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Interspecific variations in shorebird responses to management practices on protected Mediterranean saltpans.

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Waterbird responses to wetland management

1 **Interspecific variations in breeding waterbird responses to management practices on**
2 **protected Mediterranean saltpans.**

3

4 **Keywords:**

5 bayesian hierarchical model, gulls, population dynamics, Ramsar convention, salinity, water

6 levels, waterbirds, wetlands

7

8 **Abstract**

9

10 Tidal habitats sustain fragile ecosystems, undergoing pressures from coastal artificialization
11 and rising sea levels. Saltpans are a substitution habitat for birds that breed, winter or stop-
12 over along coastlands where most pristine tidal habitats have been removed. Balancing the
13 economical, patrimonial and biodiversity values of former saltpans is thus needed to
14 mitigate the threats posed by global changes on waterbirds. In this study, we scrutinized the
15 influence of management practices on waterbirds on two isolated saltpans located on the
16 French Mediterranean shore, several tens of kilometres apart from other suitable habitats.
17 We analysed three years of bird counts for nine protected species that breed, forage and
18 roost on these saltpans. We used a multispecies hierarchical model to relate variations in
19 bird counts to water levels, oxygenation and salinity, the three parameters targeted by the
20 saltpans management plan to promote bird settlement. We showed that the hypersaline
21 conditions that dominate in these saltpans are suboptimum to most species, suggesting that
22 waterbird concentrations are dictated by the lack of alternatives in the surrounding
23 landscape rather than by habitat suitability. Intraspecific variations in species' responses to
24 these variables should orient towards the creation of a habitat mosaic within the saltpans.
25 Eventually, between-site differences in bird responses to water conditions pointed the
26 effects of disturbance, predation and other landscape-level features. Our results reveal that
27 high waterbird numbers on isolated saltpans may be a misleading measure of their
28 ecological suitability, and that management on these sites needs to incorporate conflicts and
29 complementarity in species' habitat use.

30

31 **Introduction**

32

33 Wetlands, among the most biodiverse ecosystems on earth, sustain a wide range of essential
34 ecosystem services such as harvesting and fishing, water purification, floods buffering and
35 mitigation of catastrophic climatic events (Zedler & Kercher, 2005; Gardner *et al.*, 2015;
36 Montanarella *et al.*, 2018; Ramsar Convention on Wetlands, 2018). They also provide habitat
37 and resources for a high diversity of organisms organized into trophically complex
38 ecosystems. Although considered as foreground habitats for conservation and human
39 welfare, the global surface of wetlands has been reduced by 35% between 1970 and 2015
40 under various pressures, among which climate change and human land use are especially
41 prominent (Barbier *et al.*, 2011; Gardner *et al.*, 2015; Ramsar Convention on Wetlands,
42 2018). Wetlands are restricted in surface, highly unstable due to variations in water levels
43 and quality, and thus vulnerable to even small levels of disturbance (Adam, 2002; Kirwan &
44 Megonigal, 2013). Appropriate conservation effort is therefore needed to warrant the
45 maintenance of wetland-related ecosystems, and requires in-depth studies to evaluate the
46 effects of water management practices on targeted species (Clausen *et al.*, 2013).

47

48 Coastal wetlands are highly productive, yet unstable ecosystems with site-specific dynamics
49 tied to variations in sea levels, balance of freshwater and saltwater, and human usage
50 (Adam, 2002). The vulnerability of coastal wetlands facing rising sea levels as a result of
51 ongoing climate change is listed as one of the most severe threats to coastal biodiversity in
52 the coming decades (Boesch, 2000; Craft *et al.*, 2009; Hoegh-Guldberg & Bruno, 2010).
53 However, coastal wetlands are more immediately threatened by human land use, which

54 accounts for 25-50% of the decrease in their global surface cover during the past centuries
55 through direct destruction, draining for agriculture or urbanization, eutrophication, invasive
56 species and water pollution (Gedan *et al.*, 2009; Deegan *et al.*, 2012; Kirwan & Megonigal,
57 2013). As a result, many coastal wetlands are now restricted to small isolated patches of
58 marshy habitats within deeply man-modified seashores, some of which are maintained
59 artificially by conservation-oriented management, especially in northern America, western
60 Europe, and locally elsewhere (Hughes & Paramor, 2004).

61

62 Most waterbirds (mainly Charadriidae, Scolopacidae, Laridae and a few other related
63 families ; Burger & Olla, 1984) are strict invertebrate eaters or piscivores, and thus occupy a
64 top-position in trophic networks that make them suitable indicators to monitor the
65 functioning of coastal wetland ecosystems (Piersma *et al.*, 2004). Because most waterbirds
66 are migratory, the preservation of their breeding, stop-over and wintering habitats all along
67 migration routes is critical to their regional or global population persistence (Piersma *et al.*,
68 2006), for instance along the Pacific north-american coast (Velasquez, 1992), in southeastern
69 Asia (Sripanomyom *et al.*, 2011; Xia *et al.*, 2017) or on Mediterranean shores (AEWA, 2018;
70 Giosa *et al.*, 2018). Along these coasts, suitable wetlands are small and rare due to
71 topographic constraints and intense human land use (Myers, 1983; Piersma *et al.*, 2006). As
72 a consequence of climate change-induced erosion of coastal marshes and habitat loss
73 (Ramírez *et al.*, 2018), waterbird conservation thus largely benefits from the maintenance of
74 appropriate resources in artificial wetlands such as fishponds and saltpans (Velasquez, 1992;
75 Takekawa *et al.*, 2006; Giosa *et al.*, 2018). It is therefore of paramount importance to assess

76 carefully the conservation value of saltpan management practices in relation to waterbird
77 habitat and trophic requirements.

