants in spring could cause a detectable early peak of abundance in lakes with shorter hydroperiod since in these lakes the number of individuals that stay for breeding is relatively low and diminishes quickly as they dry, while in lakes with longer hydroperiod a more numerous breeding populations remains for longer time.

(a) Pied Avocet



(b) Black-winged Stilt



(c) Kentish Plover

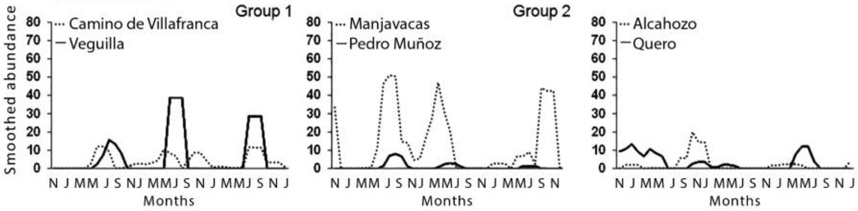
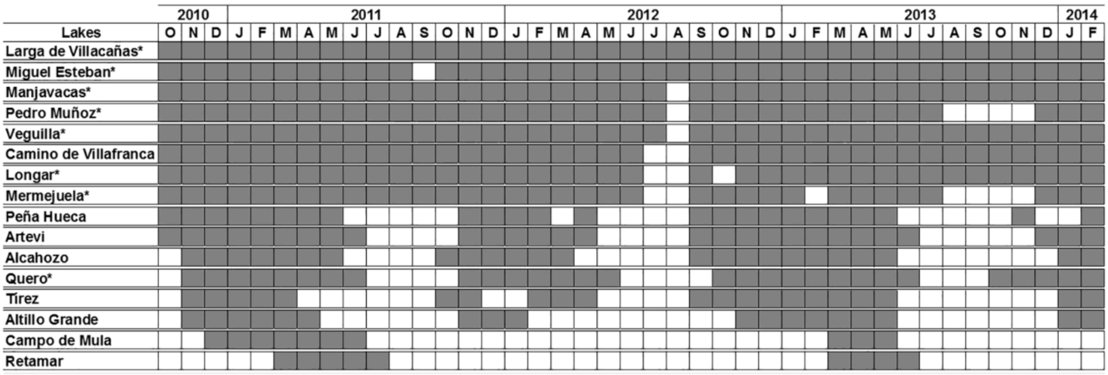


Fig. 4 Temporal variation (moving averages) of the abundance of the three wader species in the studied lakes. Groups of lakes were defined from the dendrograms in Fig. 2. For Black-winged Stilt, lakes in Group 2 are shown in two graphs for better visualization of their temporal patterns (Groups 2a and 2b). Panels without group number include the lakes that presented temporal patterns not correlated to other lakes and therefore did not join to any group identified in Fig. 2. Months are labelled alternately starting in November (N) 2010.

On other hand, later abundance peaks occurred synchronously in the same lakes for Pied Avocet and Black-winged Stilt (Lakes Veguilla and Pedro Muñoz). Lakes that receive effluents from urban wastewater treatment plants present inappropriate bio-physical conditions in late summer (Vidal et al. 2013; Anza et al. 2014), but display high organic productivity (Anza et al. 2014) and are attractive sites to waterbirds during breeding periods (Gosálvez et al. 2012). Unlike the other lakes that receive wastewater and present long hydroperiods, Veguilla and Pedro Muñoz have large concentration of emerging macrophytes on its edges, and few flat shallow areas for foraging of waders in the breeding season. However, during the summer, while other areas are dry or nearly dry, Veguilla and Pedro Muñoz gradually expose extensive mudflats in their central area that attract many waders. Consequently, the decrease of the abundance of individuals after the mid-summer in some lakes with longer hydroperiods (e.g. Manjavacas, Larga de Villafranca, Miguel Esteban, Longar and Mermejuela) and the coincident increase at Pedro Muñoz and Veguilla lakes is possibly the result of structural differences between the wetlands, which has significant effects on foraging habitat availability.

In the case of Kentish Plover the lakes that presented significant temporal correlation were those with longer hydroperiods, where this species presented peaks of abundance in midsummer, although with more variability in Manjavacas and Pedro Muñoz. On the contrary, in the lakes that usually dry in midsummer (Quero and Alcahozo), Kentish Plover showed abundance peaks in winter or spring. These alternating patterns of Kentish Plover abundance in these groups of lakes suggest that part of the population of this species could switch between wetlands depending of the fluctuating conditions in them.

The varying effect of hydroperiod on the spatial synchrony of the study species might be explained by differences in their natural history, especially related to their foraging strategy and habitat selection (Ntiamoa-Baidu et al. 1998; Granadeiro et al. 2006; Kuwae 2007). Black-winged Stilt tend to forage solitary in shallower waters than Pied Avocet, which frequently forage in flocks (Ntiamoa-Baidu et al. 1998). Therefore, as the studied lakes are shallow, the gradual loss of water during the summer may reduce faster the habitat quality for Pied Avocet, favoring the synchronization of lakes with similar hydroperiods. Kentish Plover forage in shores or shallow water (Kosztolányi et al. 2007; Hanane 2011) and their feeding efficiency decreases as saltmarshes dry, forcing parents to move with broods to lakeshores (Kosztolányi et al. 2006). This behavior could explain that, like Pied Avocet, their temporal pattern is affected by hydroperiod. The lack of effect of hydroperiod on the spatial synchrony of Black-winged Stilt, together with its capacity for living in a wider variety of aquatic environments (Hortas et al. 2012), would explain the more similar temporal pattern between lakes in this species as shown by the high correlations between lakes.



	2010			2011												2012												2013												2014	
Lakes	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F
Larga de Villacañas*	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Miguel Esteban*	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Manjavacas*	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Pedro Muñoz*	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨					▨	▨	▨
Veguilla*	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Camino de Villafranca	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨			▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Longar*	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨			▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Mermejuela*	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨			▨	▨	▨	▨	▨		▨	▨	▨	▨	▨					▨	▨	▨
Peña Hueca	▨	▨	▨	▨	▨	▨	▨	▨						▨	▨	▨	▨		▨					▨	▨	▨	▨	▨	▨	▨	▨	▨						▨			▨
Artevi	▨	▨	▨	▨	▨	▨	▨	▨	▨					▨	▨	▨	▨	▨	▨					▨	▨	▨	▨	▨	▨	▨	▨	▨	▨						▨	▨	▨
Alcahozo		▨	▨	▨	▨	▨	▨	▨					▨	▨	▨	▨	▨	▨						▨	▨	▨	▨	▨	▨	▨	▨	▨								▨	▨
Quero*		▨	▨	▨	▨	▨	▨	▨	▨					▨	▨	▨	▨	▨	▨	▨					▨	▨	▨	▨	▨	▨	▨	▨	▨				▨	▨	▨	▨	▨
Tírez		▨	▨	▨	▨	▨							▨	▨			▨	▨	▨					▨	▨	▨	▨	▨	▨	▨	▨	▨								▨	▨
Altillo Grande		▨	▨	▨	▨	▨	▨							▨	▨	▨										▨	▨	▨	▨	▨	▨	▨								▨	▨
Campo de Mula			▨	▨	▨	▨	▨	▨	▨																					▨	▨	▨									
Retamar						▨	▨	▨	▨	▨																				▨	▨	▨	▨								

Fig. 5 Hydroperiod of the 16 lakes selected for the analysis. Gray cells identify months with presence of water between October 2010 and February 2014. The lakes marked with an asterisk received wastewater.

For the three species, we also observed that the abundance peaks of the groups of lakes showed constant periodicity in study years 1 and 3, with an asynchrony found in study year 2. As many theoretical and empirical studies have observed, identifying patterns and processes of temporal population dynamics is not an easy task and it is necessary to consider also the effect of random events, like environmental and demographic stochasticity (Brown et al. 1995; Ives and Klopfer 1997). Even the lakes that received wastewater can dry in summer if the water accumulated in winter was low. This appeared to be the case of most of our study lakes in the summer of 2012, when all the sites (except Miguel Esteban and Larga de Villacañas) were completely dry in August. According to the weather data of the province of Toledo (Spanish Meteorology Agency - AEMET), the rain accumulated in previous fall and winter was lower in 2012 (109.1 mm) than in 2011 (236.1 mm) and 2013 (283 mm). In parallel, for all three species we also observed a similarity in the temporal patterns of the groups of lakes between 2011 and 2013, with distinct variation found in 2011. Specifically, the groups of lakes in 2012 tend to present earlier abundance peaks than in the other two years. This difference may be a direct response to variations in rainfall since it is known that changes in hydrological conditions affect not only food availability (Bancroft et al. 2002; Roshier et al. 2002), but also movements of individuals during the breeding periods (Borkhataria et al. 2012).

Many studies have found that different factors may act together in the formation of synchronous patterns (Ranta et al. 1999; Powney et al. 2011; Eberhart-Phillips et al. 2015; Mortelliti et al. 2015). For instance, hydrological disturbance and dispersal were important mechanisms driving spatio-temporal patterns of Everglades fish populations

(Ruetz et al. 2005). In our study, at least in one species (Pied Avocet) the distance between lakes and hydroperiod seemed to act together to cause the spatial synchronization of populations. Ranta et al. (1999) demonstrated that correlated extrinsic disturbances are capable of synchronizing population dynamics in combination with the distance effect. In our case, as in the system studied by Ruetz et al. (2005), the hydroperiod was not correlated to the distance among sites and seems to promote spatial synchrony independently from dispersal.

Distance effect and other variables

Although dispersal mechanisms have been commonly related to the spatial synchrony of many species, including birds (Koenig 1998; 2001), detecting and understanding the relationship between distance and synchronization of populations is not always easy. This is because when motivated by dispersion, spatial synchrony depends on many factors, including the dispersal ability of individuals (Sutcliffe et al. 1996), the degree of functional connectivity between patches (Powney et al. 2011), the spatial scale (Paradis et al. 1999) and presence of environmental disturbances (Ranta et al. 1999). Functional connectivity refers to the environmental permeability of a given landscape, which facilitates or hinders the movement of individuals between patches and/or fragments (Goodwin and Fahrig 2002, Powney et al. 2011). In our study, we analyzed a set of landscape variables, such as distance from human settlements, distance between lakes and number of lakes within three increasing radii as indicators of the functional connectivity of lakes (Goodwin and Fahrig 2002). We also evaluated a set of structural habitat variables and their relationship to the observed temporal patterns. None of these variables was associated with the spatial synchrony of the studied species, except distance between lakes in Pied Avocet. Given the high dispersal capacity of these species (Hötker 2002; SEO/BirdLife 2016a, b) and the relative proximity of the lakes (maximum distance 94 km), the distance seems not to be affecting the spatial synchrony of Black-winged Stilt and Kentish Plover. Only in the case of Pied Avocet we detect an effect of distance between lakes on their spatial synchrony, that was weaker than hydroperiod effect. Overall, the absence of effect of landscape and habitat variables is related to the ecology of the analyzed species, which are able to occupy sites scattered in extensively altered landscapes (Hortas et al. 2012; Hortas 2012a, b).

Conclusions

For more than three decades, inland lakes of the Iberian Peninsula have undergone significant changes in water regimes as a result of channelled surface water, overexploitation of aquifers and wastewater input. The monthly census approach conducted herein allowed us to detect how hydrological disturbance (wastewater input) affects the spatial synchrony of populations and generates diverse temporal patterns of abundance variation. Our data provide the first insights into the mechanisms that drive spatial synchrony in temporary inland lakes. Further research on this topic in central Spain wetlands, that present one of the most altered hydric functioning in the Iberian Peninsula, will help to design water management strategies that improve habitat quality for wader species.

