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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

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

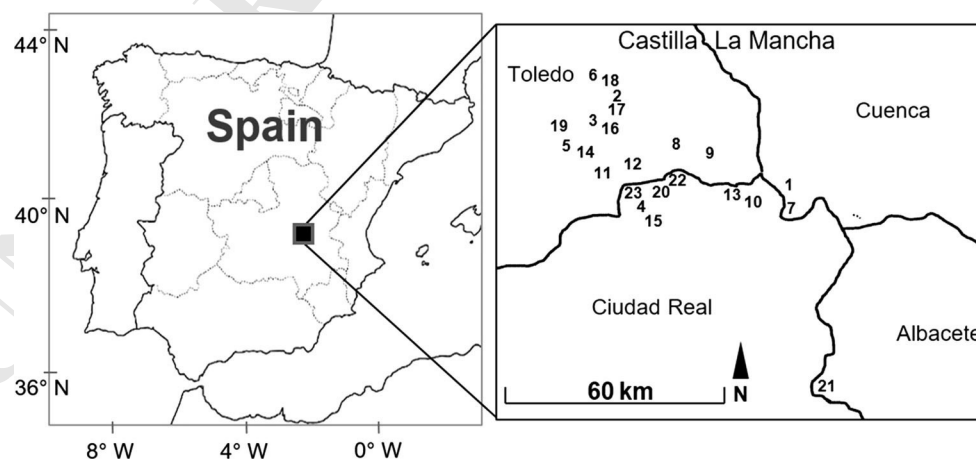


Fig. 1 Location of the 23 lakes (identified by numbers) monitored monthly between October 2010 and February 2014. The codes of each lake are available in Table 1

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	Bird counts and environmental variables	
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
	Data analysis	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 (Thioulose 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	UN	2322	UN	2322	UN	2322	UN	2322	UN	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	UN	7215	UN	7215	UN	7215	UN	7215	UN	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	UN	2708	UN	2708	UN	2708	UN	2708	UN	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	UN	9752	UN	9752	UN	9752	UN	9752	UN	9752	UN	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	UN	2322	UN	2322	UN	2322	UN	2322	UN	2322	0	2	7	7	890951	443546	447405	0	0	4.25
16	Larga de Villacañas*	472815	4384080	100	1458	1148	1148	UN	1148	UN	1148	UN	1148	UN	1148	UN	1148	UN	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 m². 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

