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## 7 Spatial synchrony of wader populations in inland lakes of the Iberian 8 Peninsula

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20 **Abstract** Spatial synchronization refers to similarity in  
21 temporal variations between spatially separated popu-  
22 lations. Three mechanisms have been associated with the  
23 spatial synchrony of populations: Moran effect, disper-  
24 sal and trophic interactions. In this study, we explored  
25 the degree of spatial synchrony of three wader species  
26 populations (Pied Avocet, Black-winged Stilt and Ken-  
27 tish Plover) using monthly estimates of their abundance  
28 in inland lakes of the Iberian Peninsula. The effect of  
29 several types of wetland variables (structural, hydrope-  
30 riod and landscape) on spatial synchronization was ex-  
31 plored. Groups of lakes with significant synchronization  
32 were identified for all three species. The lakes with  
33 wastewater input presented longer hydroperiods than  
34 those that did not receive these effluents, and this factor  
35 was positively related to the spatial synchrony of the  
36 Pied Avocet and Kentish Plover populations. The dis-  
37 tance between lakes (used as an indicator of the dispersal  
38 effect on synchronization) was significant only in Pied  
39 Avocet. No structural or landscape variables were re-  
40 lated to spatial synchronization in any species. It was  
41 impossible to identify any variable related to the spatial  
42 synchronization of Black-winged Stilt abundance as a

possible result of the high ecological plasticity of this 43  
species. Our data provides the first evidence for mech- 44  
anisms that act on the spatial synchronizing of wader 45  
populations in temporary continental lakes in central 46  
Spain, and show that the hydroperiod of lakes acts as an 47  
important factor in the spatial synchronization of 48  
aquatic species and that its effect is mediated by the 49  
reception of urban wastewater. 50

**Keywords** Similarity temporal · Spatial dynamic · 51  
Wetlands · Hydroperiod · Wastewater 52

### 53 Introduction

54 Understanding variations of abundance in space and 54  
time has been one of the major goals in ecology (Cazelles 55  
and Stone 2003; Liebhold et al. 2004). Notably, popu- 56  
lation dynamics has received plenty of attention since 57  
the models presented by Moran (1953). Moran (1953) 58  
described statistical methods to observe the temporal 59  
patterns of the Canadian lynx, and proposed a formal 60  
ecological mechanism to analyze spatial population 61  
synchrony on large geographic scales. Conceptually, 62  
spatial synchrony of populations refers to the temporal 63  
similarity of abundance (or any other characteristic of a 64  
population) between sites separated spatially (Liebhold 65  
et al. 2004). In other words, regardless of the size of the 66  
local population, two or more sites are synchronized if 67  
the curves of abundance of both sites are coupled. 68  
Spatial synchrony is one of the most important patterns 69  
in metapopulations dynamics, being observed at differ- 70  
ent scales (local, regional and global), as well as in many 71  
species groups (Holyoak and Lawler 1996; Thrall et al. 72  
2001; Post and Forchhammer 2002; Trenham et al. 2003; 73  
Liu et al. 2009; Batchelder et al. 2012; Kvasnes et al. 74  
2013). 75

76 In general, spatial synchrony of abundance has been 76  
associated to three ecological processes, which can act 77  
independently or in combination: dispersal of individu- 78  
als, environmental conditions and trophic interactions 79


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80 (Ranta et al. 1995; Bjørnstad et al. 1999). Regarding  
 81 dispersal mechanism, the populations tend to fluctuate  
 82 synchronously since the increase abundance in a specific  
 83 site raises the migration rate into adjacent areas, forcing  
 84 the spatial synchrony. As the dispersion is distant-de-  
 85 pendent, the level of synchrony tends to be higher be-  
 86 tween closer areas, decreasing as the distance between  
 87 areas increases (Ranta et al. 1995). On the other hand,  
 88 some distant sites may show high spatial synchrony of  
 89 populations as a response to correlated environmental  
 90 conditions, a process known as Moran effect (Koenig  
 91 2002). Haynes et al. (2013), for instance, noted that  
 92 precipitation acted as synchronizer factor of populations  
 93 of moths due to the similar effect on the survival and  
 94 reproduction of individuals. In this case, as in many  
 95 others, the Moran effect is mainly associated with  
 96 environmental conditions extrinsic (or exogenous),  
 97 which are common over large spatial scales (e.g. tem-  
 98 perature and precipitation). Finally, trophic interactions  
 99 between predator–prey populations may also force the  
 100 spatial synchronization of populations, as shown by Ims  
 101 and Steen (1990).