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Table 1. The environmental variables of the 16 lakes monitored monthly between October 2010 and February 2014 in the “La Mancha Húmeda” Biosphere Reserve, central Spain. Acronyms: UTM = Universal Transverse de Mercator (Datum ETRS89); Hyd = hydroperiod (% of months with water); DH = distance from human settlement (meters); D.PA/D.BS/D.KP = distance (D) in meters from the nearest lake for Pied Avocet (PA), Black-winged Stilt (BS) and Kentish Plover (KP); R = number of lakes present in radii of 2, 5 and 10 km; Veg = area covered by natural vegetation; Ni = number of islands; IsA = total area of existing islands; AD = average depth. The lakes that presented at least 4 months of occurrence of one studied species (5% of the monitoring period) were selected for the spatial synchrony analysis and are indicated with an asterisk (*) - see Methods. Flooded area, vegetation and islands coverage are in m^2. UN = lakes not analyzed for a given species.

				Hydroperiod	Anthropogenic	Landscape						Structural					
Code	Lake	UTM X	UTM Y	Hyd	DH	D.PA	D. BS	D. KP	R2	R5	R10	Area	Flooded	Veg	Ni	IsA	AD
1	Alcahozo*	510620	4360164	58.5	5509	3184	UN	3184	1	2	6	886622	690661	195961	0	0	1.75
2	Altillo Grande*	474187	4393670	43.9	2649	2260	UN	UN	2	3	4	329132	204966	124166	0	0	4.25
3	Artevi*	472611	4385210	68.2	965	9195	1155	UN	1	1	9	279171	167168	112003	0	0	4.75
4	Camino de Villafranca*	478055	4362616	95.1	2263	2322	2322	2322	0	2	10	1599214	1347179	237802	2	17233	2.25
5	Campo de Mula*	464695	4381452	21.9	5483	UN	8534	UN	0	1	6	509145	255728	253417	0	0	3.25
6	Longar*	472448	4395066	92.6	1757	2260	9627	UN	2	3	5	2595033	991391	1603642	0	0	4
7	Manjavacas*	511840	4363360	97.5	6639	3184	7215	3184	1	7	17	2628067	1978446	640048	3	9573	2.75
8	Mermejuela*	488191	4376617	82.9	4834	10843	7621	UN	0	2	5	99195	86559	12636	0	0	6.5
9	Miguel Esteban*	495294	4373855	97.5	1376	UN	7621	UN	0	1	1	922238	234238	688000	0	0	2.5
10	Pedro Muñoz*	504589	4362479	87.8	362	6460	2708	6460	2	3	11	413916	261401	152515	0	0	3.25
11	Peña Hueca*	470426	4373729	58.5	8880	3077	UN	UN	0	2	8	1588659	1326046	196325	4	66288	3.75
12	Quero*	478215	4372367	70.7	787	7907	9752	9752	1	6	16	957282	840836	116446	0	0	2
13	Retamar*	502427	4364111	21.9	2503	UN	2708	UN	0	3	7	791605	627250	164355	1	4098	3.5
14	Tírez*	469331	4376605	51.2	8546	3077	UN	UN	0	2	6	1318531	811890	506204	1	437	4.25
15	Veguilla*	479389	4360715	97.5	886	2322	2322	2322	0	2	7	890951	443546	447405	0	0	4.25

16	Larga de Villacañas*	472815	4384080	100	1458	1148	1148	UN	2	3	12	1673095	1.145.530	527565	0	0	3.25
17	Albardiosa	474994	4390229	8.3	5085	UN	UN	UN	0	3	5	718838	395178	323660	0	0	2.5
18	Altillo Pequeño	473975	4394727	55.5	1436	UN	UN	UN	2	3	5	246865	178111	68754	0	0	3
19	Camino de Turleque	464403	4384224	5.5	4082	UN	UN	UN	0	1	4	486833	394459	92374	0	0	5.25
20	Pajares	482321	4367206	39	4669	UN	UN	UN	0	1	5	235875	209027	26848	0	0	2.75
21	Redondilla	513136	4310021	26.8	171	UN	UN	UN	5	9	10	57357	35129	22228	0	0	11
22	Salicor	485033	4368502	55.5	7161	UN	UN	UN	1	2	5	814097	483899	237203	3	92995	5.75
23	Yeguas	475657	4363078	61.1	4683	UN	UN	UN	1	3	6	962659	649388	313271	0	0	2

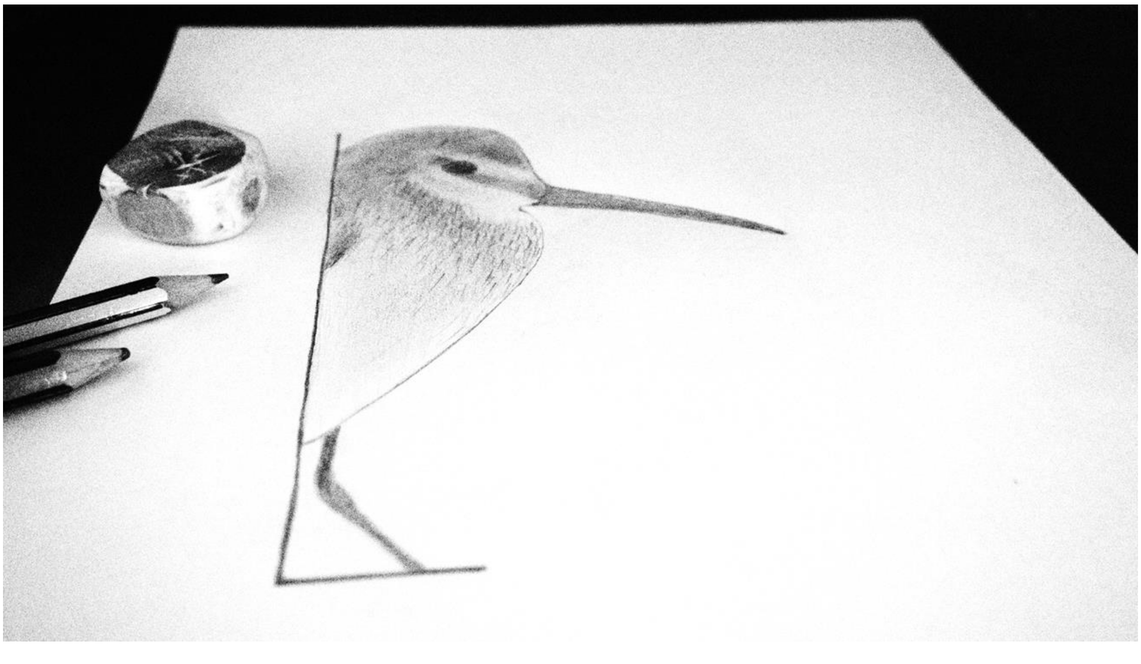
Table 2. Results of the Mantel tests run to evaluate the correlation of environmental variables with the spatial synchrony of populations. Bold values are statistically significant tests for a p-value less than 0.05.

	Pied Avocet		Black-winged Stilt		Kentish Plover	
Environmental variables	Obs	*P*-value	Obs	*P*-value	Obs	*P*-value
Hydroperiod	**0.380**	**0.004**	0.073	0.352	**0.710**	**0.043**
Distance between lakes	**0.250**	**0.046**	0.017	0.434	0.202	0.203
Distance from human settlement	0.183	0.099	0.105	0.276	–0.188	0.805
Average depth	–0.224	0.930	0.076	0.354	0.05	0.391
Total area	–0.128	0.671	–0.072	0.613	–0.303	0.823
Flooded area	–0.128	0.656	–0.091	0.613	–0.275	0.829
Vegetation Surface	–0.130	0.654	–0.218	0.788	–0.226	0.761
Island Surface	0.097	0.278	–0.217	0.790	–0.179	0.722
Number of island	0.151	0.285	–0.284	0.929	–0.105	0.450
Number lakes in 2 km	–0.080	0.756	0.022	0.396	–0.181	0.669
Number lakes in 5 km	–0.118	0.729	–0.040	0.526	–0.003	0.423
Number lakes in 10 km	–0.165	0.872	–0.034	0.547	0.008	0.419

Capítulo 4

Spatiotemporal patterns of dunlin (*Calidris alpina*) in continental lakes of the Iberian Peninsula

M. S. S. Gonçalves, J. A. Gil-Delgado, R. U. Gosálvez, G. M. López-Iborra, A. Ponz, P. Pons, & A. Velasco



Correlimos común (*Calidris alpina*)

Biorxiv, doi: https://doi.org/10.1101/434886

SPATIOTEMPORAL PATTERNS OF DUNLIN (*Calidris alpina*) IN CONTINENTAL LAKES OF THE IBERIAN PENINSULA

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Dunlin (*Calidris alpina*)

Abstract

Spatiotemporal dynamics may present different levels of regional or local stability, generally attributed to local habitat and landscape factors, reflecting the tolerances and ecological requirements of the populations. In this study, we examined the variations of dunlin abundance and occurrence in twenty-three wetlands of the “La Mancha Húmeda” Biosphere Reserve, central Spain, between October 2010 and July 2017. In addition, we observed the variations of local abundance in the lakes of the Manjavacas lagoon complex, seeking to understand the factors that determine the local movements of the wintering individuals. Eleven lakes had records of dunlin, but most of individuals (ca. 90%) were observed in the Manjavacas Lagoon Complex (Alcahozo and Manjavacas lakes). The preference for this complex associated with temporal variations of abundance between the Alcahozo and Manjavacas lagoons possibly reflects the specific characteristics of the invertebrate community available as prey, especially for the presence of anostracans and copepods. The results of this study are a first step in understanding the factors that lead this species to select continental wetlands as wintering sites.

Keywords: population, abundance, migratory birds, wading birds, inland wetlands, conservation, Biosphere Reserve

1. Introduction

Spatiotemporal dynamics may present different levels of regional or local stability, generally attributed to habitat and landscape factors, reflecting the tolerances and ecological requirements of the populations (Collins & Glenn, 1991). In waterbirds, the spatiotemporal distribution in wetland patches has often been associated to destruction and environmental fragmentation (Guadagnin & Maltchik, 2007). Inland wetland ecosystems are distributed in spots on landscape. Therefore, in order to maintain the stability of the populations, waterbirds are forced to adapt to local conditions of habitat change as well as incorporating multiple fragments or habitat patches into the daily life cycle (Guadagnin et al. 2009). Among waterbird migratory species, the recognition of these variations helps to understand the relevance of interconnected habitats between breeding, wintering and stopover areas (Andres et al. 2012).

Migratory waterbirds are often used as indicators of environmental quality (Green &Elmberg, 2013). However, for many inland wetlands of high environmental importance, there is no information on spatiotemporal dynamics of migratory waders and their correlations with environmental factors (Morrison et al. 2006). This is particularly important as significant reductions in populations of many wader species have been observed over the past 30 years (Andres et al. 2012). In this context, continental wetlands require special attention since it has demonstrated a greater loss of habitat in relation to coastal environments (Kingsford et al. 2016).

Dunlin (*Calidris alpina*)

In central Spain, "La Mancha Húmeda" Biosphere Reserve (hereafter MHBR), presents a complex and extensive network of permanent and temporary salt lakes of great relevance in the cycle of migratory waterbirds (Gosálvez et al. 2012). The MHBR is key habitat for those species that arrive from northern Europe towards the south of the continent European and African during the autumn and winter (BirdLife International, 2018). More than 25 wading species – approximately 40% of species in Spain, occupy the inland wetlands of the reserve (Gonçalves et al. 2018). According to the maps available at BirdLife International (2018), dunlin (*Calidris alpina*), together with black-tailed godwit (*Limosa limosa*) and common greenshank (*Tringa nebularia*), represent one of the most conspicuous winter migratory species in central Spain, however, little is known about their spatiotemporal patterns, especially in inland wetlands (Gosálvez et al. 2012; Gonçalves et al. 2016, 2018).

Determining routes of migratory birds, as well as their feeding and wintering areas is crucial to define and implement management actions at multiple spatial scales (Andres et al. 2012). In this study, we aim to describe the variations of dunlin abundance and occurrence in 23 wetlands of the RBMH. In addition, we observed the variations of local abundance in the lakes of the Manjavacas lagoon complex, seeking to understand the factors that determine the local movements of the wintering individuals.