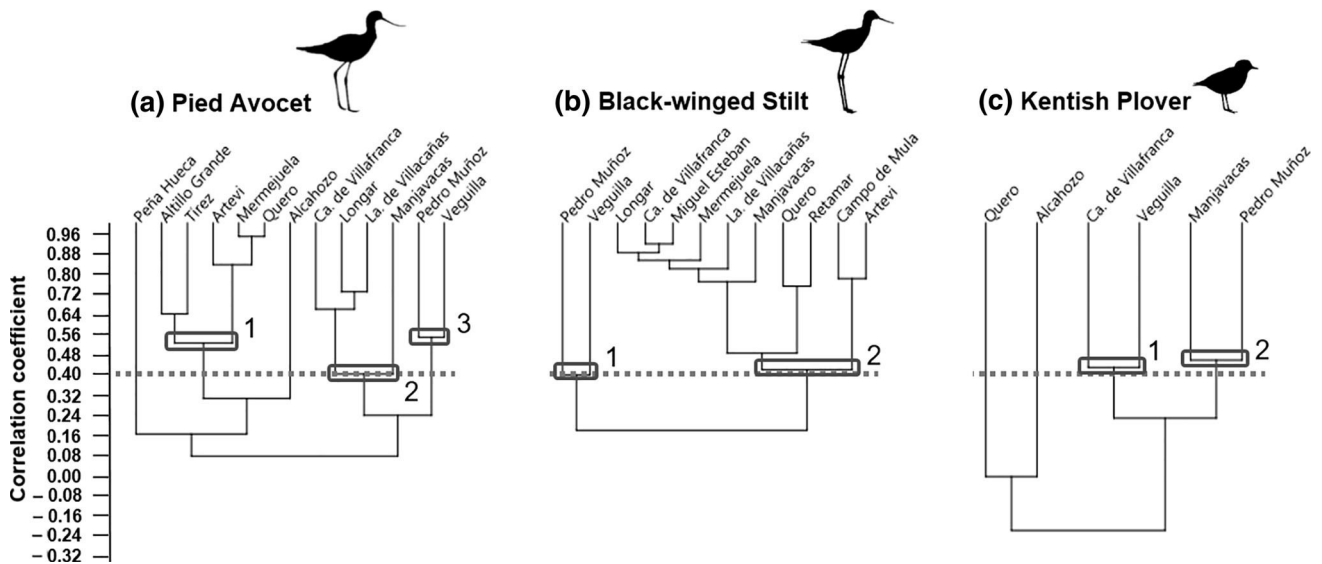


Fig. 2 Dendrogram showing the similarity of the seasonal patterns of the abundance of Pied Avocet, Black-winged Stilt and Kentish Plover in inland lakes of Central Spain. The horizontal line marks the significant correlation coefficient for a P value < 0.01 , used as a

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

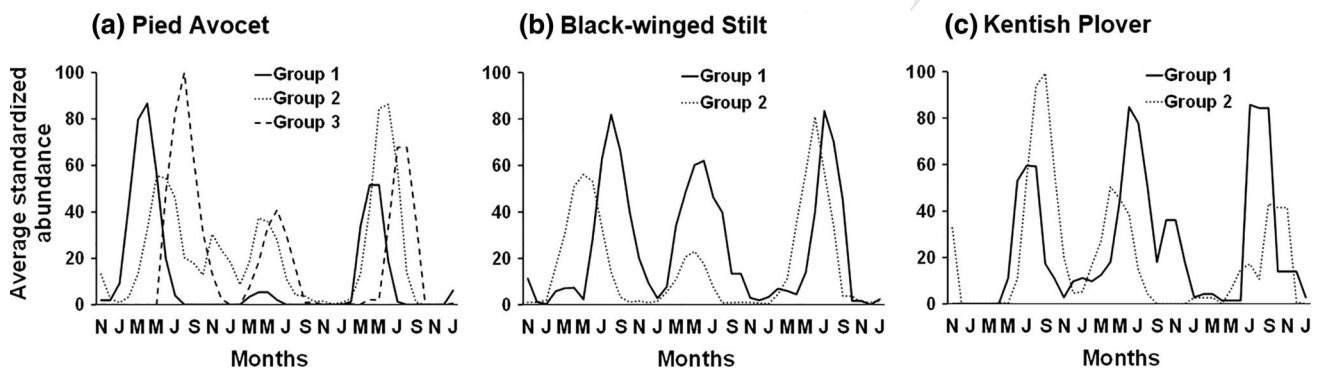


Fig. 3 Average temporal pattern of each group of lakes identified by the dendrograms of each species (Fig. 2). To generate these graphs we standardized the monthly abundance values of each lake by dividing them by the maximum abundance observed in that lake

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 Tirez)
 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