78

79 Mudflat-feeding waders (Charadriidae and Scolopacidae) account for a large proportion of
80 waterbirds biomass and thus bear a strong role on tidal trophic networks, in addition to their
81 high patrimonial value associated with hunting, conservation status and legal use as
82 indicator species (Colwell, 2010). These small-bodied species cannot cope with large
83 variations in water depth, which therefore determine habitat availability. Furthermore, the
84 abundance and quality of their invertebrate preys peaks in mesohaline waters with high
85 oxygenation levels (Velasquez, 1992; Takekawa *et al.*, 2006; Dias, 2009; Athearn *et al.*, 2012).
86 These conditions are specifically met in saltpans, in which water levels, variations in
87 physiochemical conditions and other sources of disturbance are buffered artificially by
88 hydraulic control, rendering these artificial saltmarshes suitable for high waterbird
89 concentrations (Velasquez, 1992; Sánchez *et al.*, 2006; Takekawa *et al.*, 2006).

90

91 Because waterbird numbers and diversity decrease in hypersaline conditions, the suitability
92 of saltpans to birds is conditioned to the maintenance of optimum physicochemical
93 conditions (Warnock *et al.*, 2002). Gulls (Laridae) and terns (Sternidae) breeding on saltpans
94 nest on small islets or dykes, as a substitution to sandpits or other coastal habitats subjected
95 to erosion and human disturbance (Catry *et al.*, 2004). By contrast with waders, these birds
96 benefit from higher water levels that isolate their breeding sites from predators (Warnock *et*
97 *al.*, 2002; Bluso-Demers *et al.*, 2016), although gulls also require mudflats for feeding.
98 Waterbird conservation on saltpans therefore need to accommodate conflicts in species'

99 habitat and resource requirements, which, in most instances, can only be done through
100 hydraulic management of water level and flow.

101

102 A major axis of the western Palearctic migration flyway crosses the western Mediterranean
103 on the French coast between the Rhône river and the foothills of the French Alps (Newton,
104 2003). Wetlands located in this area are therefore enlisted in the Ramsar convention among
105 priority sites for the conservation of migrating and breeding waterbirds at the scale of
106 Western Europe (Sadoul & Walmsley, 2000). Most suitable habitats have, however, been
107 eliminated by land artificialization. The two remaining significant wetlands along this stretch
108 of coast are the Camargue and, 120 km farther east, a small complex of two former saltpans
109 located three kilometers apart of each other on the highly urbanized Hyères peninsula. This
110 small isolated site has therefore become the only substantial habitat patch for waterbirds at
111 the eastern limit of the French Mediterranean shore and is an important breeding area for
112 several species of conservation concern at the national or regional scale, such as Kentish
113 Plover (*Charadrius alexandrinus*) and Black-headed Gull (*Chroicocephalus ridibundus*).
114 However, in spite of the essential role of these saltpans for bird conservation, an evaluation
115 of management practices still needs to determine whether local water management
116 adequately balances the species' ecological requirements according to their various habitat
117 uses.

118

119 We therefore framed a study on the following question: how do breeding shorebirds
120 respond to management practices in this isolated protected coastal wetland? The critical
121 importance of this site for coastal wetland breeders and migrants, the lack of any alternative

122 habitat for breeding birds around this point of the Mediterranean coast, and the strong
123 pressure from surrounding urbanization, are exemplary to evaluate the conservation value
124 of local saltpan management practices. Additionally, the absence of any substantial patch of
125 alternative habitat within a 100 km radius of dry and artificialized coast concentrates birds
126 inside this specific site, ensuring that once accounted for seasonal phenology, their
127 abundance variations are dictated by local conditions only. However, breeding species have
128 conflicting requirements, since colonial nesters (such as terns and gulls) favour high water
129 levels to ensure protection against predation pressure and feed on water, while waders
130 require large extents of emerged mudflats to forage on ground.

131

132 We specifically addressed three questions: (i) are bird counts high because water levels and
133 physiochemical properties encompass species' optimum values, or because of the lack of
134 alternative sites? (ii) do species with different habitat and trophic requirements respond
135 synchronically or idiosyncratically to variations in water physiochemical parameters? (iii) to
136 what extent are species' responses dictated by the way birds use these two saltpans? We
137 addressed these questions through a three-years monitoring based on decadal bird counts,
138 concentrating on nine breeding species prioritized by the site management plan. We
139 focused on variations in water levels, salinity and oxygen concentration, which are identified
140 as the most limiting physicochemical variables for waterbirds frequenting saltpans (Warnock
141 *et al.*, 2002; Takekawa *et al.*, 2006, 2015).