2. Methods

Study area

“La Mancha Húmeda" Biosphere Reserve was created in 1981 initially with a surface of 25,000 ha (Crespo et al. 2011). Additionally, in agreement with the document of the Ministry of Agriculture, Food, and Environment (2014), this area was enlarged to about 420,000ha, inserting a large number of legally protected wetlands inside reserve. Although the relief of central Spain is marked by a great geological and geomorphological diversity, much of the reserve landscape is dominated by slightly undulating fields and extensive cereal and vineyards plantations the most important economic activity of the region (Ruiz-Pulpón, 2013; 2015). The rainfall of the region is low, varying between 300 and 500 mm annually and, combined with a warmest summer. The higher temperatures and lower rainfalls since the endo of spring, forces the lakes to a natural temporary variation in water levels (Martinez-Santos et al., 2008). Thus, from the end of July to the first rainfalls of autumn the lakes are dry. In its domains, two important conservation sites are inserted: Tablas de Daimiel National Park (approximately 2,000 hectares) and Ruidera Natural Park (3,772 hectares). Further, other wetlands are also classified as Ramsar sites and/or inserted into Natura 2000 network (Gonçalves et al. 2018).

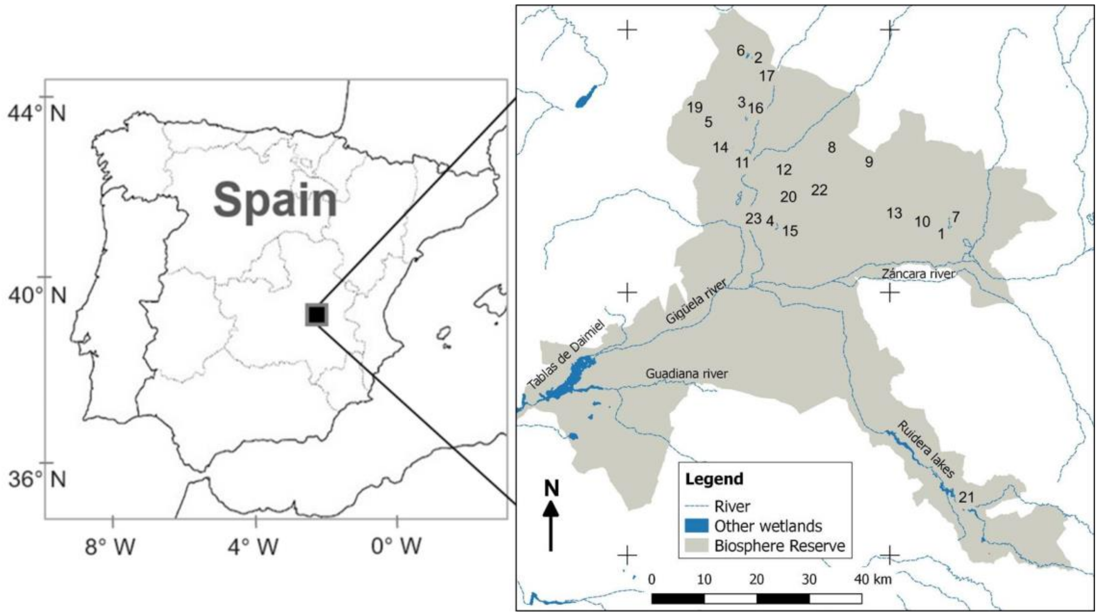

Fig. 1.La Mancha Húmeda” Biosphere Reserve and location of the twenty-three lakes (identification codes are in Table 1) monitored between 2010 and 2017.

Bird protocol and statistical analyzes

Dunlins were counted monthly in 23 lakes between October 2010 and July 2017 (Table 1). Except for Redondilla lake, the selected lakes are concentrated in the north of the "La Mancha Húmeda" Biosphere Reserve. The 23 lakes represent in large part the high heterogeneity of the wetlands of the region, especially in relation to hydrological dynamics and in physical characteristics (Gonçalves et al. 2016). Counts were made at the end of each month between 08:00-12:00, always on favorable weather conditions (little wind or no rain). Telescopes and binoculars were used during countings.

Frequency of occurrence (expressed in % of months with species) and dominance (expressed in % of records in relation to total recorded individuals) were calculated for each lake in two periods: wintering (November to March) and non-wintering (April to October). The higher number of the records of individuals was concentrated in two lakes of the Manjavacas Lagoon Complex. Thus, to determine possible patterns of local movement of individuals within this area, we evaluated the level of correlation of the monthly abundance variations between the two lakes using the Pearson's Correlation Coefficient (r). The analysis was calculated from the time series of smoothed monthly abundance of each lake. This analysis was performed using PAST software (Hammer et al. 2001). Smoothing was performed to reduce the effect of daily and monthly variability and focussing on the temporal behavior of abundance curves. Thus, the monthly data series was smoothed out by calculating the central moving average for each month using a three-month window, i.e. mean between the month, the previous month, and the subsequent month; the first and last month were excluded from the analysis.

3. Results

Of the 23 lakes monitored monthly between October 2010 and July 2017, eleven had records of dunlin. A total of 5707 records were accumulated throughout the study period, with a high dominance of the individuals recorded from Alcahozo and Manjavacas lakes – approximately 90% of dominance (Table 2). During the wintering period, the Alcahozo lake had the highest average monthly abundance of individuals (81.1 ± 99.7) and the highest frequency of occurrence (54.2%). Out of the wintering period, this lake presented low values of average abundance (0.4 ± 3.1) and frequency of occurrence (4.2%). For this period, the Manjavacas and Camino de Villafranca lagoons were the most used by the species (Table 2; Fig. 1).

Temporal variations of abundance in two lakes concentrated most of the records, Alcahozo and Manjavacas, presented a low correlation (r = 0.3). In five of the seven winter seasons, abundance values reached the first peaks or occurred exclusively at Lake Alcahozo. Subsequently, abundance reductions in this lake were followed by an increase of individuals in Lake Manjavacas (Fig. 2).

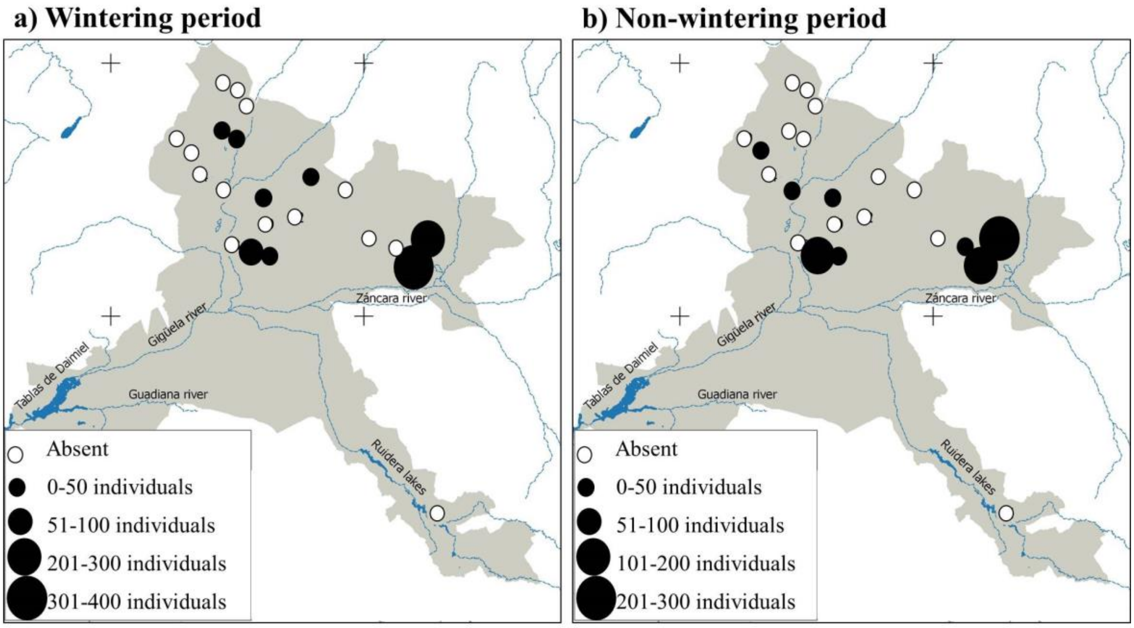

Fig. 2. Distribution of the highest values of dunlin abundance observed in a single month for the wintering (a) and non-wintering (b) periods.

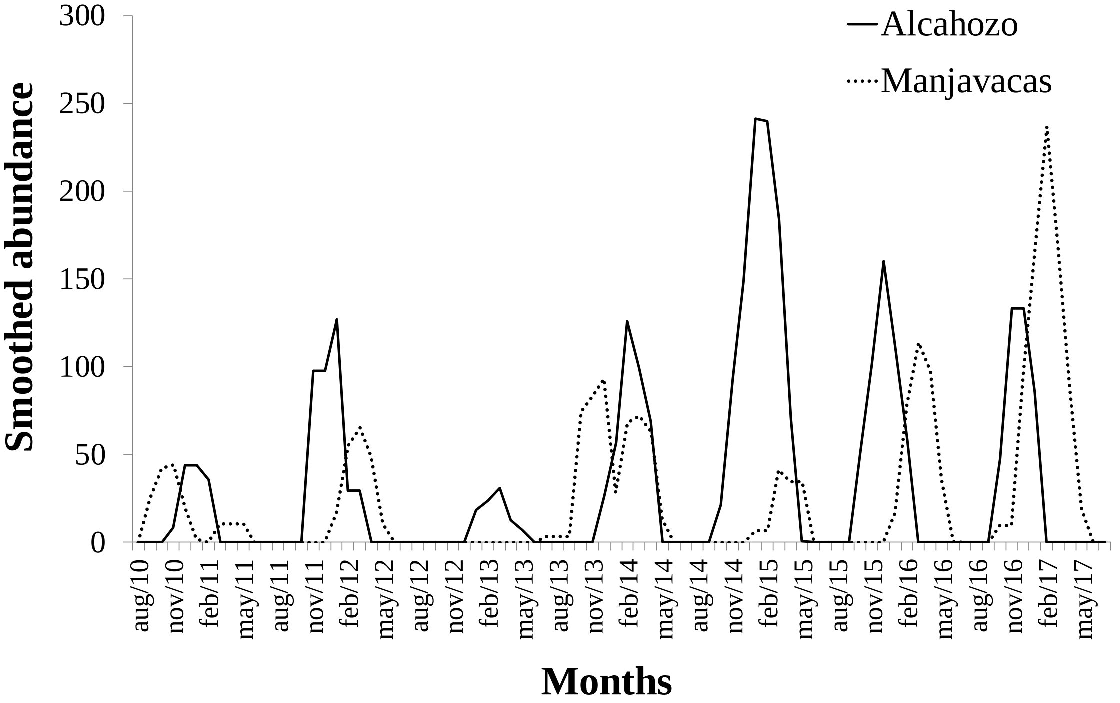

Fig. 3.Temporal variation (moving averages) of the abundance of dunlin in two lakes of the Manjavacas Lagoon Complex.

4. Discussion

According to the atlas of birds in winter in Spain (Seo/BirdLife International 2012), which shows a retrospective of the annual abundance values of the migratory species, our data indicate that approximately 3% of the wintering population of dunlin is in our study areas. The values of FO and monthly average abundance for each pond per period indicate that few ponds concentrate the vast majority of individuals during the wintering and non-wintering periods.