102 Although long-term monitoring has been conducted  
 103 in many world regions, little is known about the syn-  
 104 chronicity of bird populations in continental wetlands.  
 105 In addition, most animal ecology studies have sought to  
 106 identify synchronization patterns of annual periodicity  
 107 (e.g. Koenig 2001; Bellamy et al. 2003; Williams et al.  
 108 2003; Eberhart-Phillips et al. 2015; Mortelliti et al.  
 109 2015). This temporal scale prevents closer relations be-  
 110 tween the intra-annual variability of ecosystems and  
 111 spatial population dynamics from being detected. For  
 112 example, many inland lakes in the Iberian Peninsula  
 113 have a naturally short hydroperiod due to the small  
 114 expanse of their basin and poor annual precipitations,  
 115 while others have larger basins or receive some inputs  
 116 from groundwater or rivers, and hold water for most of  
 117 the year. To this natural variability, the contribution of  
 118 urban wastewater has been added in recent decades

(Martinez-Santos 2008). In these environments, where  
 119 hydric changes are rapid, it is likely that annual sam-  
 120 pling programs would not reveal the processes behind  
 121 population fluctuations, even if they have been per-  
 122 formed for many years.  
 123

124 In this paper we explored the degree of spatial syn-  
 125 chrony of the populations in this type of Mediterranean  
 126 wetlands using monthly estimates of abundance. We  
 127 employed three wader species distributed in a set of  
 128 saline lakes of central Spain as a model system: Black-  
 129 winged Stilt (*Himantopus himantopus*), Pied Avocet  
 130 (*Recurvirostra avosetta*) and the Kentish Plover (*Char-  
 131 adrius alexandrinus*). These are species with a good dis-  
 132 persion ability between wetlands and are good study  
 133 subjects to observe the patterns and processes associated  
 134 with spatial synchrony. Specifically, we explored whe-  
 135 ther habitat and landscape factors were related to the  
 136 spatial synchrony of populations and we expected to  
 137 find high levels of synchronization as a possible result of:  
 138 (1) hydrodynamics, including the potential effect of  
 139 wastewater inputs; (2) distance between lakes, as an  
 140 indicator of a dispersal limitations effect and; (3) vari-  
 141 ability in the structural and landscape features of the  
 142 lakes.

## 143 Methods

### 144 Study area

145 The study area is located in the “La Mancha Húmeda”  
 146 Biosphere Reserve (hereafter MHBR), in the Castilla-La  
 147 Mancha region, central Spain (Fig. 1). The MHBR is  
 148 one of the most important wetland complexes of the  
 149 Iberian Peninsula (Florín et al. 1993), with a network of  
 150 over 190 wetlands spread over three geographical areas—  
 151 Campo de San Juan, Campo de Montiel and the  
 152 Serrania de Cuenca (Gosálvez et al. 2012), of which 50  
 153 are temporary lakes (Florín and Montes, 1999). The

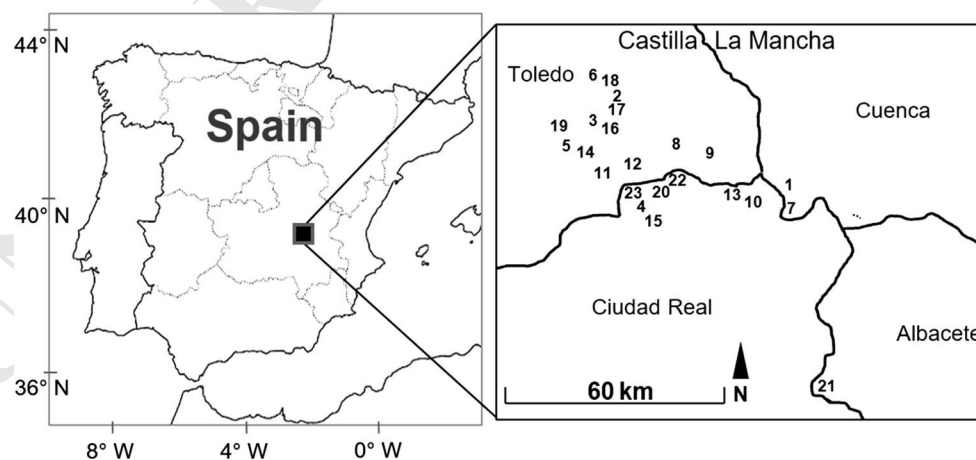


Fig. 1 Location of the 23 lakes (identified by numbers) monitored monthly between October 2010 and February 2014. The codes of each lake are available in Table 1