142

143 **Material and methods**

144

145 *Study area*

146

147 The study site comprises two former saltpans (hereafter “Pesquiers” and “Vieux Salins”)
148 located three kilometres apart in a small peninsula of the eastern French Mediterranean
149 coast (43°05’N ; 006°11’E , Fig. 1), property of the Conservatoire du Littoral, a French agency
150 for the protection of coastal habitats. It is enlisted in the Ramsar convention (criterion 2:
151 supports vulnerable species ; criterion 3: supports populations of animal species important
152 for maintaining the biological diversity of the biogeographic region ; criterion 4: supports
153 animal species at a critical stage in their life cycles, or provides refuge during adverse
154 conditions ; Ramsar Convention, 1971).

155

156 The closest substantial site offering permanently suitable conditions for waterbirds is the
157 Camargue (>19000 ha of protected area, 120 km to the west). Our study site is therefore a
158 small islet of protected wetlands which warrants a resting, breeding and feeding area to
159 waterbirds throughout the year in an otherwise unsuitable landscape matrix formed by low
160 dry mountains and a heavily urbanized coast. Both saltpans are strictly closed to the public
161 and are protected as part of Port Cros National Park, which prevents any kind of exploitation
162 or human activities unrelated to biodiversity protection. Management is largely dedicated to
163 bird breeding and is ensured by fieldworkers from the municipality.

164

165 The Pesquiers (Fig. 1c) are a 650 ha saltpan located on a narrow sandy peninsula and used
166 for commercial exploitation from 1848 to 1995. It consists in a single large unit comprising
167 32 ponds (average surface 14.9 ha \pm 22.3 ha, all uncertainties in standard deviation units
168 unless otherwise stated), close to or below the sea level (-1.19 to +0.6 m depending on
169 ponds). Hydraulic pumps and sluice gates distribute water across the ponds from a belt canal
170 connected to the adjacent sea, and the saltpan is encircled by a road. Dykes separating the
171 ponds are covered by sparse herbaceous vegetation and scattered bushes.

172

173 The Vieux Salins (Fig. 1d) are located inland in a less urbanized area bordered by vineyards
174 and fields at its northern end; the southern end is separated from the coast by a tree hedge
175 and a track. They cover a smaller extent (350 ha) with 34 ponds that result from the
176 grouping of several old familial units exploited from the 13rd century to 1995 (7.19 ha \pm 5.46
177 ha). The ponds are mostly above the sea level (from -0.7 to +1.7 m); hydraulic pumps are
178 used to supply and distribute water from the adjacent sea, and sluice gates regulate water
179 flow inside ponds. The dykes and immediate surroundings are covered by a continuous
180 herbaceous cover with scattered bushes and small woods.

181

182 Modulations of water levels and flow are decided by the site manager on a day-to-day basis
183 and operated by local technicians. These controlled variations aim to secure the settlement
184 of breeding birds, trying to balance the requirements of foraging waders and those of other
185 species, with a specific focus on gull-tern colonies and Kentish Plover (*Charadrius*
186 *alexandrinus*, listed as vulnerable at a national level, Appendix S1, Table S1.1). On both sites,
187 the control of water levels is mainly limited by pump flow and tide ; desired levels are usually

188 reached within a few hours, up to a day. Shallow water enters the circuit only through
189 infiltrations, precipitations and casual drainage from surrounding hills after floods.

190

191 *Bird data*

192

193 Standardized bird counts have been performed on all the ponds of the two saltpans since
194 2005, but we restricted the dataset to the 12 ponds (7 on Vieux Salins and 5 on Pesquiers)
195 and three years (2014-2016) with complete physicochemical records (Fig. 1); these ponds
196 account for 62% of all bird counts for the species and years considered (from 32%, Little Tern
197 to 82%, Kentish Plover). Counts were performed by a trained ornithologist, on a weekly
198 (April-September) or ten-days (October-March) basis, at strategic locations maximizing
199 coverage along a standardized 77 km track covering all ponds within the two sites. Counts
200 started at sunrise and the whole track was sampled in a single day, usually in five hours. All
201 birds seen or heard were recorded, except flyovers or birds flying from a pond to another.
202 Bird flocks usually stayed together and remained well identifiable, allowing the observer to
203 minimize the risk of double counts. Counts were not replicated, but all species considered in
204 the studies feed on well-visible bare ground, mudflats or low waters, ensuring near-
205 exhaustive detection and counts. Identification errors were unlikely given the commonness
206 and overall low diversity of targeted species.