Alcahozo and Manjavacas lakes, were the most important sites during the wintering period, accounting for almost 90% of the accumulated records. The lakes of this complex are marked by different hydrological dynamics (Gonçalves et al. 2016), with significant effects on quality of its waters and, consequently, on the structure of invertebrate communities.The only complex included in our study area that resembles these lakes is the Alcazar de San Juan Complex, which integrates the lakes Camino de Villafranca, Yeguas and Veguilla. However, this complex does not have a composition of invertebrates similar to the Manjavacas' lakes (unpublished data from Ecolake Project, University of Valencia, Spain). Specifically, the set of invertebrate species of the lagoon complex of Manjavacas is marked by the abundance of copepods and anostracans (Pons et al. 2018). This is particularly important since the combination of anostracans and microcrustaceans has been referred to as key factors in the selection of foraging areas during the migratory cycle of waders (Horváth et al. 2013), which could explain such preference for the lakes Alcahozo and Manjavacas during the wintering, and, at least in part, for non-wintering period.

The temporal variations of abundance observed for Alcahozo and Manjavacas lakes indicate local movements of individuals within the Manjavacas complex as winter progresses. The first groups of wintering individuals tend to be observed first in the Alcahozo lake and, later, in the Manjavacas lake. This pattern may be associated with the aquatic invertebrate life cycle of both wetlands. Specifically, the main species of anostracan – *Branchinectella media* – is present only in Alcahozo lake. This species, besides being an indicator of environmental quality and being absent in polluted wetlands (Alonso 1996), such as the Manjavacas lake, is one of the first invertebrate species to appear at the beginning of the hydrological cycle (Jocque et al. 2010). Anostracans also present a fast growth and a high biomass when compared to the other invertebrate species occurring in Manjavacas lake (cladocers, copepods, and ostracods) (Alonso 1996). In this sense, the selection of the Alcahozo lake in early winter could indicate a response to the nutritional quality of prey, at least until the end of the life cycle of *B. media*, usually at the end of winter (Pons et al., 2017), when dunlins begin to occupy the Manjavacas lake. This process could also explain the importance of the Manjavacas lake during the non-wintering period, when this lake remains part of time with water and presents great abundance of invertebrates (Boronat et al. 2001).

The recognition of spatiotemporal patterns of wintering populations helps to understand the factors that influence their habitat needs, as well as the recognition of the conservation status of their ecosystems (Lunardi et al. 2012). Our data help to understanding some of factors that influence of the distribution of dunlin during the wintering and non-wintering period in the "La Mancha Húmeda" Biosphere Reserve. Notably, we highlight that the main wintering area of the species – Manjavacas Lagoon Complex – is under strong anthropic pressure, because there is failures in the treatment of its wastewater, as well as under constant changes as a consequence of the surrounding agricultural activities. Finally, our data suggest that the lagoons belonging to this complex constitute of faithful wintering sites of the species and that conservation and improvement measures should be taken to keep viable the presence of these populations.

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Table 1. Twenty-three lakes monitored between October 2010 and July 2017 in "La Mancha Húmeda" Biosphere Reserve (see Figure 1). UTM – Datum ETRS89; Area (ha); Flooded surface (ha); Veg – area covered by natural vegetation (ha); Ni – number of sedimentary islands; IsA – total area of existing sedimentary islands (ha); AD – average depth (meters); Hyd – hydroperiod (% of months with water); Leng – shoreline length (meters) and; SDI – Shoreline Development Index.

Code	Lake	UTM X	UTM Y	Area	Flooded	Veg	Ni	IsA	AD	Hyd	Leng	SDI
1	Alcahozo*	510620	4360164	88.6	69	19.5	0	0	1.75	58.5	4805	1,63
2	Altillo Grande	474187	4393670	32.9	20.4	12.4	0	0	4.25	43.9	2932	1,82
3	Artevi	472611	4385210	27.9	16.7	11.2	0	0	4.75	68.2	3102	2,14
4	Camino de Villafranca	478055	4362616	159.9	134.7	23.7	2	1.7	2.25	95.1	9181	2,23
5	Campo de Mula	464695	4381452	50.9	25.5	25.3	0	0	3.25	21.9	4038	2,25
6	Longar	472448	4395066	259.5	99.1	160.3	0	0	4	92.6	5895	1,67
7	Manjavacas	511840	4363360	262.8	197.8	64.0	3	9	2.75	97.5	9872	1,98
8	Mermejuela	488191	4376617	9.9	8.6	1.2	0	0	6.5	82.9	1374	1,31
9	Miguel Esteban	495294	4373855	92.2	23.4	68.8	0	0	2.5	97.5	3966	2,31
10	Pedro Muñoz	504589	4362479	41.3	26.1	15.2	0	0	3.25	87.8	5936	3,27
11	Peña Hueca	470426	4373729	158.8	132.6	19.6	4	6.6	3.75	58.5	11146	2,73
12	Quero	478215	4372367	95.7	84.0	11.6	0	0	2	70.7	4991	1,53

13	Retamar	502427	4364111	79.1	62.7	16.4	1	4	3.5	21.9	5217	2,21
14	Tírez	469331	4376605	131.8	81.1	50.6	1	0.04	4.25	51.2	6112	1,91
15	Veguilla	479389	4360715	89.0	44.3	44.7	0	0	4.25	97.5	9607	4,06
16	Larga de Villacañas	472815	4384080	167.3	114.5	52.7	0	0	3.25	100	9648	2,54
17	Albardiosa	474994	4390229	71.8	39.5	32.3	0	0	2.5	8.3	3557	1,59
18	Altillo Chica	473975	4394727	24.6	17.8	6.8	0	0	3	55.5	2200	1,47
19	Camino de Turleque	464403	4384224	48.6	39.4	9.2	0	0	5.25	5.5	3097	1,39
20	Pajares	482321	4367206	23.5	20.9	2.6	0	0	2.75	39	2360	1,45
21	Redondilla	513136	4310021	5.7	3.5	2.2	0	0	11	26.8	981	1,47
22	Salicor	485033	4368502	81.4	48.3	23.7	3	9.2	5.75	55.5	5159	2,09
23	Yeguas	475657	4363078	96.2	64.9	31.3	0	0	2	61.1	4593	1,6

Table 2. Lakes monitored between October 2010 and July 2017 and their respective dominance values (% Dom; distribution of accumulated records by period), average monthly abundance (average (SD)) and frequency of occurrence (FO%; number of months with presence of dunlin).

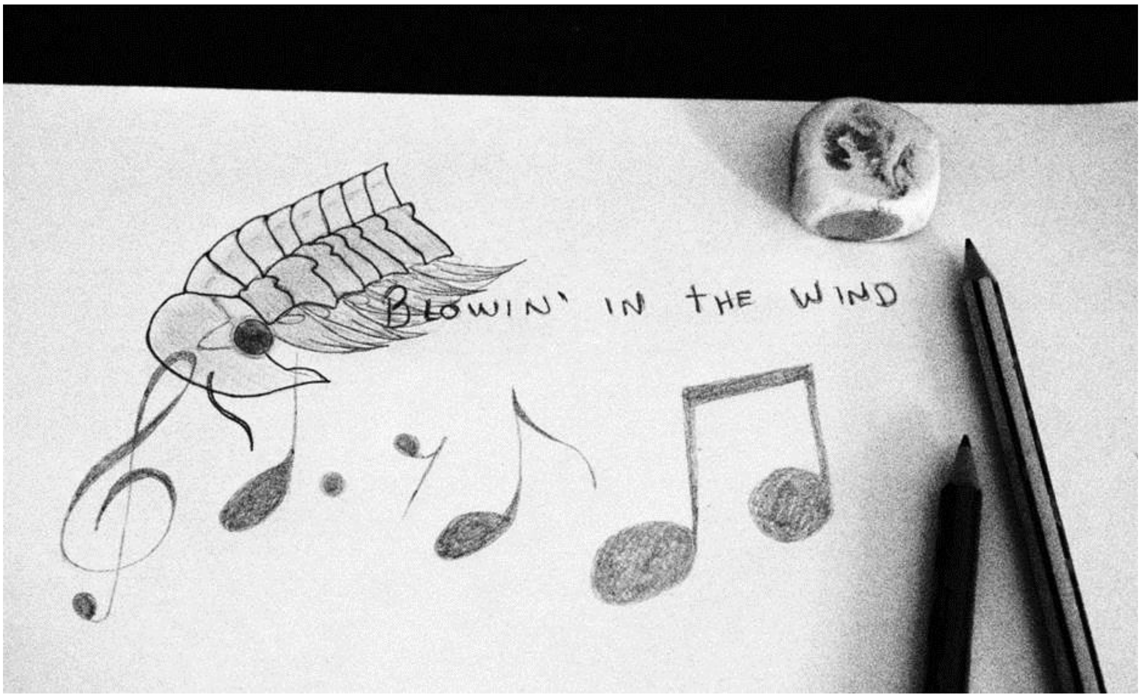
	All period			**Wintering period**			**Non-wintering period**		
Lakes	**%Dom**	**Average (SD)**	**FO%**	**%Dom**	**Average (SD)**	**FO%**	**%Dom**	**Average (SD)**	**FO%**
Alcahozo	50,1	34,9 (76,1)	25,6	64,0	81,1 (99,7)	54,3	1,8	0,4 (3,7)	4,2
Manjavacas	37,2	25,8 (58,7)	30,5	28,8	36,5 (71,9)	40	66,6	17,9 (45,7)	23,4
Camino de Villafranca	8,0	5,5 (20,4)	29,3	5,0	6,2 (13,1)	37,1	18,7	5 (24,6)	23,4
Veguilla	2,2	1,5 (7,4)	4,88	0,3	0,4 (2,5)	2,9	8,9	2,4 (9,5)	6,3
Quero	0,9	0,5 (2,1)	9,76	0,7	0,8 (2)	17,1	1,5	0,4 (2,2)	4,2
Artevi	0,6	0,4 (3,8)	1,22	0,8	1 (5,9)	2,9	0	0	0
Larga de Villacañas	0,3	0,1 (1,7)	1,22	0,4	0,4 (2,7)	2,9	0	0	0
Pedro Muñoz	0,2	0,1 (0,9)	3,66	0	0	0	0,9	0,2 (1,2)	6,3
Campo de Mula	0,2	0,1 (1,1)	1,22	0	0	0	0,8	0,2 (1,4)	2,1
PeñaHueca	0,2	0,1 (0,7)	2,44	0	0	0	0,7	0,1 (0,9)	4,2
Mermejuela	0,1	0,07 (0,6)	1,22	0,1	0,1 (1)	2,9	0	0	0
Albardiosa	0	0	0	0	0	0	0	0	0
Altillo Chica	0	0	0	0	0	0	0	0	0
Altillo Grande	0	0	0	0	0	0	0	0	0
Camino de Turleque	0	0	0	0	0	0	0	0	0
Longar	0	0	0	0	0	0	0	0	0
Miguel Esteban	0	0	0	0	0	0	0	0	0
Pajares	0	0	0	0	0	0	0	0	0
Redondilla	0	0	0	0	0	0	0	0	0
Retamar	0	0	0	0	0	0	0	0	0

Salicor	0	0	0	0	0	0	0	0	0
Tírez	0	0	0	0	0	0	0	0	0
Yeguas	0	0	0	0	0	0	0	0	0

Capítulo 5

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

M. S. S. Gonçalves, J. A. Gil-Delgado, G. M. López-Iborra, & P. Pons



Cabeza y somitos torácicos de *Branchinectella media*. Música de Bob Dylan

Animal Biodiversity and Conservation, Vol 42

WIND EFFECTS ON HABITAT USE BY WINTERING WADERS IN AN INLAND LAKE OF THE IBERIAN PENINSULA

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Abstract

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 in days with different wind speed (smooth and strong). Visual counts of potential prey items (zooplankton) in mud and water habitats were also performed. Under the smooth wind conditions, wader flocks selected mostly the shallow water located on the lake's leeward. On the contrary, under strong wind conditions birds tended to forage on the windward shore, with similar frequency in mud and shallow water habitats. The abundance of prey items in mud and water column varied according to wind conditions, being higher in the sites preferred by waders. Our findings add to the knowledge about how small-sized waders cope with environmental dynamics in wind in non-tidal lakes.