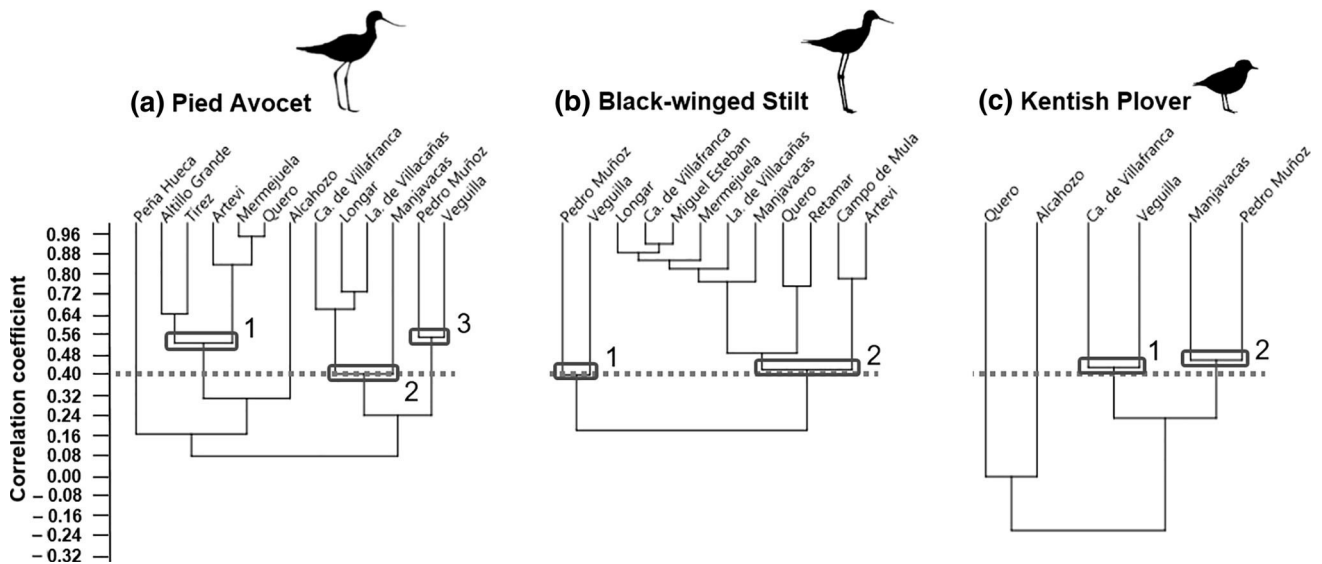
154	average temperature in the region is 14 °C, and the	208
155	minimum temperature in extreme years can reach	209
156	−20 °C in winter and the maximum can rise to 42 °C in	210
157	July. The seasons with the highest rainfall are winter and	
158	spring, and annual precipitation varies between 300 and	
159	400 mm (Martinez-Santos et al. 2008). The landscape is	
160	predominantly agricultural, characterized by vineyards,	
161	cereal crops, olive groves, forestry and pastures. There	
162	are many types of wetlands in the MHBR, which range	
163	from temporary lakes to floodplains and permanent or	
164	episodically flooded. There are also natural or artificial	
165	lakes, some of which receive wastewater from adjacent	
166	urban centers (Florín et al. 1993; Florín and Montes	
167	1999). In our study, most wetlands were temporary	
168	lakes, either with or without wastewater input. In gen-	
169	eral, the vegetation surrounding lakes was predomi-	
170	nantly halophilous and some lakes were characterized by	
171	vegetation islands dominated by Reed ( <i>Phragmites aus-</i>	
172	<i>tralis</i> ), Cattail ( <i>Typha dominguensis</i> ), Common Club-	
173	rush ( <i>Schoenoplectus lacustris</i> ) and Alkali-bulrush ( <i>Bol-</i>	
174	<i>boschoenus maritimus</i> ) (Gosálvez et al. 2012).	
175	<b>Bird counts and environmental variables</b>	
176	Monthly counts of Pied Avocet, Black-winged Stilt and	
177	Kentish Plover were conducted in 23 wetlands between	
178	October 2010 and February 2014. The study wetlands	
179	were selected as a representative sample of the types and	
180	conditions of lakes in the region within the framework of	
181	a previous project on the ecology of inland lakes in	
182	Central Spain (Gosálvez et al. 2012). They cover a wide	
183	range of sizes, depths, extent of vegetation in the edges	
184	(Table 1), as well as salinity (Florín et al. 1993). Counts	
185	were performed at fixed observation points and always	
186	by the same researchers. These points were selected to	
187	obtain the best view of the complementary sectors in the	
188	lagoon area in order to avoid loss of the individuals near	
189	or behind emergent plants. Counts were made in the last	
190	week of each month and conducted between 08:00 h and	
191	about 12:00 h, after ensuring favourable climatic con-	
192	ditions (little wind and no rain). Telescopes and binoc-	
193	ulars were utilized in samples.	
194	Twelve environmental variables were analyzed per	
195	lake (Table 1). These variables can be classified into four	
196	groups: (1) hydroperiod, i.e. percentage of months with	
197	water; (2) anthropogenic, i.e. distance from human set-	
198	tlements; (3) landscape, i.e. distance between lakes and	
199	number of lakes within three radii (2, 5 and 10 km); and	
200	(4) structural, i.e. average depth, total lake surface,	
201	flooded surface, surface with natural vegetation sur-	
202	rounding the lake, number of islands and total surface of	
203	islands. The average depth was obtained by the differ-	
204	ence between the average of the altitude at the four	
205	cardinal points on the lake border, obtained from a	