207

208 We focused on nine protected waterbird species specifically targeted by the saltpans
209 management plan due to their French and regional conservation status (species list,

210 conservation status, mean counts per site and number of pairs in Appendix S1, Table S1.1).
211 All but Greater Flamingo breed on at least one of the two saltpans, and all are regularly
212 present and forage onsite, although terns also fish at sea. All the species are at least partly
213 migratory or erratic in winter : for each species, we therefore limited our study to the period
214 corresponding to 95% of its annual counts to distinguish absences due to species' phenology
215 from temporary absences resulting from local environmental conditions (Appendix S1, Table
216 S1.1: "Period of inclusion"). So doing, we also eliminated casual counts of late or early
217 migrants.

218

219 *Physicochemical variables*

220

221 Three physicochemical variables have been monitored since 2014 by the reserve's
222 fieldworkers every 15 days at 14 fixed sampling points (nine on Pesquiers, five on Vieux
223 Salins, Fig. 1c,d), alternating each saltpan on a weekly basis (quantitative summary in
224 Appendix S1, Table S1.2 and Fig.S1.1). Some sampling events were offset by a few days in
225 case of bad weather, and 2% of the recordings could not be performed due to persisting
226 unsuitable weather or device breakdowns. Water level (cm) corresponded to the height of
227 the water column and was measured to the nearest cm using permanent limnometric scales.
228 Salinity was measured to the nearest g.L^{-1} with a probe (Consort C562, probe SK23T) up to its
229 saturation level (120 g.L^{-1}). Higher concentrations (20% of the recordings) needed to be
230 measured by a mechanical densimeter which was not systematically used by field
231 technicians for practical reasons: we therefore truncated all salinity measurements to 120
232 g.L^{-1} . Oxygen concentration was measured with a probe (Consort C562, probe SZ10T-PB) to

233 the nearest 10^{-4} mg.L⁻¹. These three variables were uncorrelated (R^2 from 0.08 to 0.05).
234 Physicochemical measurements and bird counts were not performed simultaneously; we
235 therefore matched each bird count with the closest measurement event (mean offset = 0 ± 2
236 days, from -6 (1 sample) to +6 (1 sample) days).

237

238 *Statistical Analyses*

239

240 We related species' abundances to variations in water levels, salinity and oxygen
241 concentration with a hierarchical autoregressive generalized linear model implemented in a
242 bayesian framework (Royle & Dorazio, 2008; Kery & Royle, 2015). We modelled species
243 counts $N_{i,t,k,s}$ of species (s) at monitoring event (t), year (k) and pond (i) as a Poisson
244 distribution with mean $\lambda_{i,t,k,s}$:

$$245 N_{i,t,k,s} \sim \text{Poisson}(\lambda_{i,t,k,s}) \quad (1)$$

246 We predicted λ with a pond-varying intercept (α), saltpan-specific linear (β) and quadratic (γ)
247 effects of water level (WAL), salinity (SAL) and Oxygen concentration (OXY), plus a temporal
248 overdispersion term (ϵ). The effects of salinity > 120 g.L⁻¹ was modelled by the saltpan-
249 specific conditional intercept α^{120} . All terms were species-specific :

$$250 \log(\lambda_{i,t,k,s}) = \alpha_{i,s} + \beta_{1,site(i),s} \times WAL_{i,t} + \gamma_{1,site(i),s} \times WAL_{i,t}^2 + (1 - I_{SAL_{i,t} < 120}) \times$$
$$251 \alpha_{site(i),s}^{120} + I_{SAL_{i,t} < 120} \times (\beta_{2,site(i),s} \times SAL_{i,t} + \gamma_{2,site(i),s} \times SAL_{i,t}^2) + \beta_{3,site(i),s} \times OXY_{i,t} +$$
$$252 \gamma_{3,site(i),s} \times OXY_{i,t}^2 + \epsilon_{t,k,s} \quad (2)$$

253 Where $I_{SAL_{i,t} < 120}$ indicates whether salinity is above the censoring threshold of 120g.L⁻¹:

254
$$I_{SAL_{i,t} < 120} = \begin{cases} 1 & \text{if the salinity of the pond } i \text{ at time } t \text{ is } < 120 \text{ g.L}^{-1} \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

255 Since data for water levels, salinity or oxygen were missing in 14% of the recordings, we
256 modelled missing values assuming that all variables were normally distributed around the
257 observed mean and with the observed standard deviation.

258

259 We nested pond-level intercepts $\alpha_{i,s}$ within the two saltpans for each species to reflect
260 saltpan-dependent suitability to birds:

261
$$\alpha_{i,s} \sim \text{Norm}(\mu_{site(i)}, \tau) \quad (4)$$

262 We also imposed species-level priors to regression coefficients $\beta_{k,site(i),s}$:

263
$$\beta_{k,site(i),s} \sim \text{Norm}(B_s, T_s) \quad (5)$$

264 Although we were interested in saltpan-level coefficients, these hyperpriors were necessary
265 to model species-level responses to variations in physico-chemical variables. This
266 hierarchical formulation is equivalent to a mixed model with nested pond and site random
267 effects on α and with a species random effect on β_k (Zuur, 2011).