Keywords: abiotic factors, foraging habitat, saline lakes, shorebirds, wintering season

Resumen

Nuestro objetivo fue identificar los efectos de la dirección y velocidad del viento en el uso del hábitat de alimentación de correlimos común y correlimos menudo en un lago interior de la Península Ibérica. El hábitat de alimentación de grupos de limícolas (superficie fangosa o aguas poco profundas) y la ubicación en el lago con respecto a la dirección del viento (barlovento y sotavento) se evaluaron 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. Bajo las suaves condiciones del viento, el grupo de limícolas seleccionaron principalmente el agua poco profunda ubicada a sotavento del lago. Por el contrario, bajo condiciones de fuerte viento, las aves tendieron a buscar comida en la orilla de barlovento, con una frecuencia similar en los hábitats de lodo y aguas poco profundas. La abundancia de elementos de presa en la columna de lodo y agua varió según las condiciones del viento, siendo más alta en los sitios preferidos por los limícolas. Nuestros hallazgos se suman al conocimiento de cómo los limícolas de tamaño pequeño hacen frente a la dinámica ambiental del viento en lagos no mareales.

Palabras clave: aves acuáticas, factores abióticos, hábitat de forrajeo, shorebirds, lagunas salinas, período invernal

1. Introduction

Multiple environmental components act independently or in association to influence habitat selection and use by birds (Jones, 2001). The choice of the foraging sites by waders is fundamentally a consequence of the balance of costs and benefits of feeding in many potential foraging habitats, defined mainly by depth of the water column, as well as quality and quantity of prey (e.g. Piersma, 2006; Granadeiro et al., 2007; Beerens et al., 2015a, b). Additionally, other important factors, such as predation risk (Mikula et al., 2018), anthropic disturbances (Holm & Laursen, 2009), eco-physiological adaptations (Gutiérrez et al., 2012, Lourenço & Piersma, 2015) or roost location and landscape attributes (Dias et al., 2014; Santiago-Quesada et al., 2014) are associated to habitat selection by waders outside the breeding season, but 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 & Barton, 2017). For waders, aquatic invertebrates are the main food supply, which can be detected and captured visually or using tactile sensibility (Piersma et al., 1996). Many waders, especially scolopacid species, have 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 & Masero, 2007; Estrella et al., 2007).

Wind can act of two different ways on the aquatic invertebrate distribution. On the one hand, in foraging grounds where the preys are distributed along the water column, wind can move and concentrate them in specific sites of the wetland, facilitating the visual strategy (Verkuil et al., 1993). On the other hand, wind 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 are focused in coastal systems, where most migratory wader populations spend the wintering season (van de Kam et al., 2004). Dunlin (*Calidris alpina*) and little stint (*C. minuta*) are two of the most abundant wintering waders in the Iberian Peninsula, where 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 carried on habitat selection by waders wintering in Iberia, they were performed on intertidal habitats or coastal areas (e.g. Masero et al. 2000, Masero & Pérez-Hurtado 2001, Dias, 2009; Lourenço et al. 2013; Martins et al. 2016), and there is no information on habitat use or selection during the winter period in continental Iberian wetlands by foraging waders.

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). Specifically, we investigated the relationship between wind direction and wind speed and the selection of two foraging habitats – mud and shallow water. According to Verkuil et al. (1993), we expected significant effects of wind direction and speed on the spatial distribution of aquatic invertebrates and, consequently, on the habitat use by foraging waders.

2. 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 Alcahozo lake (Coord. N 39º 23’ 26,7” / W 2º 52’ 35,7”), a temporary natural wetland located in this reserve (Figure 1). The Alcahozo lake has a roughly circular shape and covers an area of approximately 88 ha, including 19 ha of natural halophile vegetation surrounding the lake (Gonçalves et al., 2016). It presents homogeneously flat shores and a maximum depth of approximately 45 cm. There are no sedimentary islands within this lake.

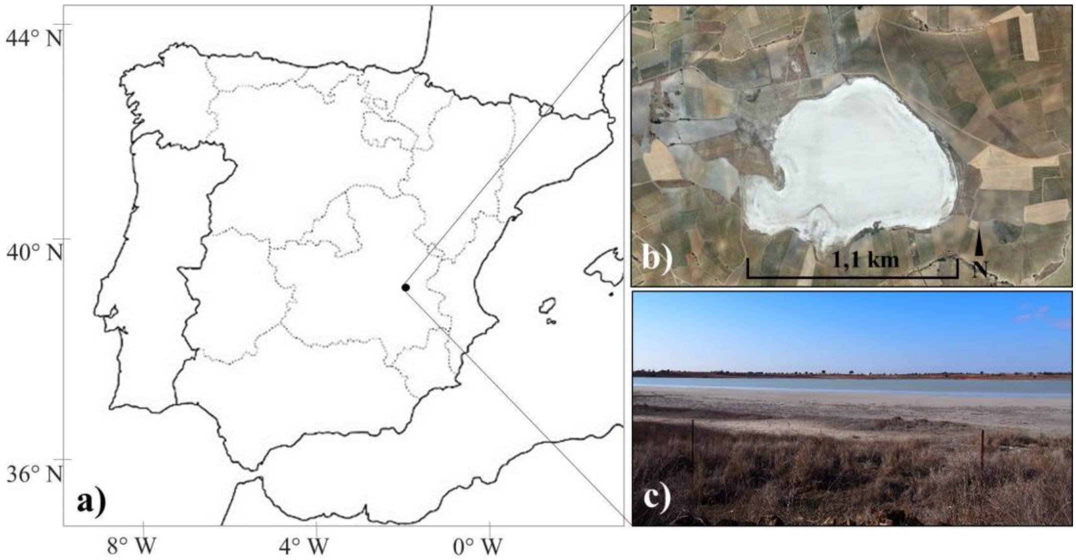


Figure 1. Location (a) and view (b and c) of the Alcahozo lake, in "La Mancha Húmeda" Biosphere Reserve, Spain.

Data collection and sampling design

To evaluate the foraging habitat use, we applied an *used vs 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 interval 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 during 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) (Figure 2). After that, we identified their position in relation to wind direction as windward or leeward (Figure 2). In this way, the wader flocks could be found in the following four situations: mud/leeward, mud/windward, water/leeward and water/windward. Additionally, two wind speed classes were defined – smooth (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.

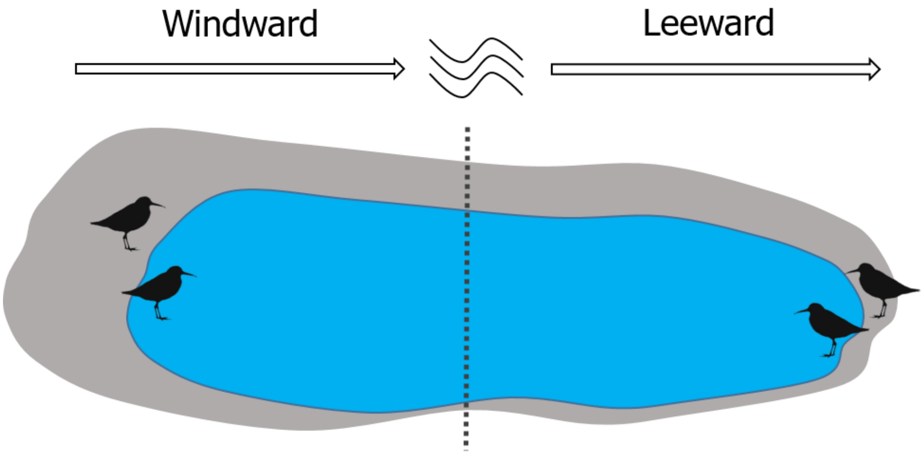


Figure 2. Scheme showing the four possible distributions of the flocks (represented by a single bird) of waders during the wintering period in the Alcahozo lake. In each observation, only one of four situations was possible: windward or leeward and mud (gray) or shallow water (blue).

Anostracans and copepods are abundant in the Alcahozo lake, 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 with a cautious approach and by remaining motionless, these and other groups like ostracods could be visually detected at a close distance. Although the best method to quantify the abundance of invertebrates is the collection of water samples and subsequent 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 & Townsend, 1996). In this sense, as a way of observing if the 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 (Figure 2). Samplings were performed between January and February 2016. Invertebrate counts were performed in six days in each wind speed class. Five plots of 40 cm x 40 cm distributed every 2 meters 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 rest at places representative of the other three categories not used at that moment; thus, the location of the plots varied at each sampling occasion, since it depended on the location of the waders and wind direction.

Data analysis

We used log-linear models to evaluate if the observations of wader flocks were associated preferentially 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 (smooth/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.

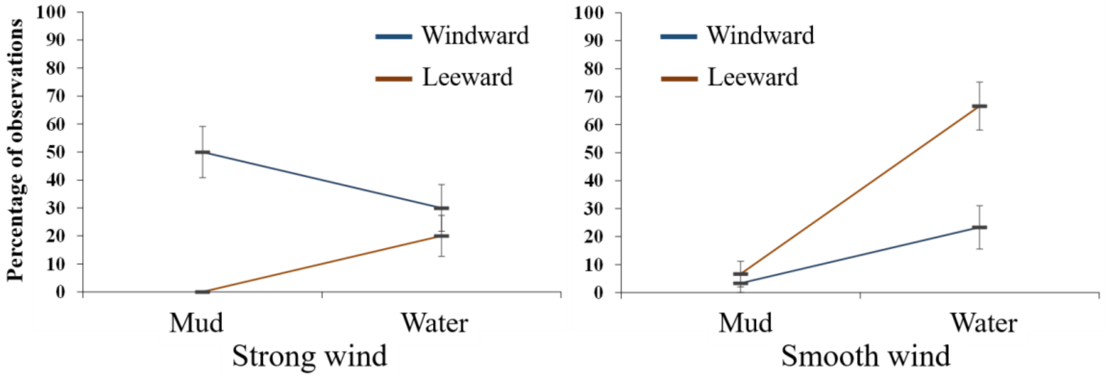
For the invertebrates abundance, the effects of abundance of the same factors cited above were tested using Generalized Linear Mixed Models (GLMMs) with Poisson distribution. The total number of invertebrates counted in each plot was the response variable. Habitat type, position relative to wind and wind speed category were factors included as fixed effects. The sampling day was considered as 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 Core Team, 2014). The GLMMs were performed using the package 'lme4' (Bates et al., 2013).

3. Results

In smooth wind conditions, 74% of the observations of foraging flocks were made at leeward of the lake, mainly of birds feeding in the water column (67%) (Figure 3a). On the other hand, under strong wind conditions, 80% of foraging flocks were found at the windward side, with 50% and 30% of flocks using the mud and the water column, respectively (Figure 3a). All possible interactions were significant (Table 1).

For invertebrates, three taxonomic groups were identified during the visual counts: Anostraca, Copepoda, and Ostracoda. Under smooth wind conditions, the greatest invertebrates' abundance was observed in the shallow water, with the highest values located at the leeward side (Figure 3b). However, under strong wind conditions, invertebrate abundance was much higher in mud than in water at the windward side, while at the leeward side their abundance was low and similar low in both habitat types (Figure 3b). The interaction between the three factors (wind speed, direction and habitat type) was not significant (χ^2= 0.95; df= 1; p= 0.32), but the two-way interactions were all significant ($p < 0.01$, in all cases) (Table 1).

a) Birds



b) Invertebrates

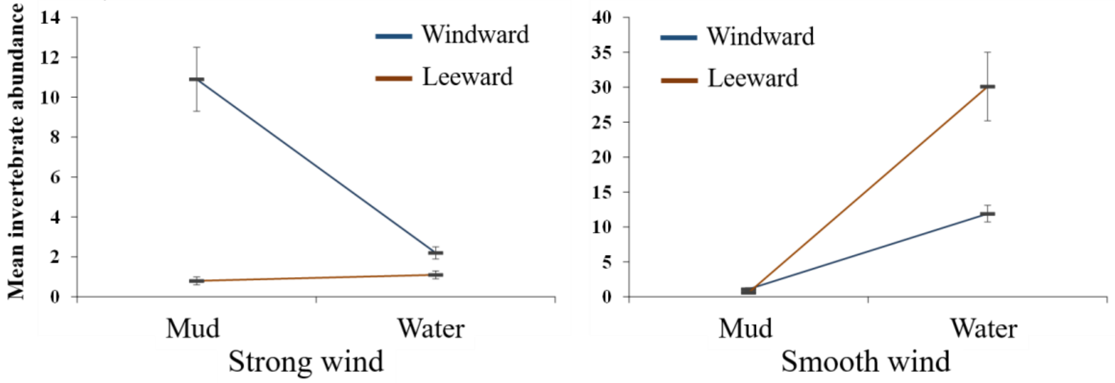


Figure 3. a) Percentage of observations of the waders flock based on 30 flocks observed under each wind speed category (±SE calculated using binomial distribution) and b) invertebrates abundance (±SE) between mud and water habitats in relation to the direction (windward or leeward) and wind category (strong or smooth).