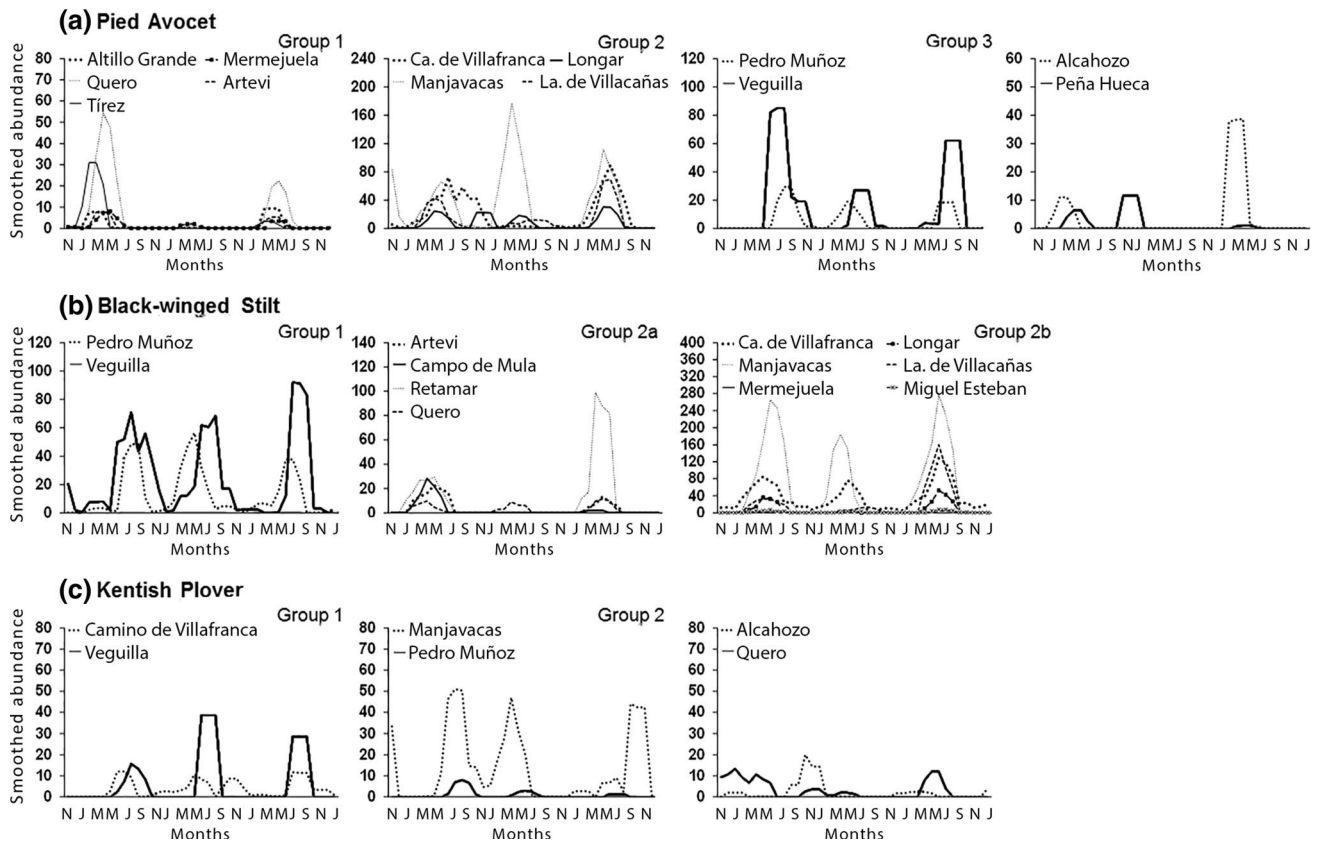


Fig. 4 Temporal variation (moving averages) of the abundance of the three water species in the studied lakes. Groups of lakes were defined from the dendrograms in Fig. 2. For Black-winged Stilt, lakes in Group 2 are shown in two graphs for better visualization of their temporal patterns (Groups 2a and 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 hydrope-
328 riod of lakes, which in turn is altered by wastewater
329 input.

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	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

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 (Ntiamao-
 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 (Ntiamao-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

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 syn-
 chrony 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 connec-
 tivity 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

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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525 References

526 Anderson MJ, Walsh DCI (2013) PERMANOVA, ANOSIM, and
527 the Mantel test in the face of heterogeneous dispersions: what
528 null hypothesis are you testing? *Ecol Monograph* 83:557–574.
529 doi:10.1890/12-2010.1

530 Anza I, Vidal MD, Laguna C, Díaz-Sánchez S, Sánchez S, Chicote
531 A, Florin M, Mateo R (2014) Risk factors for avian botulism
532 outbreaks in wetlands receiving effluents from urban wastewa-
533 ter treatment plants: eutrophication and bacterial pathogens.
534 *Appl Environ Microbiol* 80:4251–4259. doi:10.1128/AEM.
535 00949-14

536 Bancroft GT, Gawlik DE, Rutchey K (2002) Distribution of
537 wading birds relative to vegetation and water depths in the
538 northern Everglades of Florida, USA. *Waterbirds* 25:265–277.
539 doi:10.1675/1524-4695(2002)025[0265:DOWBRT]2.0.CO;2

540 Batchelder HP, Mackas DL, O’Brien TD (2012) Spatial-temporal
541 scales of synchrony in marine zooplankton biomass and
542 abundance patterns: a world-wide comparison. *Prog Oceanog*
543 97–100:15–30. doi:10.1016/j.pocean.2011.11.010

544 Bellamy PE, Rothery P, Hinsley SA (2003) Synchrony of woodland
545 bird populations: the effect of landscape structure. *Ecography*
546 26:338–348. doi:10.1034/j.1600-0587.2003.03457.x

Bjørnstad ON, Ims RA, Lambin X (1999) Spatial population
547 dynamics: analyzing patterns and processes of population syn-
548 chronicity. *Trends Ecol Evolut* 14:427–432. doi:
549 10.1016/S0169-5347(99)01677-8 550