268

269 We divided the overdispersion term $\varepsilon_{t,k,s}$ into a within-year error (ε_1) reflecting species'
270 seasonal phenology and a between-years error (ε_2) accounting for temporal autocorrelation
271 across consecutive breeding seasons :

272
$$\varepsilon_{t,k,s} = \varepsilon_{1,t,s} + \varepsilon_{2,k,s} \quad (5)$$

273 We assumed that ε_1 and ε_2 were normally distributed first-order autoregressive terms (Zuur,
274 2011) :

$$275 \quad \varepsilon_{1,t,s} \sim \text{Norm}(\varphi_{1,s} \times \varepsilon_{1,t-1,s}, \tau_1) \quad (6)$$

$$276 \quad \varepsilon_{2,k,s} \sim \text{Norm}(\varphi_{2,s} \times \varepsilon_{2,k-1,s}, \tau_2) \quad (7)$$

277 In these equations, φ_1 and φ_2 quantify respectively the magnitude of intra- and inter-annual
278 autocorrelations.

279

280 We specified flat gaussian priors for all higher-level hyperparameters and ran three Monte-
281 Carlo Markov chains under JAGS 4.3.0 (Plummer, 2003), each with 10^6 burn-in iterations and
282 10^6 iterations for inference, thinned by 1000. The script of the model in BUGS language is
283 provided in Appendix S3. We computed the Gelman-Rubin statistics (Gelman *et al.*, 2004) for
284 all parameters and considered that a value below 1.1 indicated adequate convergence. We
285 assessed model fit with a Bayesian posterior predictive check based on a comparison of
286 observed and modelled species' abundances (Gelman & Hill, 2007).

287 **Results**

288

289 *Model fit and convergence*

290

291 The Bayesian posterior predictive check indicated varying fits according to species, from $p =$
292 0.26 to $p = 0.7$ ($p = 0.5$ indicates perfect fit; all results in Appendix S2, Fig S2.1). The poorest
293 fits corresponded to gregarious species that form large flocks (Black-headed Gull and
294 Greater Flamingo) or to semi-colonial species that aggregate in space (Stilt and Avocet). All
295 parameters converged adequately according to Gelman-Rubin's statistics (Appendix S2,
296 Table S2.1) and visual checks of chain stability. Autocorrelation was non-significant at both
297 intra- and inter-annual scales for most species (Appendix S1, Table S1.1), indicating that
298 temporal variations in counts were well captured by the variables considered.

299

300 *Site effect*

301

302 Species-level raw counts were lower in the smaller inland Vieux Salins than in the wide
303 coastal Pesquiers (Appendix S1, Table S1.1, which also displays the average number of pairs
304 per year on the two sites). This difference persisted once water level, salinity and dissolved
305 oxygen concentration were fixed to their average value over the two sites (Appendix S2, Fig.
306 S2.2). Species-specific variations unrelated to physiochemical parameters were not

307 explained by pond size only (maximum Pearson's R^2 between counts and pond area = 0.33 in
308 Greater Flamingo).

309

310 *Responses to physiochemical variables*

311

312 All physiochemical variables were non-linearly related to variations in species counts. Counts
313 varied by 0 to 100% along the range of variation of the three variables, with strong
314 interspecific variation (Fig. 2-4 : estimated marginal variation in species' counts against a
315 given physiochemical variable, holding all other fixed to their average value). Hence, none of
316 the variables considered had an unambiguously higher influence than the others, which
317 implies that species' responses to management practices were dictated by a balance of
318 multiple physiochemical features rather than merely by water levels.

319

320 Water level is the only lever available to the reserve managers to modulate water conditions
321 on the two saltpans, and the most integrative of the three variables considered. Waders,
322 which nest and forage on emerged ground, exhibited a bell-shaped response to variations in
323 water level on at least one of the two sites (Fig. 2), with flatter responses in four of the five
324 islet-breeding species (Slender-billed Gull, Fig. 2d and Terns, Fig. 2g, h, i, but not Black-
325 headed Gull, Fig. 2f). This result is explained by the need of these species to preserve their
326 nests from predators, but also by the fact that they tend to forage more frequently on open
327 waters. Leaving aside credible intervals, maximum counts were attained within the range of
328 water level variations for eight and five out of nine species in Pesquiers and Vieux Salins,

329 respectively (Appendix S2, Table S2.2, range of covariates in Appendix S1, Table S1.2 for
330 comparison). However, response curves differed sharply between the two saltpans without
331 any systematic pattern (compare blue and black curves in Fig. 2). For instance, Flamingo's
332 optimum was close to 22 cm in Vieux Salins, while its counts increased monotonically in
333 Pesquiers all over the water levels range (Fig. 2c and Table S2.2). These site-dependent
334 optimums imply that species-dependent factors unrelated to the tested variables contribute
335 to these response curves.