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 chi-square test.

Interaction	Chi square	df	p-value
Wader flock habitat			
wind speed x position x habitat	3,95	1	0,0468
Invertebrate abundance			
wind speed x position x habitat	0,95	1	0,3288
wind speed x position	82,79	1	< 0,001
wind speed x habitat	588,27	1	< 0,001
position x habitat	69,59	1	< 0,001

4. 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 that could be potentially associated to the wind effects. Our results showed that under smooth wind conditions, foraging birds selected mostly shallow water, on the lake’s leeward. On the contrary, under strong wind conditions, birds tend to forage on the windward shore and they used both mud and shallow water microhabitats. Similarly, invertebrate abundance in mud and water microhabitats varied with wind conditions, being higher in the sites preferred by waders.

In shallow lakes, such as our study area, strong winds move the water column rapidly affecting the spatial distribution of zooplankton organisms (Cardoso & Marques, 2009) and raising sediments in suspension that may increase turbidity (G-Tóth et al., 2011). Therefore, in these ecosystems wind has the potential of affecting wader prey abundance and detectability. Our results agree with the general patterns observed in shallow lagoons in the Ukraine region by Verkuil et al. (1993, 2003). Under smooth wind conditions, most feeding wader flocks used the water habitat at the leeward coast. This pattern is possibly a response to the smooth displacement of prey items towards the leeward shore. In addition, the smooth wind keeps water turbidity low, facilitating visual detection and predation on invertebrates. In this situation, the distribution of feeding waders flocks mirrors almost perfectly the variations in invertebrate abundance.

On the other hand, under strong wind conditions, wader flocks used mainly the windward side for foraging activities. This may be due to two causes: the area of exposed mud is greatly reduced at the leeward shore and the water column moves so rapidly that preys are exposed on the muddy surface at the windward shore (Verkuil et al., 1993), facilitating predation. In addition, under strong wind conditions, the prey abundance index is quite low at the water column in the two positions relative to the wind, while the frequency of waders feeding in water is not so different in leeward and windward sides. This suggests that 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 & Masero, 2007).

The visual counts of invertebrates identified Anostraca, Copepoda, and Ostracoda as the main groups of invertebrates. At the Alcahozo lake, these groups are represented by *Branchinectella media* (Anostraca), *Arctodiaptomus salinus* (Copepoda) (Pons et al., 2018) and *Heterocypris barbara* (Ostracoda) (Castillo-Escrivà et al., 2015). Notably, information about spatial distribution and habitat selection is available only for *B. media*. Pons et al. (2018) investigated the spatial distribution of *B. media* in days without wind and observed that adult individuals tend to occur on the central region of the lake, while juveniles are most commonly observed at 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 the sites with the higher abundance of prey, which 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 irrespective of wind. Although we have not observed any predation attempts, the approximation of some species as lesser black-backed gull (*Larus fuscus*), black-headed gull (*L. ridibundus*) and Eurasian marsh harrier (*Circus aeruginosus*) often forced the flocks to change their foraging behavior. Specifically, the waders presented three responses: short distance displacement and 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 1500 gulls (*Larus* spp.) gather to spend the night in the Alcahozo lake and, depending on the chosen position to rest, could be a physical barrier to the habitat use of the waders. However, gulls always roosted at 50-60 meters from the shoreline and therefore did not influence directly the habitat use of waders. Future research should consider these effects on the habitat selection by waders using these inland wetlands.

This study adds to our understanding about the 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 for most of the lakes there is no physical protection limiting the advance of the agricultural frontier (Gonçalves et al., 2018). The shore topography of some of these lakes has been modified in the past by agricultural or infrastructure works, including transformations for receiving wastewater from nearby towns (Gonçalves et al., in press). Thus, artificial modifications of the topography of inland lakes that prevent some of the preferred habitats to be available under some wind situation could reduce the suitability of these wetlands for wintering waders.

5. Acknowledgments

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Capítulo 6

Resumen global

1. Resumen ampliado

Esta tesis doctoral trata de las aves limícolas de las zonas húmedas continentales de España. Estos ambientes se incardinan en un contexto de paisajes con una fuerte presión ambiental y, en consecuencia, marcados con innumerables figuras de espacios protegidos de importancia internacional (Infante et al., 2011). En particular, esta tesis hace referencia especial a las aves migratorias y residentes que utilizan la región durante los períodos de reproducción, invernado y de paso, y que taxonómicamente pertenecen al orden de los Charadriformes (Piersma & Lindström, 2004). Como parte central, buscamos comprender cómo las variables correspondientes al hábitat y / o al paisaje se asociaron a los patrones observados en diferentes niveles en ecología, específicamente la riqueza de especies, la dinámica espacial y temporal de poblaciones y el uso del hábitat a escala local.

Una constelación de áreas húmedas en la región central de España, conocida como La Mancha, está clasificada o insertada en importantes figuras de protección, especialmente la Reserva de la Biosfera de la UNESCO, áreas RAMSAR y red Natura 2000 (Infante et al., 2011). Sin embargo, históricamente, la región ha sido modificada por actividades humanas y, en los últimos 30 años, la canalización y / o sustracción de aguas subterráneas para irrigación de los cultivos agrícolas está presente en toda la región central de España (Infante et al., 2011). Esto está en el marco de lo que en nuestro días conocemos como intensificación de la agricultura y que engloba al conjunto de manejos que actúan sobre los cultivos desde el uso de los nuevos pesticidas hasta la plantación de variedades con mayor producción (Chamberlain et al., 2010). Tales cultivos se localizan en las inmediaciones de las zonas húmedas y no son raras las situaciones en que adentran en los espacios lagunares. Además, las lagunas han sido objeto de vertidos de aguas residuales procedentes de zonas urbanas, sin recibir un adecuado tratamiento de la calidad del agua y una completa comprensión de sus efectos en la estructuración espacial y temporal de la biodiversidad acuática.

En este sentido, el primer paso de esta tesis fue comprender el efecto de factores ambientales en un importante indicador de la diversidad biológica – la riqueza de especies (capítulo 2). Se sabe que la conservación de los humedales depende del conocimiento de cómo una amplia lista de factores de hábitat y paisaje afectan la riqueza de especies en diferentes períodos del año (Ma et al., 2010). Así, para alcanzar este primer objetivo, exploramos la información del número de especies de aves limícolas de 23 lagunas. Los datos fueron obtenidos a partir de una amplia serie temporal de censos mensuales. Para ello, la riqueza de especies fue determinada para dos importantes períodos del ciclo anual de aves limícolas en la región de La Mancha – período de reproducción (mayo a julio) y período invernal (diciembre a febrero). Hemos identificado 26 especies de limícolas, de las cuales ocho son residentes y 18 son invernantes. Cuatro especies pertenecen a categorías formales de amenaza de extinción: el correlimos zarapitín (*Calidris ferruginea*), la aguja colinegra (*Limosa limosa*), el zarapito real (*Numenius arquata*) y la avefría (*Vanellus vanellus*). Las mayores riquezas para ambos períodos se observaron en las lagunas que reciben aguas residuales y, por lo tanto, tiene su período de inundación ampliado. Pocas variables se asociaron a los patrones de riqueza de especies. Un fenómeno ampliamente conocido en los patrones de riqueza de especies – relación especie-área (Brown & Dinsmore, 1986; Rosselli &

Stiles, 2012) – fue importante sólo para el período invernal, probablemente como respuesta a la estabilidad hídrica de la región durante el invierno. Para el período de reproducción, el principal factor fue el hidroperíodo de las lagunas, probablemente porque en esta estación las lagunas que no reciben aguas residuales comienzan a presentar bajos niveles de volumen de agua durante la primavera y verano, potenciando el uso de lagunas con hidroperíodo más largo. En un grado menor tanto para el período de reproducción como para el período invernal, el número de lagunas dentro de un radio de 10 km se asoció a la riqueza de especies, indicando que las aves son influenciadas, al menos en parte, por el grado de conectividad de las lagunas.

A partir de la misma base de datos exploramos un fenómeno ecológico poco conocido para zonas húmedas continentales – la sincronía espacial de las poblaciones (capítulo 3). Para ello, tres especies fueron utilizadas como modelo – avoceta común (*Recurvirostra avosetta*), cigueñuela común (*Himantopus himantopus*) y chorlitejo patinegro (*Charadius alexandrinus*). Con este enfoque, evaluamos la semejanza de las curvas de abundancia mensual entre los lagos y probamos si el nivel de sincronía de las curvas se asoció con diferentes factores del hábitat y del paisaje. Este fenómeno es uno de los más importantes en la dinámica de poblaciones y, aunque sea poco conocido para aves limícolas, ha sido observado en diferentes escalas espaciales para muchas especies (ver Liebhold et al., 2004). Las tres especies mostraron variaciones de abundancia sincronizadas entre grupos de lagunas analizadas, de forma que fue posible identificar grupos de lagunas con picos de abundancia en diferentes fases de tiempo. El hidroperíodo de aquellos lagos que reciben aguas residuales fue más largo en aquellas lagunas que no reciben estos aportes y que dependen exclusivamente del régimen de las lluvias. Este factor estuvo positivamente relacionado con la sincronía espacial de avoceta común y chorlitejo patinegro. En particular, las variaciones de abundancia de estas dos especies formaron grupos de lagunas con patrones constantes en el tiempo. En concreto, lagunas con un hidroperíodo corto presentaron los primeros picos de abundancia que posteriormente se observaron en las lagunas con largos hidroperíodos. Estos resultados evidenciaron un movimiento de individuos entre estos dos grupos de lagunas, posiblemente como respuesta a las mejores condiciones de hábitat para alimentarse en los inicios y finales del verano. Para la avoceta común, los patrones sincrónicos también estuvieron asociados a la distancia entre los lagos, un factor usado como indicador del efecto de dispersión. Ninguna variable fue capaz de explicar los altos niveles de sincronía entre las diferentes lagunas para la cigüeñuela común. Esta especie presentó igualmente dos grupos de lagunas sincronizados, uno formado por un gran número de áreas heterogéneas y otro formado por dos lagunas similares en estructura de la vegetación y que sostienen ambientes con agua durante más tiempo durante el verano. Estos resultados para la cigüeñuela común posiblemente reflejan la alta plasticidad ecológica de la especie en relación a otras especies de limícolas. Adicionalmente, un análisis del hidroperíodo más refinado, como por ejemplo la profundidad de las lagunas y la superficie de inundación mensual, podrían tener un mayor potencial para responder a las variaciones temporales de abundancia de esa especie. Debido al régimen temporal de las lagunas y por reproducirse las tres especies en la región, todas ellas reducen sus valores de abundancia en los meses de otoño e invierno y aumentan sus poblaciones en los meses de primavera y verano. Por este motivo, aunque un efecto estacional ha sido esperado previamente, nuestro enfoque se centró en el acoplamiento de las curvas entre las diferentes áreas y estos resultados presentan las primeras evidencias sobre los procesos que conducen la sincronía espacial de poblaciones de aves limícolas reproductoras en el centro de España.