Borkhataria RR, Frederick PC, Keller RA, Collazo JA (2012)
551 Temporal variation in local wetland hydrology influences
552 postdispersal survival of juvenile Wood Storks (*Mycteria*
553 *americana*). *Auk* 129:517–528. doi:10.1525/auk.2012.11244 554

Brown JH, Mehlman DW, Stevens GC (1995) Spatial variation in
555 abundance. *Ecology* 76:2028–2043. doi:10.2307/1941678 556

Cazelles B, Stone L (2003) Detection of imperfect population
557 synchrony in an uncertain world. *J Anim Ecol* 72:953–968. doi:
558 10.1046/j.1365-2656.2003.00763.x 559

Eberhart-Phillips L, Hudgens BR, Colwell MA (2015) Spatial
560 synchrony of a threatened shorebird: regional roles of climate,
561 dispersal and management. *Bird Conserv Int*. CJO 2015. doi:
562 10.1017/S0959270914000379 563

Florin M, Montes C (1999) Functional analysis and restoration of
564 Mediterranean lagunas in the Mancha Húmeda Biosphere Re-
565 serve (Central Spain). *Aquat Conserv Mar Freshw Ecosyst*
566 9:97–109. doi:10.1002/(SICI)1099-0755(199901/02)9:1 <97:AID-
567 AQC329 > 3.0.CO;2-F 568

Florin M, Montes C, Rueda F (1993) Origin, hydrologic func-
569 tioning and mor-phometric characteristics of small, shallow,
570 semiarid lakes (Lagunas) in La Mancha, central Spain. *Wet-*
571 *lands* 13:247–259. doi:10.1007/BF03161291 572

Goodwin BJ, Fahrig L (2002) How does landscape structure
573 influence landscape connectivity? *Oikos* 99:552–570. doi:
574 10.1034/j.1600-0706.2002.11824.x 575

Gosálvez R, Gil-Delgado JA, Vives-Ferrándiz C, Sánchez G,
576 Florin M (2012) Seguimiento de aves acuáticas amenazadas en
577 lagunas de la Reserva de la Biosfera de La Mancha Húmeda
578 (España Central). *Polígonos, Revista de Geografía* 22:89–122.
579 doi:10.18002/pol.v0i22.101 (in Spanish) 580

Granadeiro JP, Dias MP, Martins RC, Palmeirim JM (2006)
581 Variation in numbers and behaviour of waders during the tidal
582 cycle: implications for the use of estuarine sediment flats. *Acta*
583 *Oecol* 29:293–300. doi:10.1016/j.actao.2005.11.008 584

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Palaeontolog-
585 ical Statistics Software Package for education and analysis, ver.
586 3.04. *Palaeontol Electr* 4:9 587

Hanane S (2011) Breeding ecology of Kentish Plovers *Charadrius*
588 *alexandrinus* in rocky and sandy habitats of north-west Mor-
589occo (North Africa). *Ostrich* 82:217–223. doi:
590 10.2989/00306525.2011.616681 591

Haynes KJ, Bjørnstad ON, Allstadt AJ, Liebhold AM (2013)
592 Geographical variation in the spatial synchrony of a forest-
593 defoliating insect: isolation of environmental and spatial driv-
594 ers. *Proc R Soc B Biol Sci* 280:20130112. doi:10.1098/rspb.
595 2012.2373 596

Holyoak M, Lawler SP (1996) Persistence of an extinction-prone
597 predator-prey interaction through metapopulation dynamics.
598 *Ecology* 77:1867–1879. doi:10.2307/2265790 599

Hortas F (2012a) Cigueñuela (*Himantopus himantopus*). In: SEO/
600 BirdLife (ed) Atlas de las aves en invierno en España
601 2007–2010. Ministerio de Agricultura, Alimentación y Medio
602 Ambiente—SEO/BirdLife, Madrid, pp 222–223 (in Spanish) 603

Hortas F (2012b) Acoveta común (*Recurvirostra avosetta*). In:
604 SEO/BirdLife (ed) Atlas de las aves en invierno en España
605 2007–2010. Ministerio de Agricultura, Alimentación y Medio
606 Ambiente—SEO/BirdLife, Madrid, pp 224–225 (in Spanish) 607