336

337 Responses to salinity were monotonically negative for six large islet-breeding species
338 (Avocet, Stilt, Slender-billed Gull, Kentish Plover, Black-headed Gull and Little Tern), the
339 three others exhibiting non-linear curves (Fig. 3). Estimates of species' abundances when
340 salinity exceeded the 120g.L^{-1} threshold imposed by our probe were consistent with these
341 curves in all species (Fig. 3). Interestingly, seven out of nine species reached a minimum
342 abundance within the salinity range observed in the Pesquiers, the main foraging site for
343 most of them, but only three in Vieux Salins, which birds use more for roosting (Table S3.2).
344 This pattern was reversed for Flamingo (maximum counts for 51g.L^{-1}), which however uses
345 little Vieux Salins in the breeding season. Conversely, response curves were negative or flat
346 for three species which breed and feed on the two saltpans although usually more tied to
347 less saline waters, Black-headed Gull (Fig. 3f), Little Tern (Fig. 3h) and Common Tern (Fig. 3i).
348 Most species' responses to salinity were flatter in Vieux Salins, and even positive for Stilt
349 (Fig. 3b) and Black-headed Gull (Fig. 3f), although salinity varied within the same range in
350 both saltpans (Table S3.2).

351

352 The effect of dissolved oxygen concentration was also species- and saltpan-dependent with
353 no general pattern, although response curves were flatter in Vieux Salins than in Pesquiers
354 (Fig. 4). Species' optimums were inconsistent across the two saltpans, except for Avocet
355 which peaked around 7 mg.L-1 in both (Fig. 4a and Appendix S2, Table S2.2). Flamingo
356 exhibited similar monotonic decreases with increasing oxygen concentrations in the two
357 saltpans (Fig. 4c), suggesting that this particular parameter might act as a strong limiting
358 factor to this species.

359

360 Discussion

361

362 Most species exhibited strong non-linear responses to at least one of the three variables
363 investigated, supporting the hypothesis that water level, salinity and dissolved oxygen
364 concentration are relevant parameters to control saltpans suitability to waterbirds, in line
365 with previous studies in other biogeographic areas (Velasquez, 1992; Warnock *et al.*, 2002;
366 Giosa *et al.*, 2018). As a general pattern, macroinvertebrate species diversity peak at mid-
367 salinity (Britton & Johnson, 1987), which in turn forces a decrease in bird occurrence
368 towards hypersaline waters due to a lack of prey and osmoregulation stress (Gutiérrez *et al.*,
369 2011). Salinity is thus crucial for waterbird assemblages through its direct influence on
370 trophic resources fluctuations (Warnock *et al.*, 2002; Takekawa *et al.*, 2006; Ramírez *et al.*,
371 2018). In our study, all species tied to saltpans for foraging, except flamingo (*i.e.*, all but
372 terns, which also fish at sea), exhibited negative response curves to salinity at least on
373 Pesquiers, which points that water on this saltpan is overly saline to most breeding
374 waterbirds. Accordingly, the levels of salinity recorded in our study site were well above the

375 range found in comparable protected saltpans elsewhere in the world (e.g. in San Francisco
376 bay, Warnock *et al.*, 2002). In line with studies on other artificial marshes (Takekawa *et al.*,
377 2006; Bellio *et al.*, 2009; Giosa *et al.*, 2018), these patterns imply that our study site is a
378 suboptimum and stressful habitat which waterbirds are forced to use by the lack of more
379 suitable marshes in the vicinity, the closest coastal wetland to our study site being the
380 Camargue, 120 km to the west.

381

382 While increasing salinity had clearly detrimental effects on most species, the effects of water
383 levels and dissolved oxygen were more species-specific, reflecting both species' habitat
384 preferences and site use. Waders and gulls peaked at low to intermediate water levels,
385 consistent with their need of mudflats for foraging (Piersma *et al.*, 2004), while terns, which
386 fish on open waters, exhibited flatter responses explained by the fact that they breed on
387 ponds where water levels are maintained permanently high. At the other extreme, the
388 particular ecology of flamingo, a large-bodied specialist of highly saline waters relying on
389 saltpans as up to 60% of its habitat (Béchet *et al.*, 2009), explains its maximum counts at
390 lower oxygenation, higher salinity and higher water levels than most other species. Its
391 unexpected apparent reluctance to high salinity in Vieux Salins can be explained by the
392 confusing fact that the few sufficiently large and deep ponds on this saltpan also happen to
393 be the least saline. In sum, waterbirds' responses to changes in water physicochemical
394 parameters were highly asynchronic across species and consistent with their differential use
395 of the saltpans, either for breeding, foraging or both.

396

397 Although species' responses to the three studied variables were generally well explained by
398 breeding and feeding behaviours, we observed marked differences between the two studied
399 salt pans suggesting the interplay of additional factors not accounted for in our study. Most
400 notably, responses to all tested variables were more marked, and abundances were higher,
401 on the barren Pesquiers salt pans than on the more vegetated Vieux Salins, reflecting the
402 tendency of shorebirds to forage and breed preferentially in open habitats (Tavares *et al.*,
403 2015; Źmihorski *et al.*, 2016). This discrepancy between the two sites may also imply that
404 breeding waterbirds limit distances between breeding and foraging areas to reduce energy
405 expenditure and predation risk. Among undesired effects which may also contribute to inter-
406 site differences, herbaceous cover and wooded areas can increase predation pressure by
407 wild boar, red fox, yellow-legged gull, falcons and sparrowhawk (Źmihorski *et al.*, 2016), and
408 the small size of Vieux Salins exposes birds more to external disturbance (in particular the
409 proximity of an airport), although both sites are permanently closed to the public. These
410 speculations based on field experience demand formal testing with dedicated data, which
411 were not available during our study. Our results suggest, however, that waterbirds'
412 responses to water parameters interact with landscape and habitat-level determinants,
413 calling for an ecosystem-based management approach (Ma *et al.*, 2010; Clausen *et al.*,
414 2013), which would account for habitat complementation behaviours in the species under
415 focus.