206	geographical viewer (see below), and the altitude of the	
207	deepest point of the lake. Structural variables were ob-	
	tained by fieldwork and from the geographical viewer	208
	Iberpix (Spanish National Geographic Institute) and	209
	Google Earth Pro Version 2015.	210
	<b>Data analysis</b>	211
	The analysis to detect the spatial synchrony of abun-	212
	dance and its associations with the habitat and land-	213
	scape features was performed for each species	214
	separately. For each studied species we selected the lakes	215
	where it occurred in at least 5 % of the months (Pied	216
	Avocet, 13 lakes; Black-winged Stilt, 12 lakes; Kentish	217
	Plover, 6 lakes). To avoid the effect of the daily vari-	218
	ability of censuses and to focus on the main temporal	219
	pattern of each lagoon, the series of monthly abun-	220
	dances were smoothed by calculating the central moving	221
	average for each month, with the exception of the first	222
	and last month in the series, using a window size of	223
	3 months. Therefore the smoothed abundance in each	224
	month was obtained by averaging the census for that	225
	month and the censuses of the previous and subsequent	226
	months.	227
	The degree of spatial synchrony between lakes was	228
	evaluated using Pearson's correlation coefficient (r),	229
	calculated from the time series of smoothed monthly	230
	abundance in each lake. For each species, a dendrogram,	231
	showing the resemblance of lakes in temporal pattern,	232
	was generated using the correlations of smoothed	233
	abundances between all pairs of lakes as a measure of	234
	similarity. Dendrograms were built with the PAST	235
	software (Hammer et al. 2001) following the UPGMA	236
	method. To identify groups of lakes with similar tem-	237
	poral patterns, we used the significant value of correla-	238
	tion for 37 degrees of freedom (number of values in the	239
	smoothed time series minus 2) and <i>P</i> value <0.01	240
	( <i>r</i> = 0.408) as a threshold.	241
	The matrix of correlations between wetlands calcu-	242
	lated for each species was transformed to a dissimilarity	243
	matrix using the formula $(1 - r)/2$ , where <i>r</i> is Pearson's	244
	correlation coefficient, to generate values that ranged	245
	between 0 and 1. A dissimilarity matrix was also built	246
	for each environmental variable after standardization	247
	using Euclidean distance. The relation between these	248
	two dissimilarity matrices (bird temporal patterns and a	249
	matrix for each environmental variable) was assessed by	250
	the Mantel Test, a statistical procedure that evaluates	251
	the correlation between two matrices (Anderson and	252
	Walsh 2013). The Monte Carlo method with 9999 ran-	253
	dom permutations was used to assess the significance of	254
	the Mantel Test (Zar 2010). Significant <i>p</i> -values were	255
	considered to be <0.05. These analyses were performed	256
	with the "ade4" package (Thioulouse et al. 1997) in the	257
	R-Program, v. 3.1.3 (R Development Core Team 2014).	258
	Finally, we used the Mann–Whitney U-test to compare	259
	the average hydroperiod between the lakes with and	260
	without wastewater input.	261