Hortas F, Amat JA, Figuerola J (2012) Chorlitojeo Patinegro
608 (*Charadrius alexandrinus*). In: SEO/BirdLife (ed) Atlas de las
609 aves en invierno en España 2007–2010. Ministerio de Agricul-
610 tura, Alimentación y Medio Ambiente—SEO/BirdLife, Ma-
611 drid, pp 234–235 (in Spanish) 612

Hötker H (2002) Arrival of Pied Avocets *Recurvirostra avosetta* at
613 the breeding site: effects of winter quarters and consequences
614 for reproductive success. *Ardea* 90:379–387 615

Ims RA, Steen H (1990) Geographical synchrony in microtine
616 population cycles: a theoretical evaluation of the role of no-
617 madic predators. *Oikos* 57:381–387. doi:10.2307/3565968 618



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- 619 Ives AR, Klopfer ED (1997) Spatial variation in abundance created
620 by stochastic temporal variation. *Ecology* 78:1907–1913.
621 doi:10.1890/0012-9658(1997)078[1907:SVIACB]2.0.CO;2
- 622 Koenig WD (1998) Spatial autocorrelation in California land birds.
623 *Conserv Biol* 12:612–620. doi:10.1111/j.1523-1739.1998.97034.x
- 624 Koenig WD (2001) Spatial autocorrelation and local disappear-
625 ances in wintering North American birds. *Ecology*
626 82:2636–2644. doi:10.1890/0012-9658(2001)082[2636:
627 SAALDI]2.0.CO;2
- 628 Koenig WD (2002) Global patterns of environmental synchrony
629 and the Moran effect. *Ecography* 25:283–288. doi:10.1034/j.
630 1600-0587.2002.250304.x
- 631 Kosztolányi A, Székely T, Cuthill IC, Yılmaz KT, Berberoğlu S
632 (2006) Ecological constraints on breeding system evolution: the
633 influence of habitat on brood desertion in Kentish Plover.
634 *J Anim Ecol* 75:257–265. doi:10.1111/j.1365-2656.2006.01049.x
- 635 Kosztolányi A, Székely T, Cuthill IC (2007) The function of habitat
636 change during brood-rearing in the precocial Kentish plover
637 *Charadrius alexandrinus*. *Acta Ethol* 10:73–79. doi:10.1007/s10
638 211-007-0032-z
- 639 Kuwae T (2007) Diurnal and nocturnal feeding rate in Kentish
640 plovers *Charadrius alexandrinus* on an intertidal flat as recorded
641 by telescopic video systems. *Mar Biol* 151:663–673. doi:
642 10.1007/s00227-006-0506-y
- 643 Kvasnes MAJ, Storaas T, Pedersen HC, Bjørk S, Nilsen EB (2013)
644 Spatial dynamics of Norwegian tetraonid populations. *Ecol Res*
645 25:367–374. doi:10.1007/s11284-009-0665-7
- 646 Liebhold A, Koenig WD, Bjørnstad ON (2004) Spatial synchrony
647 in population dynamics. *Ann Rev Ecol Evol Syst* 35:467–490.
648 doi:10.1146/annurev.ecolsys.34.011802.132516
- 649 Liu Z, Gao M, Li Z, Liu H (2009) Dispersal, colored environ-
650 mental noise, and spatial synchrony in population dynamics:
651 analyzing a discrete host–parasitoid population model. *Ecol*
652 *Res* 24:383–392. doi:10.1007/s11284-008-0513-1
- 653 Martínez-Santos P, De Stefano L, Llamas MR, Martínez-Alfaro
654 PE (2008) Wetland restoration in the Mancha Occidental
655 aquifer, Spain: a critical perspective on water, agricultural, and
656 environmental policies. *Restor Ecol* 16:511–521. doi:
657 10.1111/j.1526-100X.2008.00410.x
- 658 Moran PAP (1953) The statistical analysis of the Canadian lynx
659 cycle. *Aust J Zool* 1:291–298. doi:10.1071/ZO9530291
- 660 Mortelliti A, Westgate M, Stein J, Wood J, Lindenmayer DB
661 (2015) Ecological and spatial drivers of population synchrony
662 in bird assemblages. *Basic Appl Ecol* 16:269–278. doi:
663 10.1016/j.baae.2015.01.008
- 664 Ntiamoa-Baidu Y, Piersma T, Wiersma P, Poot M, Battley P,
665 Gordon C (1998) Water depth selection, daily feeding routines
666 and diets of waterbirds in coastal lagoons in Ghana. *Ibis*