416

417 The restoration of a natural connexion between the sea and inland waters is the most
418 efficient option to create vast expands of suitable wetlands to waterbirds and the associated
419 trophic network. This solution is however out of reach where dykes warrant protection

420 against coastal erosion and secure human land use : saltpans then become the only
421 substitution habitat for waterbirds in highly artificialized matrices, such as in our study site,
422 elsewhere in the Mediterranean basin (Paracuellos *et al.*, 2002), in western United States
423 (Takekawa *et al.*, 2006; Athearn *et al.*, 2012) or in south-eastern Asia (Lei *et al.*, 2018). To
424 ensure the efficiency of this artificial conservation solution, our results suggest that saltpans
425 management choices should be based on the ecological preferences of functional guilds
426 rather than, as is often favoured by managers for practical or communication reasons, on
427 flagship species. Distinguishing ponds matching the requirements of mudflat-feeding birds,
428 including shorebirds and gulls, from others dedicated to water-feeding species (here only
429 terns) or to flamingo (due to its specific ecology) would likely capture most of this ecological
430 variability. However, this segregation might need to be adjusted seasonally to account for
431 the requirements of passing-through migrants and wintering species (Bellio *et al.*, 2009;
432 Tavares *et al.*, 2015). Based on our results, a viable strategy to promote the simultaneous co-
433 occurrence of these two guilds would be to maintain a mosaic involving low-salinity (20 to 40
434 g.L⁻¹) ponds with water levels below 20 cm and emerged mudflats (shorebirds and gulls),
435 mid-salinity (40-80 g.L⁻¹) ponds with 20 cm of water (mainly flamingo) and ponds with higher
436 water levels protecting colonies from predation and offering foraging areas to terns.

437

438 Furthermore, contrary to Athearn *et al.* (2012), we found no evidence that hypersaline
439 conditions above 40 g.L⁻¹ favour any of the functional guilds present on our study site. This
440 discrepancy suggests regional and intra-guild species-specific variations in the range of
441 suitable water properties. Any reduction of salinity should furthermore be applied reversibly
442 to avoid undesired cascading effects on the trophic network through eutrophication and

443 competition induced by local invaders (Takekawa *et al.*, 2015). Our results additionally
444 suggest that birds' sensitivity to salinity is exacerbated on foraging sites due to its structuring
445 impact on trophic networks, while water levels are more critical on roosting and breeding
446 sites. This pattern implies that species' optimum responses to water physico-chemical
447 parameters are not just explained by trophic requirements and physiological stress, but also
448 by contextual effects associated with habitat complementation behaviours, landscape,
449 predation pressure and disturbance, calling for management decisions based on local
450 estimations of species' requirements rather than on external results.

451

452 It is tempting to believe that a more complete assessment of water physico-chemical
453 characteristics, including direct measurements of photosynthetic activity, evaluation of prey
454 resources, and a finer spatial resolution in water level measurements would yield a more
455 biologically realistic model and more precise management recommendations. These data
456 are, however, rarely available and the required sampling effort may not be sustainable for
457 managers over the long-term at a frequency compatible with the rapid environmental
458 changes observed in saltpans (a few days to a few weeks). Our dataset is therefore
459 representative of the actual data available in practice to decide on management options,
460 which are largely tied to a single lever, water levels. The resulting water flow modulates
461 directly salinity and oxygen, which in turn determine prey availability to waterbirds
462 (Velasquez, 1992; Athearn *et al.*, 2012) and can thus be considered suitable proxies of the
463 dynamics of the trophic chains (Takekawa *et al.*, 2015). We suggest however that a two-tier
464 monitoring of environmental variables on saltpans, coupling regular measurements of these
465 synthetic proxies with more spaced exhaustive analyses of water and geolocated bird

466 records, would substantially improve model-based assessments of management practices
467 and subsequent choices.