**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

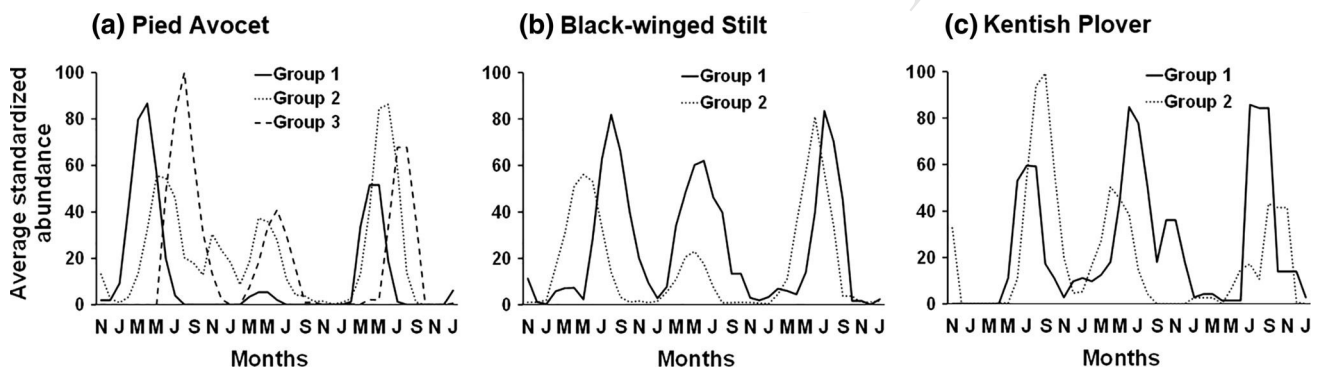
Code	Lake	UTM X				UTM Y				Hydroperiod				Anthropogenic				Landscape				Structural							
		D	PA	BS	KP	R2	R5	R10	R10	Area	Flooded	Veg	Ni	IsA	AD	D	PA	BS	KP	R2	R5	R10	R10	Area	Flooded	Veg	Ni	IsA	AD
1	Alcahozo*	510620	4360164	58.5	5509	3184	UN	3184	UN	3184	UN	3184	UN	3184	UN	3184	UN	3184	UN	2	3	4	6	886622	690661	195961	0	0	1.75
2	Altillo Grande*	474187	4393670	43.9	2649	2260	UN	2260	UN	2260	UN	2260	UN	2260	UN	2260	UN	2260	UN	2	3	4	4	329132	204966	124166	0	0	4.25
3	Artevi*	472611	4385210	68.2	965	9195	1155	9195	1155	UN	1155	UN	1155	UN	1155	UN	1155	UN	1155	1	1	9	9	279171	167168	112003	0	0	4.75
4	Camino de Villafraanca*	478055	4362616	95.1	2263	2322	2322	2322	2322	2322	2322	2322	2322	2322	2322	2322	2322	2322	2322	0	2	10	10	1599214	1347179	237802	2	17233	2.25
5	Campo de Mula*	464695	4381452	21.9	5483	UN	8534	UN	8534	UN	8534	UN	8534	UN	8534	UN	8534	UN	8534	0	1	6	6	509145	255728	253417	0	0	3.25
6	Longar*	472448	4395066	92.6	1757	2260	9627	UN	9627	UN	9627	UN	9627	UN	9627	UN	9627	UN	9627	2	3	5	5	2595033	991391	1603642	0	0	4
7	Manjavacas*	511840	4363360	97.5	6639	3184	7215	3184	7215	3184	7215	3184	7215	3184	7215	3184	7215	3184	7215	1	7	17	17	2628067	1978446	640048	3	9573	2.75
8	Mermejuela*	488191	4376617	82.9	4834	10843	7621	UN	7621	UN	7621	UN	7621	UN	7621	UN	7621	UN	7621	0	2	5	5	99195	86559	12636	0	0	6.5
9	Miguel Esteban*	495294	4373855	97.5	1376	UN	6460	UN	6460	UN	6460	UN	6460	UN	6460	UN	6460	UN	6460	0	1	1	1	922238	234238	688000	0	0	2.5
10	Pedro Muñoz*	504589	4362479	87.8	362	6460	2708	6460	2708	6460	2708	6460	2708	6460	2708	6460	2708	6460	2708	2	3	11	11	413916	261401	152515	0	0	3.25
11	Peña Hueca*	470426	4373729	58.5	8880	3077	UN	3077	UN	3077	UN	3077	UN	3077	UN	3077	UN	3077	UN	0	2	8	8	1588659	1326046	196325	4	66288	3.75
12	Quero*	478215	4372367	70.7	787	7907	9752	7907	9752	9752	9752	9752	9752	9752	9752	9752	9752	9752	9752	1	6	16	16	957282	840836	116446	0	0	2
13	Retamar*	502427	4364111	21.9	2503	UN	2708	UN	2708	UN	2708	UN	2708	UN	2708	UN	2708	UN	2708	0	3	7	7	791605	627250	164355	1	4098	3.5
14	Tirez*	469331	4376605	51.2	8546	3077	UN	3077	UN	3077	UN	3077	UN	3077	UN	3077	UN	3077	UN	0	2	6	6	1318531	811890	506204	1	437	4.25
15	Veguilla*	479389	4360715	97.5	886	2322	2322	2322	2322	2322	2322	2322	2322	2322	2322	2322	2322	2322	2322	0	2	7	7	890951	443546	447405	0	0	4.25
16	Larga de Villacañas*	472815	4384080	100	1458	1148	1148	1148	1148	1148	1148	1148	1148	1148	1148	1148	1148	1148	1148	2	3	12	12	1673095	1.145.530	527565	0	0	3.25
17	Albardiosa	474994	4390229	8.3	5085	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	0	3	5	5	718838	395178	323660	0	0	2.5
18	Altillo Pequeño	473975	4394727	55.5	1436	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	2	3	5	5	246865	178111	68754	0	0	3
19	Camino de Turleque	464403	4384224	5.5	4082	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	0	1	4	4	486833	394459	92374	0	0	5.25
20	Pajares	482321	4367206	39	4669	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	0	1	5	5	235875	209027	26848	0	0	2.75
21	Redondilla	513136	4310021	26.8	171	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	5	9	10	10	57357	35129	22228	0	0	11
22	Salicor	485033	4368502	55.5	7161	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	1	2	5	5	814097	483899	237203	3	92995	5.75
23	Yéguas	475657	4363078	61.1	4683	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	UN	1	3	6	6	962659	649388	313271	0	0	2

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<sup>2</sup>. 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, UN lakes not analyzed for a given species