667 140:89–103. doi:10.1111/j.1474-919X.1998.tb04545.x
- 668 Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1999) Dis-
669 persal and spatial scale affect synchrony in spatial population
670 dynamics. *Ecol Lett* 2:114–120. doi:10.1046/j.1461-0248.1999.
671 22060.x
- 672 Post E, Forchhammer MC (2002) Synchronization of animal
673 population dynamics by large-scale climate. *Nature* 420:168–
674 171. doi:10.1038/nature01064
- Powney GD, Roy DB, Chapman D, Brereton T, Oliver TH (2011)
675 Measuring functional connectivity using long-term monitoring
676 data. *Methods Ecol Evol* 2:527–533. doi:10.1111/j.2041-210X.
677 2011.00098.x
- R Development Core Team (2014) R: a language and environment
679 for statistical computing. R Foundation for Statistical Com-
680 puting, Vienna
- Ranta E, Kaitala V, Lindstrom J, Linden H (1995) Synchrony in
682 population dynamics. *Proc R Soc B Biol Sci* 262:113–118. doi:
683 10.1098/rspb.1995.0184
- Ranta E, Kaitala V, Lindstrom J (1999) Spatially autocorrelated
685 disturbances and patterns in population synchrony. *Proc R Soc*
686 *B Biol Sci* 266:1851–1856. doi:10.1098/rspb.1999.0856
- Roshier DA, Robertson AI, Kingsford RT (2002) Responses of
688 waterbirds to flooding in an arid region of Australia and
689 implications for conservation. *Biol Conserv* 106:399–411. doi:
690 10.1016/S0006-3207(01)00268-3
- Ruetz CR III, Trexler JC, Jordan F, Loftus WF, Perry SA (2005)
692 Population dynamics of wetland fishes: spatio-temporal pat-
693 terns synchronized by hydrological disturbance? *J Anim Ecol*
694 74:322–332. doi:10.1111/j.1365-2656.2005.00926.x
- SEO/BirdLife (2016a) *Himantopus himantopus*. Distribución de
696 aves anilladas en España recuperadas por país. [http://www.
697 anillamientoseo.org/](http://www.anillamientoseo.org/). Accessed 08 Sep 2016 (in Spanish)
- SEO/BirdLife (2016b) *Charadrius alexandrinus*. Distribución de
699 aves anilladas en España recuperadas por país. [http://www.
700 anillamientoseo.org/](http://www.anillamientoseo.org/). Accessed 08 Sep 2016 (in Spanish)
- Sirot E, Touzalin F (2014) Temporal patterns of arrival from
702 migration as a response to competition for breeding space.
703 *J Avian Biol* 45:109–112. doi:10.1111/j.1600-048X.2013.00184.x
- Sutcliffe LO, Thomas CD, Moss D (1996) Spatial synchrony and
705 asynchrony in butterfly population dynamics. *J Anim Ecol*
706 65:85–95. doi:10.2307/5702
- Thioulouse J, Chessel D, Dolédec S, Olivier JM (1997) ADE-4: a
708 multivariate analysis and graphical display software. *Stat*
709 *Comput* 7:75–83. doi:10.1023/A:1018513530268
- Thrall PH, Burdon JJ, Bock CH (2001) Short-term epidemic
711 dynamics in the *Cakile maritima*–*Alternaria brassicicola* host–
712 pathogen association. *J Ecol* 89:723–735. doi:10.1046/j.0022-
713 0477.2001.00598.x
- Trenham PC, Koenig WD, Mossman MJ, Stark SL (2003) Re-
715 gional dynamics of wetland-breeding frogs and toads: turnover
716 and synchrony. *Ecol Appl* 13:1522–1532. doi:10.1890/02-5206
- Vidal D, Anza I, Taggart MA, Ramírez-Pérez E, Crespo E, Hofle
718 U, Mateo R (2013) Environmental factors influencing the
719 prevalence of a *Clostridium botulinum* type C/D mosaic strain in
720 nonpermanent Mediterranean wetlands. *Appl Environ Micro-*
721 *biol* 80:4264–4271. doi:10.1128/AEM.01191-13
- Williams CK, Ives AR, Applegate RD (2003) Population dynamics
723 across geographical ranges: time-series analyses of three small
724 game species. *Ecology* 84:2654–2667. doi:10.1890/03-0038
- Zar JH (2010) Biostatistical analysis, 5th edn. Prentice-Hall,
726 Englewood Cliffs 727