Dando continuidad a la observación de los patrones espaciales y temporales de abundancia de las poblaciones, seleccionamos como objeto de estudio una de las aves limícolas invernantes más abundantes en la Península Ibérica – el correlimos común (*Calidris alpina*) (capítulo 4). El conocimiento de las rutas de aves migratorias, así como sus áreas de alimentación e invernada, es crucial para definir e implementar acciones de manejo a múltiples escalas espaciales (Andres et al., 2012). Así, en este capítulo analizamos de forma descriptiva la frecuencia de ocurrencia (FO%) y el porcentaje total de los individuos (dominancia %) de correlimo común registrados en las mismas lagunas estudiadas en los capítulos anteriores entre los años 2010 y 2017. Los resultados de estos análisis detectaron que el correlimos común se encontró en menos del 50% de las áreas estudiadas y casi el 90% de los individuos registrados pertenecían a apenas dos lagunas – lagunas Alcahozo y Manjavacas – ambas situadas en el Complejo Lagunar de Manjavacas. Así, de forma complementaria, evaluamos el grado de correlación de las curvas de abundancia de los correlimos comunes entre estas dos áreas, buscando comprender los posibles movimientos locales de los individuos. Se observó que los picos de abundancia presentaron un patrón similar a los observados para las especies reproductoras estudiadas en el capítulo 2. Específicamente, la laguna de Alcahozo, que no recibe aguas residuales, mostró picos de abundancia más adelantados en relación a la laguna Manjavacas– laguna con un amplio hidroperíodo y que recibe aguas depuradas. Tanto la clara preferencia por el complejo lagunar de Manjavacas, como el patrón de abundancia entre las lagunas, parecen estar directamente asociados a la composición y abundancia de los invertebrados de ambas lagunas en relación al resto de las lagunas estudiadas. Horváth et al. (2013), en zonas húmedas continentales de Hungría, demostraron que algunas especies de limícolas están más influidas por la composición y abundancia de crustáceos que otras especies.

Específicamente, estos autores observaron que los anostráceos tienen un papel importante en la estructuración de las comunidades de aves acuáticas. En adición, los anostráceos junto con los copépodos, notablemente, la especie del genero *Arctodiaptomus*, constituyen invertebrados atractivos como alimento para las aves limícolas durante el período de migración (Horváth et al., 2013). De acuerdo con el listado de especies de invertebrados del Laboratorio de Microbiología y Ecología de la Universidad de Valencia para las lagunas estudiadas, entre las cuatro lagunas del Complejo Lagunar de Manjavacas hay una composición particular de especies entre anostráceos y copépodos que, de acuerdo com la observaciones de Horváth et al. (2013), se podría explicar la concentración de correlimos comunes en estos lagos. Respecto a las variaciones temporales de abundancia entre los lagos de Manjavacas y Alcahozo, los primeros picos de la población de correlimos común que se asocia a la laguna de Alcahozo se podrían explicar probablemente por la presencia de *B. media* en esta laguna. Para las dos lagunas del complejo lagunar de Manjavacas que fueron estudiadas (Alcahozo y Manjavacas), esta especie es observada solo en Alcahozo. *B. media* posee un desarrollo más rápido y una biomasa considerablemente mayor que las especies de invertebrados presentes en Manjavacas.

En la laguna Alcahozo, los correlimos menudos y comunes forman grupos mixtos para alimentarse durante el invierno. Se sabe que la elección de los sitios de alimentación por las aves limícolas es fundamentalmente una consecuencia del equilibrio de costos y beneficios entre muchos hábitats potenciales de alimentación, definidos principalmente por la profundidad de la columna de agua, y por la calidad y la cantidad de presas (Piersma, 2006). En consecuencia, estos factores deben de influir en la dinámica temporal y los niveles de estabilidad de las poblaciones de limícolas en las diferentes escalas espaciales (Ranta et al., 1995). En este trabajo, hemos buscado reconocer a escala local, cómo las condiciones del viento influyeron en el uso del hábitat por las dos especies mencionadas en la laguna Alcahozo. Hemos investigado la relación entre la dirección y la velocidad del viento y el uso de dos hábitats de forrajeo – lodo de la orilla y aguas poco profundas. Para valuar las variaciones en la abundancia de presas potenciales en estos hábitats realizamos conteos visuales de invertebrados. Esperábamos encontrar efectos significativos de la dirección y de la velocidad del viento sobre la disponibilidad de presas y, en consecuencia, sobre cómo utilizan el lago estas especies de limícolas. Nuestros resultados mostraron que en condiciones de viento suave, los limícolas seleccionan generalmente las aguas rasas a sotavento del lago. Por el contrario, bajo condiciones de fuerte viento, las aves tienden a alimentarse en la orilla de barlovento y utilizan tanto el lodo como las aguas poco profundas. De manera similar, la abundancia de invertebrados en el lodo y el agua varió con las condiciones del viento, siendo más alta en los sitios preferidos por estas aves. Nuestros resultados coinciden con los patrones generales observados en las lagunas poco profundas en la región de Ucrania (Verkuil et al., 1993, 2003). La topografía de la orilla de las lagunas de La Mancha sufre con los efectos de los cultivos agrícolas en el entorno inmediato lo que puede hacer que algunos de los hábitats de forrajeo, especialmente bajo cierta situación de viento, sean afectados y no utilizados por las aves invernantes.

2. Discusión y perspectivas

Aunque muchos estudios en la región mediterránea tienen como objeto de investigación las aves limícolas, estos están en general limitados tanto en el tiempo como en el espacio. Específicamente, la mayoría de los estudios se han realizado con periodicidad anual o estacional y en cortas series temporales, dificultando la interpretación de los efectos de factores ambientales dinámicos e intermitentes, tales como el hidroperíodo de las lagunas temporales. Además, los patrones de distribución espacial de las aves limícolas y sus factores asociados son ampliamente conocidos para la zona costera de la Peninsula Ibérica – región en que se concentran gran parte de sus poblaciones – y se conoce menos en las áreas húmedas continentales (Masero & Pérez-Hurtado, 2001, Lourenço et al., 2013; Martins et al., 2016). De esta manera, el conjunto de la información acumulada en esta tesis presenta un interés y relevancia en tres niveles distintos – relevancia teórica, aplicada y ecosistémica. En primer lugar, las relaciones observadas entre los factores de hábitat y/o de paisaje en los diferentes niveles de ecología tratados en este trabajo – comportamiento (uso del hábitat), ecología de poblaciones (dinámica espacio-temporal) y ecología de comunidades (riqueza de especies) – proporcionan las primeras evidencias de los mecanismos que actúan sobre la distribución espacial y temporal de las aves limícolas en lagunas continentales en el centro de España, y muestran que el hidroperíodo de las lagunas actúa como un factor importante en la estructuración de la diversidad biológica de La Mancha, y que su efecto es mediado, por lo menos en parte, por la recepción de aguas residuales urbanas.

El conjunto de evidencias presentadas en los capítulos es particularmente importante dado que los enfoques integrados entre diferentes niveles jerárquicos en ecología se han convertido en una herramienta útil para comprender la distribución de las especies y sus posibles mecanismos y estrategias para la conservación (Weimerskirch, 2018). Las aves limícolas registradas en nuestros estudios representan aproximadamente el 40% de las especies limícolas con potencial de registro en España. Un pensamiento está implícito en la biología moderna y es que, a lo largo de la evolución, la selección natural ha favorecido a los organismos con ciertos genotipos, dotándolos con características que les permitan resolver problemas ambientales de una manera optimizada para la supervivencia y la reproducción (Smith & Winterhalder, 2017). Todas las especies registradas presentan una capacidad alta de desplazamiento, ocupan hábitats restringidos (lodo y aguas poco profundas) y destacan por una amplia diferenciación morfológica entre las especies, especialmente en la longitud y el formato del pico, la longitud de las patas y la biomasa (Piersma et al., 1996). Este conjunto de características puede, en parte, reducir los efectos de factores limitantes como son la dispersión y la exclusión competitiva. Por otro lado, los cambios constantes en el paisaje y en la calidad de los hábitats de alimentación, en asociación a unas condiciones abióticas desfavorables, pueden constituirse en las barreras más importantes para la persistencia de estas especies en la región de estudio, ya que estos factores imponen necesidades adaptativas no sólo ecológicas sino también fisiológicas. Para la región central de España, la dispersión y las interacciones ecológicas no constituyen barreras ecológicas, las características efímeras de los ambientes temporales, las alteraciones ambientales a partir de las actividades agrícolas, así como de los aportes de aguas provenientes de los vertidos parecen ser los principales factores ambientales que determinen el uso de los humedales por estas especies. Por ejemplo, el carácter temporal de las precipitaciones puede hacer que las lagunas se queden secas o con poca agua durante el verano y que en los años secos se mantengan estas condiciones en buena parte del invierno, lo que impediría o retrasaría el ciclo de las especies zooplanctónicas, y por consiguiente la oferta de alimento. Por otra parte, en el invierno, las lagunas pueden quedar congeladas durante algunos días consecutivos como consecuencia de temperaturas que pueden llegar hasta -20ºC en años extremos. Además, los vientos fuertes y constantes también pueden afectar la distribución y disponibilidad de las presas al mover fácilmente la columna de agua. En este sentido, los artículos presentados en esta tesis abordan algunos de estos factores ambientales. En general, el hidroperíodo fue un factor importante en relación a los patrones observados, tanto respecto a los valores de riqueza de especies reproductoras como respecto a la dinámica y sincronización de las poblaciones. Esta interacción nos indica un cierto grado de adaptación y plasticidad ecológica frente a los cambios y calidad de los hábitats de alimentación dependientes del hidroperíodo. Las estrategias del uso del hábitat en relación con las condiciones abióticas – notablemente el efecto de la dirección y la intensidad del viento y la selección de áreas que combinan grupos específicos de invertebrados (i.e. anostráceos e copépodos) constituyen igualmente indicadores de adaptación ecológica y, posiblemente, fisiológica, favoreciendo la ocupación de una región con condiciones ambientales aparentemente desfavorables.

En las discusiones de los capítulos de esta tesis se ha tratado siempre sobre el hidroperíodo, pues intervienen directa o indirectamente en los patrones observados. En aquellos lagos que no reciben aguas residuales, el hidroperíodo tiende a ser cada vez más corto en función de la captación y canalización del agua para los cultivos agrícolas. Mientras tanto, es sabido que el aporte de aguas residuales disminuye la salinidad y aumenta la materia orgánica en lagos poco profundos, y como respuesta a las altas temperaturas en verano puede aumentar el riesgo de brotes de botulismo (Anza et al., 2014). Este ha sido reportado como un factor clave en la reducción de las poblaciones de aves acuáticas en todo el mundo. Particularmente para la región MHBR, más de 2000 individuos de 19 especies murieron entre 1978 y 2008 (Anza et al., 2014).

Desde hace más de dos décadas se han producido advertencias sobre las consecuencias negativas de las aguas residuales y las necesidades de restaurar las áreas húmedas continentales de España (Florín & Montes 1999). Además, en los lagos estudiados no existen esfuerzos para la recuperación de su dinámica hídrica original y de la calidad de sus aguas. De acuerdo con el plan de gestión para la conservación de la Reserva de la Mancha Húmeda de la Red Natura 2000 Humedales de la Mancha (Cubero-Rivera, 2015), la calidad del efluente de los sistemas de tratamiento de aguas residuales debería mejorarse eliminando el lodo acumulado en los humedales como consecuencia de la entrada de las aguas residuales.