**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

262 **Results**

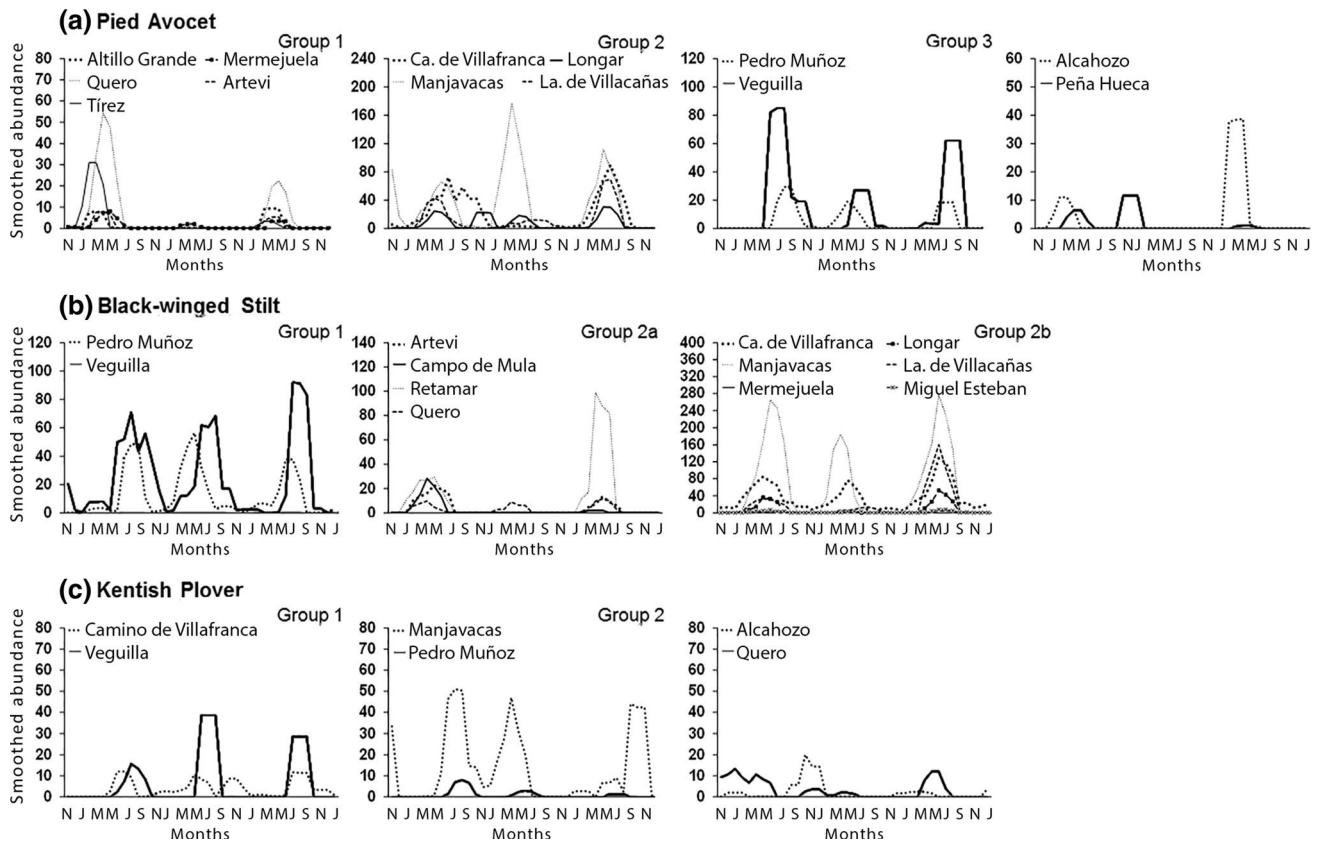
263 Groups of lakes with significant synchronization were  
 264 identified for the three species. A few lakes showed  
 265 temporal patterns which did not correlate to the others  
 266 (Fig. 2). The groups of lakes also presented a coincident  
 267 pattern of fluctuation between years—the groups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

271 *Pied Avocet*. Three groups of lakes with significant  
 272 temporal similarity were identified (Figs. 2, 3). Group 1  
 273 (Quero, Mermejuela, Artevi, Altillo Grande and Tírez)  
 274 showed earlier peaks of abundance, which occurred in  
 275 late winter and early spring (Figs. 3, 4a). Group 2 pre-  
 276 sented later and more long-lasting periods of high  
 277 abundance, which extended from late spring to late

278 summer. In this group, Manjavacas lake had large  
 279 numbers of Pied Avocets during the 2012 breeding sea-  
 280 son (year 2), when the abundance in the rest of the lakes  
 281 sharply dropped. Group 3 (Veguilla and Pedro Muñoz)  
 282 presented abundance peaks later (late summer-early  
 283 fall).

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

290 *Kentish Plover*. Two groups with two lakes each were  
 291 formed, but the similarity between lakes in the same  
 292 group was relatively low (Figs. 3, 4c). Lakes Alcahozo  
 293 and Quero showed particular temporal patterns (Fig. 4  
 294 c).  
 295



**Fig. 4** Temporal variation (moving averages) of the abundance of the three water 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

295 Environmental correlates of temporal similarity

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

301 For Pied Avocet, the environmental variables that  
302 correlated to spatial synchrony were hydroperiod  
303 (Mantel Test,  $r = 0.380$ ;  $P = 0.004$ ) and distance between  
304 lakes (Mantel Test,  $r = 0.250$ ;  $P = 0.046$ ). In  
305 Kentish Plover, the hydroperiod was the only variable  
306 that was related to the temporal patterns of the lakes  
307 (Mantel Test,  $r = 0.710$ ;  $P = 0.043$ ). None of the  
308 environmental variables was related to the high spatial  
309 synchrony levels observed for Black-winged Stilt (Table  
310 2).

311 The lakes that received wastewater presented longer  
312 hydroperiods than those that did not receive such  
313 effluents ( $U = 4.00$ ;  $P < 0.001$ ) (Fig. 5). Seven of the  
314 eight lakes with no input of wastewater had marked  
315 seasonality of presence of water and were flooded between  
316 22 and 68 % of the months (except lake Camino  
317 de Villafranca) (Fig. 5). The eight lakes that received

wastewater presented water for most of the study period 318  
(71–100 %). 319

**Discussion** 320

321 Our results show that the degree of spatial synchrony of  
322 the populations of Pied Avocet, Black-winged Stilt and  
323 Kentish Plover in inland lakes of Iberian Peninsula is  
324 significant. However, the patterns of synchrony of the  
325 three species showed different levels of responses to the  
326 set of variables explored. The spatial synchrony of Pied  
327 Avocet and Kentish Plover is affected by the hydroperiod  
328 of lakes, which in turn is altered by wastewater input. 329

Spatial synchrony and hydroperiod effect 330

331 In partial agreement to our first hypothesis, the  
332 hydroperiod effect was important on temporal patterns  
333 of two of the three species: Pied Avocet and Kentish  
334 Plover. For Pied Avocet, we observed the formation of  
335 three groups of spatially synchronized lakes: groups with

**Table 2** Results of the Mantel tests run to evaluate the correlation of environmental variables with the spatial synchrony of populations

Environmental variables	Pied Avocet		Black-winged Stilt		Kentish Plover	
	Obs	<i>P</i> value	Obs	<i>P</i> value	Obs	<i>P</i> value
Hydroperiod	<b>0.380</b>	<b>0.004</b>	0.073	0.352	<b>0.710</b>	<b>0.043</b>
Distance between lakes	<b>0.250</b>	<b>0.046</b>	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

Bold values are statistically significant tests for a *P* value less than 0.05

336 earlier peaks of abundance, intermediate peaks and later  
 337 peaks. The group of lakes with earlier peaks (beginning  
 338 of spring) were also characterized by shorter hydrope-  
 339 riods (flooded between 22 and 68 % of the months) and  
 340 they did not receive wastewater (except Lake Quero).  
 341 Unlike the lakes that received wastewater, unaltered  
 342 lakes tend to rapidly dry in the spring and summer.  
 343 Temporal variation of abundance depends not only on  
 344 movements for tracking the spatial changes in resources  
 345 availability (Borkhataria et al. 2012), but also on large-  
 346 scale migratory movements and reproduction output  
 347 (Sirot and Touzalin 2014). Therefore, the passing of  
 348 migrants in spring could cause a detectable early peak of  
 349 abundance in lakes with shorter hydroperiod since in  
 350 these lakes the number of individuals that stay for  
 351 breeding is relatively low and diminishes quickly as they  
 352 dry, while in lakes with longer hydroperiod a more  
 353 numerous breeding populations remains for longer time.

354 On other hand, later abundance peaks occurred syn-  
 355 chronously in the same lakes for Pied Avocet and Black-  
 356 winged Stilt (Lakes Veguilla and Pedro Muñoz). Lakes  
 357 that receive effluents from urban wastewater treatment  
 358 plants present inappropriate bio-physical conditions in  
 359 late summer (Vidal et al. 2013; Anza et al. 2014), but  
 360 display high organic productivity (Anza et al. 2014) and  
 361 are attractive sites to waterbirds during breeding periods  
 362 (Gosálvez et al. 2012). Unlike the other lakes that receive  
 363 wastewater and present long hydroperiods, Veguilla and  
 364 Pedro Muñoz have large concentration of emerging  
 365 macrophytes on its edges, and few flat shallow areas for  
 366 foraging of waders in the breeding season. However,  
 367 during the summer, while other areas are dry or nearly  
 368 dry, Veguilla and Pedro Muñoz gradually expose exten-  
 369 sive mudflats in their central area that attract many wa-  
 370 ders. Consequently, the decrease of the abundance of  
 371 individuals after the mid-summer in some lakes with  
 372 longer hydroperiods (e.g. Manjavacas, Larga de Vil-  
 373 lafranca, Miguel Esteban, Longar and Mermejuela) and

374 the coincident increase at Pedro Muñoz and Veguilla  
 375 lakes is possibly the result of structural differences be-  
 376 tween the wetlands, which has significant effects on for-  
 377 aging habitat availability.