La falta de tratamiento de las aguas residuales es una constante en nuestra área de estudio, especialmente par al Complejo Lagunar de Manjavacas, que necesita de una mejora en el tratamiento de las aguas depuradas que recibe. Sin embargo, este no parece ser un caso aislado de las lagunas continentales de España. Un ejemplo que ilustra el tamaño del descuido con la conservación de los ecosistemas húmedos es el hecho de que España haya sido recientemente condenada a pagar una multa de 12 millones de euros por no atender a la Directiva Europea sobre la conservación y tratamiento de las aguas residuales (ECLI: EU: C: 2018: 606). Tal situación no está de acuerdo con la tradicional historia española en relación a las zonas húmedas. En particular, la primera ley española sobre el agua fue promulgada en 1749 y, en 1926, España se convirtió en un país pionero en la gestión de recursos hídricos considerando no solo la escala local sino el abordaje en escala regional. Más recientemente, la necesidad de concentrar esfuerzos en un monitoreo de larga duración en las lagunas continentales españolas ganó fuerza a partir del primer Inventario Nacional de Zonas Húmedas y Lagos, concluido en 1990 y actualizado en 1996. Este inventario no es reconocido oficialmente y, como consecuencia, una constelación de al menos 1.500 pequeños sistemas húmedos continentales que se distribuyen por miles de hectáreas de superficie, ni siquiera existe legalmente. Se suma a eso, el bajo grado de inversión en ciencia desde décadas, tema este recientemente abordado por Martín-Moro (2018) en Science en el artículo Spain's good news. A este artículo de Moro-Martín, como resultado de los hallazgos y revisiones realizadas durante la construcción de esta tesis, se hizo un pequeño comentario publicado como eLetter en la misma revista (Gonçalves et al., 2018) que se destaca más abajo (Box 1). En este comentario, destacamos la peculiar situación de las zonas húmedas continentales que poseen un elevado número de figuras de protección, pero una completa ineficiencia en las acciones conservacionistas.

Box 1. Una reflexión crítica referente al artículo Spain's good news de Moro-Martín (2018) publicado como eLetter en Science.

“Spanish too low emphasis on science does not help either with wetlands. *Recent news in Science and Policy report Trump officials’ argue against Obama’s wetlands protection rule having put ‘too much emphasis’ on science, instead of on its legal history (Wittenberg, 2018). Spain could humbly shed light into this open controversy, since its administration is not suspicious of supporting science (Moro-Martín, 2018a, b). Besides, thousands of hectares of small, inland wetlands are recognized in Spain by arsenals of natural reserves and offer a wide range of public goods and services, including tourism and freshwater supply (Crespo et al., 2011). With such a great environmental, social and economic importance, it could be hardly imagined that wetlands conservation is not among top priorities of public policies. However, the overall lack of Spanish wetlands delineation and physical protection favor their destruction (Crespo et al., 2011). Inland wetlands hydrological functioning and survival suffered from aquifer overexploitation for irrigation agriculture during decades (Llamas, 1988), and diffuse and point pollution alter their trophic status and ecological state because of insufficient wastewater treatment and abusive crop fertilization (Laguna et al., 2016). This situation causes regular avian botulism outbreaks (Anza et al., 2014), trivializing biodiversity. Microplastics in waterbirds feces (Gil-Delgado et al., 2017) show that uncontrolled tons of plastics used in agriculture for decades are starting to affect food chains. Water rules do not help, because wetland management policy schemes are poorly implemented by water authorities (Martínez Santos et al., 2008), allowing all kind of misdeeds in private lands where wetland sites are located. Surprisingly, wetlands located in public lands are even in worse ecological conditions, sharing impacts with private ones (Florín & Montes, 1999), and adding to these threats managing actions driven by a sort of Enlightened Despotism of the 21st century, that prioritizes the execution of the budget, employment generation, and the concealment of impacts to effective protection, ecological functioning, and ecosystem restoration. Subsequent revocation of wetlands status as Biosphere Reserves and Ramsar sites could only be stopped after scientists set an agenda against Spanish administration contempt for research and environmental protection (Crespo et al., 2011).”*

De esta manera, la información que presentamos muestra la relevancia para el manejo y conservación de los ecosistemas húmedos, dado el carácter holístico en un ecosistema en el que la conservación es prioritaria para el mantenimiento de la biodiversidad. Las estrategias de conservación de aves en MHBR se han centrado tradicionalmente en el gran grupo de aves acuáticas, pero algunas características de los humedales que benefician muchos grupos de aves acuáticas afectan negativamente a las aves limícolas. Un ejemplo que ilustra este contexto es la profundidad de los cuerpos de agua, que están positivamente relacionados con la diversidad de anátidas, pero negativamente con los limícolas. El enfoque de este estudio sobre las aves limícolas ha identificado factores que podrían ser manejados para la conservación de estas especies, aunque serían necesarios más estudios para entender su compleja dinámica poblacional. Ya hay una serie de estrategias de gestión para mejorar los hábitats para las aves limícolas y cumplir con las obligaciones de conservación nacional e internacional (Barbosa, 1997), pero deben llevarse a la práctica. Finalmente, pocos trabajos se realizaron en lagunas continentales con series temporales tan largas como las que hemos utilizado en este trabajo, y nuestros resultados ayudarán a comprender mejor la relación entre la estabilidad de estos ecosistemas, su comunidad biológica y su complejidad estructural.

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Capítulo 7

Conclusiones

1. El hidroperíodo de las lagunas está influenciado por aguas residuales y constituye un importante mecanismo en la dinámica espacial y temporal de las aves limícolas. Las variaciones en el nivel de agua de las lagunas son más intensas en la primavera y el verano. Para este período, las lagunas con hidroperíodo más largo presentan mayor riqueza de aves limícolas reproductoras, posiblemente como reflejo de la entrada de aguas residuales y oferta de hábitat adecuado en un período de elevado déficit hídrico. Por otro lado, durante el período de lluvias (otoño e invierno), todas las lagunas presentan mayor estabilidad hídrica, reduciendo el efecto del hidroperíodo de manera la riqueza de aves invernantes aumenta con la superficie de inundación.

2. Con respecto a los patrones temporales de abundancia, se observaron grupos de lagos sincronizados para aves limícolas reproductoras – *Recurvirostra avosetta*, *Himantopus himantopus* y *Charadrius alexandrinhos*. Los picos de abundancia de las tres especies ocurrieron antes en las lagunas con hidroperíodos más cortos y fueron más tardíos en las lagunas que reciben aguas residuales. Aunque no se ha probado efectivamente, la cantidad de lluvia parece ser un factor determinante en el nivel de sincronización temporal en las tres especies, pues los años 2011 y 2013 fueron similares en relación a los niveles de precipitación y presentaron curvas temporales de abundancia más constantes y similares en

comparación con las curvas de 2012, año considerablemente más seco que los demás.

3. Los factores de hábitat y de paisaje actuaron diferencialmente en los patrones sincrónicos de cada especie. La sincronía espacial de *Charadrius alexandrinus* fue influida por el hidroperíodo. Este factor, junto a la distancia entre lagos, también influyó sobre la sincronía espacial de *Recurvirostra avosetta*. Por otro lado, no se detecta ninguna variable ambiental asociada a los fuertes niveles de sincronía espacial de *Himantopus himantopus*, sugiriendo que la especie posee gran plasticidad ecológica, ocupando concomitantemente lagunas estructuralmente diferentes.

4. El Complejo Lagunar de Manjavacas es un importante sitio de invernada para correlimos comunes. De los complejos lagunares observados, este es el único que posee entre sus lagunas la combinación de anostráceos y copépodos – presas reconocidas como altamente atractivas y decisivas en la selección de áreas de descanso o invernadero de limícolas migratorias.

5. Similarmente a los patrones observados para las aves reproductoras, los primeros picos de abundancia de correlimos común en el Complejo Lagunar de Manjavacas tienden a concentrarse en la laguna Alcahozo, la cual no recibe aguas residuales. Estos resultados posiblemente reflejan la presencia y abundancia de *Branchinectella media* – especie indicadora de calidad de hábitat y que una vez la laguna inundada, presenta elevada abundancia, rápido crecimiento y mayor biomasa entre los invertebrados presentes en las demás lagunas del complejo.

6. En esta misma laguna (Alcahozo), grupos mixtos de correlimos común y correlimos menudo presentan estrategias de forrajeo y uso de hábitat que varían en función de la dirección e intensidad del viento. En condiciones de viento suave, las aves tienden a forrajear mayoritariamente en el ambiente de agua rasa, generalmente a sotavento del lago. En condiciones de viento fuerte, las aves buscan forrajear a barlovento del lago, especialmente en el ambiente de lodo.
7. Las lagunas estudiadas constituyen importantes áreas de descanso, alimentación, invernada o reproducción para un gran número de aves limícolas. Cuatro especies están amenazadas de extinción – *Calidris ferruginea*, *Limosa limosa*, *Numenius arquata* y *Vanellus vanellus*. No existen programas de conservación orientados a estas especies en la región central de España. Paradójicamente, muchas figuras de protección abarcan todas las lagunas estudiadas, pero no existen prácticas de manejo y conservación efectivas con el objetivo de reducir los efectos de la falta de tratamiento de las aguas residuales y de las actividades agrícolas adyacentes.

Conclusions

1. The hydroperiod of the lakes is influenced by wastewater and constitutes an important mechanism in the spatial and temporal dynamics of the studied waders. The variations in the water level of the lagoons are more intense in the spring and summer. For this period, the lakes with the longest hydroperiod have a greater richness of breeding waders, possibly as a resulted of the entrance of wastewater and suitable habitat supply in a period of high water deficit. On the other hand, during the rainy season (autumn and winter), all the lagoons present greater water stability, reducing the effect of the hydroperiod. In that period, the richness of wintering waders increases with the flooded surface.
2. With respect to the temporal patterns of abundance, groups of synchronized lakes were observed for the three breeding wader birds studied – *Recurvirostra avosetta, Himantopus himantopus,* and *Charadrius alexandrinhos*. The peaks of abundance of the three species were earlier in the lagoons with shorter hydroperiods and were later in the lagoons that receive wastewater. Although it has not been tested, the amount of rainfall seems to be a determining factor in the level of temporal synchronization in the three species, since the years 2011 and 2013 were similar in relation to the levels of precipitation and presented similar curves of abundance.
3. The factors of habitat and landscape acted differentially in the synchronic patterns of each species. The spatial synchrony of *Charadrius alexandrinus* was influenced by the hydroperiod. This factor, together with the distance between lakes, also influenced the spatial synchrony of *Recurvirostra avosetta*. On the other hand, no environmental variable associated with the strong levels of spatial

synchrony of *Himantopus himantopus* was detected, suggesting that the species has great ecological plasticity, occupying concomitantly habitat in different conditions.

4. The Manjavacas Lagoon Complex is an important wintering site for dunlins. Of the observed lagoon complexes, this is the only one that has among its lagoons the combination of anostraceans and copepods – preys recognized as highly attractive and decisive in the selection of resting or wintering sites for migratory waders.
5. Similar to the patterns observed for breeding birds, the first peaks of abundance of dunlins in the Manjavacas complex tend to be concentrated in the Alcahozo lake, which does not receive wastewater. These results possibly reflect the presence and abundance of Branchinectella media – an indicator of habitat quality and that once the lake flooded, has rapid growth, abundance and greater biomass among the invertebrates present in the other lakes of the complex.
6. In this same lake (Alcahozo), mixed groups of dunlins and little stints often present foraging strategies and habitat use that vary depending on the direction and intensity of the wind. In smooth wind conditions, birds tend to forage mostly in the clean water environment, usually at leeward of the lake. In strong wind conditions, birds seek to forage windward of the lake, especially in the mud environment.
7. The lakes studied constitute important areas of resting, feeding, wintering or breeding for a large number of waders. Four species are threatened with extinction - *Calidris ferruginea*, *Limosa limosa*, *Numenius arquata*, and *Vanellus vanellus*. There is no conservation programs aimed at these species in central Spain. Paradoxically, many protection figures cover all the wetlands

studied, but there are no effective management and conservation practices with the objective of reducing the effects of the lack of treatment of wastewater and adjacent agricultural activities.