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

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

Lakes	2010			2011					2012					2013					2014									
	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
Larga de Villacañas*																												
Miguel Esteban*																												
Manjavacas*																												
Pedro Muñoz*																												
Veguilla*																												
Camino de Villafranca																												
Longar*																												
Mermejuela*																												
Peña Hueca																												
Artevi																												
Alcahozo																												
Quero*																												
Tirez																												
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

412 For the three species, we also observed that the  
 413 abundance peaks of the groups of lakes showed constant  
 414 periodicity in study years 1 and 3, with an asynchrony  
 415 found in study year 2. As many theoretical and empirical  
 416 studies have observed, identifying patterns and processes  
 417 of temporal population dynamics is not an easy task and  
 418 it is necessary to consider also the effect of random  
 419 events, like environmental and demographic stochasticity  
 420 (Brown et al. 1995; Ives and Klopfer 1997). Even the  
 421 lakes that received wastewater can dry in summer if the  
 422 water accumulated in winter was low. This appeared to  
 423 be the case of most of our study lakes in the summer of  
 424 2012, when all the sites (except Miguel Esteban and  
 425 Larga de Villacañas) were completely dry in August.  
 426 According to the weather data of the province of Toledo  
 427 (Spanish Meteorology Agency - AEMET), the rain  
 428 accumulated in previous fall and winter was lower in  
 429 2012 (109.1 mm) than in 2011 (236.1 mm) and 2013  
 430 (283 mm). In parallel, for all three species we also ob-  
 431 served a similarity in the temporal patterns of the groups  
 432 of lakes between 2011 and 2013, with distinct variation  
 433 found in 2011. Specifically, the groups of lakes in 2012  
 434 tend to present earlier abundance peaks than in the  
 435 other two years. This difference may be a direct response  
 436 to variations in rainfall since it is known that changes in  
 437 hydrological conditions affect not only food availability  
 438 (Bancroft et al. 2002; Roshier et al. 2002), but also  
 439 movements of individuals during the breeding periods  
 440 (Borkhataria et al. 2012).

441 Many studies have found that different factors may  
 442 act together in the formation of synchronous patterns  
 443 (Ranta et al. 1999; Powney et al. 2011; Eberhart-Phillips  
 444 et al. 2015; Mortelliti et al. 2015). For instance, hydro-  
 445 logical disturbance and dispersal were important mech-  
 446 anisms driving spatio-temporal patterns of Everglades  
 447 fish populations (Ruetz et al. 2005). In our study, at least  
 448 in one species (Pied Avocet) the distance between lakes  
 449 and hydroperiod seemed to act together to cause the  
 450 spatial synchronization of populations. Ranta et al.  
 451 (1999) demonstrated that correlated extrinsic distur-

bances 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 independ-  
 ently from dispersal.

#### Distance effect and other variables

452 Although dispersal mechanisms have been commonly  
 453 related to the spatial synchrony of many species,  
 454 including birds (Koenig 1998, 2001), detecting and  
 455 understanding the relationship between distance and  
 456 synchronization of populations is not always easy. This  
 457 is because when motivated by dispersion, spatial syn-  
 458 chrony depends on many factors, including the dispersal  
 459 ability of individuals (Sutcliffe et al. 1996), the degree of  
 460 functional connectivity between patches (Powney et al.  
 461 2011), the spatial scale (Paradis et al. 1999) and presence  
 462 of environmental disturbances (Ranta et al. 1999).  
 463 Functional connectivity refers to the environmental  
 464 permeability of a given landscape, which facilitates or  
 465 hinders the movement of individuals between patches  
 466 and/or fragments (Goodwin and Fahrig 2002, Powney  
 467 et al. 2011). In our study, we analyzed a set of landscape  
 468 variables, such as distance from human settlements,  
 469 distance between lakes and number of lakes within three  
 470 increasing radii as indicators of the functional connec-  
 471 tivity of lakes (Goodwin and Fahrig 2002). We also  
 472 evaluated a set of structural habitat variables and their  
 473 relationship to the observed temporal patterns. None of  
 474 these variables was associated with the spatial synchrony  
 475 of the studied species, except distance between lakes in  
 476 Pied Avocet. Given the high dispersal capacity of these  
 477 species (Hötcker 2002; SEO/BirdLife 2016a, b) and the  
 478 relative proximity of the lakes (maximum distance  
 479 94 km), the distance seems not to be affecting the spatial  
 480 synchrony of Black-winged Stilt and Kentish Plover.  
 481 Only in the case of Pied Avocet we detect an effect of



489 distance between lakes on their spatial synchrony, that  
490 was weaker than hydroperiod effect. Overall, the ab-  
491 sence of effect of landscape and habitat variables is re-  
492 lated to the ecology of the analyzed species, which are  
493 able to occupy sites scattered in extensively altered  
494 landscapes (Hortas et al. 2012; Hortas 2012a, b).

## 495 Conclusions

496 For more than three decades, inland lakes of the Iberian  
497 Peninsula have undergone significant changes in water  
498 regimes as a result of channelled surface water, overex-  
499 ploitation of aquifers and wastewater input. The  
500 monthly census approach conducted herein allowed us  
501 to detect how hydrological disturbance (wastewater in-  
502 put) affects the spatial synchrony of populations and  
503 generates diverse temporal patterns of abundance vari-  
504 ation. Our data provide the first insights into the  
505 mechanisms that drive spatial synchrony in temporary  
506 inland lakes. Further research on this topic in central  
507 Spain wetlands, that present one of the most altered  
508 hydric functioning in the Iberian Peninsula, will help to  
509 design water management strategies that improve habi-  
510 tat quality for wader species.

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