468

469 As pressure on coastal wetlands increases worldwide under the effects of sea level rise and
470 artificialization (Ma *et al.*, 2009; Traill *et al.*, 2011; Osland *et al.*, 2016), decommissioned
471 saltpans appear as a cost-effective way to preserve breeding and stopping-over habitats for
472 waterbirds and their associated trophic network (Green *et al.*; Masero, 2003; Athearn *et al.*,
473 2012). Although their small size cannot compensate the loss of large extents of wetlands,
474 they serve as essential stepping stones in connectivity networks (Volenec & Dobson, 2019)
475 and can sustain viable populations of vulnerable species (Márquez-Ferrando *et al.*, 2014),
476 making the protection of these artificial habitats central to preserve waterbirds along coastal
477 landscapes undergoing strong human pressure. Our study showed however that in such
478 isolated contexts, waterbirds may be forced to use saltpans by the absence of any
479 alternative habitat, in spite of the stress implied by hypersaline conditions. Balancing water
480 levels and flow aimed to match the preferences of functional guilds instead of focusing on
481 flagship species may be an effective way to solve this issue, but this local-level management
482 also needs to consider supplementary factors which influence waterbirds' behaviour, such as
483 site size, vegetation and direct disturbance. Implementing multi-species, multi-scale
484 management schemes is therefore likely the key to sustain the role of saltpans as
485 substitution habitats facing anthropogenic pressure on coastal wetlands.

486

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488

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490

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647

648 **Supplementary Materials**

649

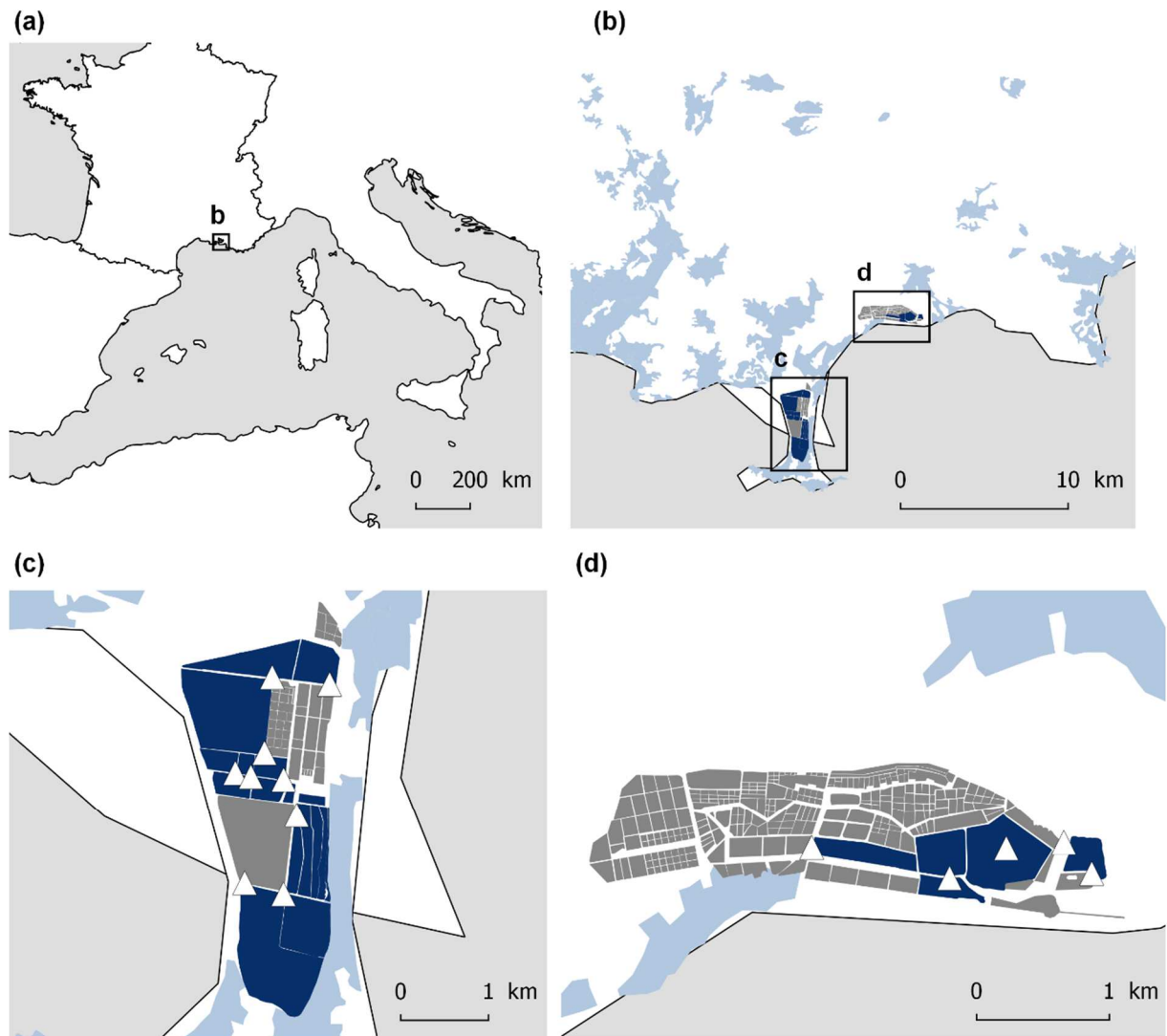
650 Appendix S1: Complementary information on the data set

651 Appendix S2: Complementary results on the model

652 Appendix S3: Script of the multispecies model in BUGS language

653

654 **Figures.**

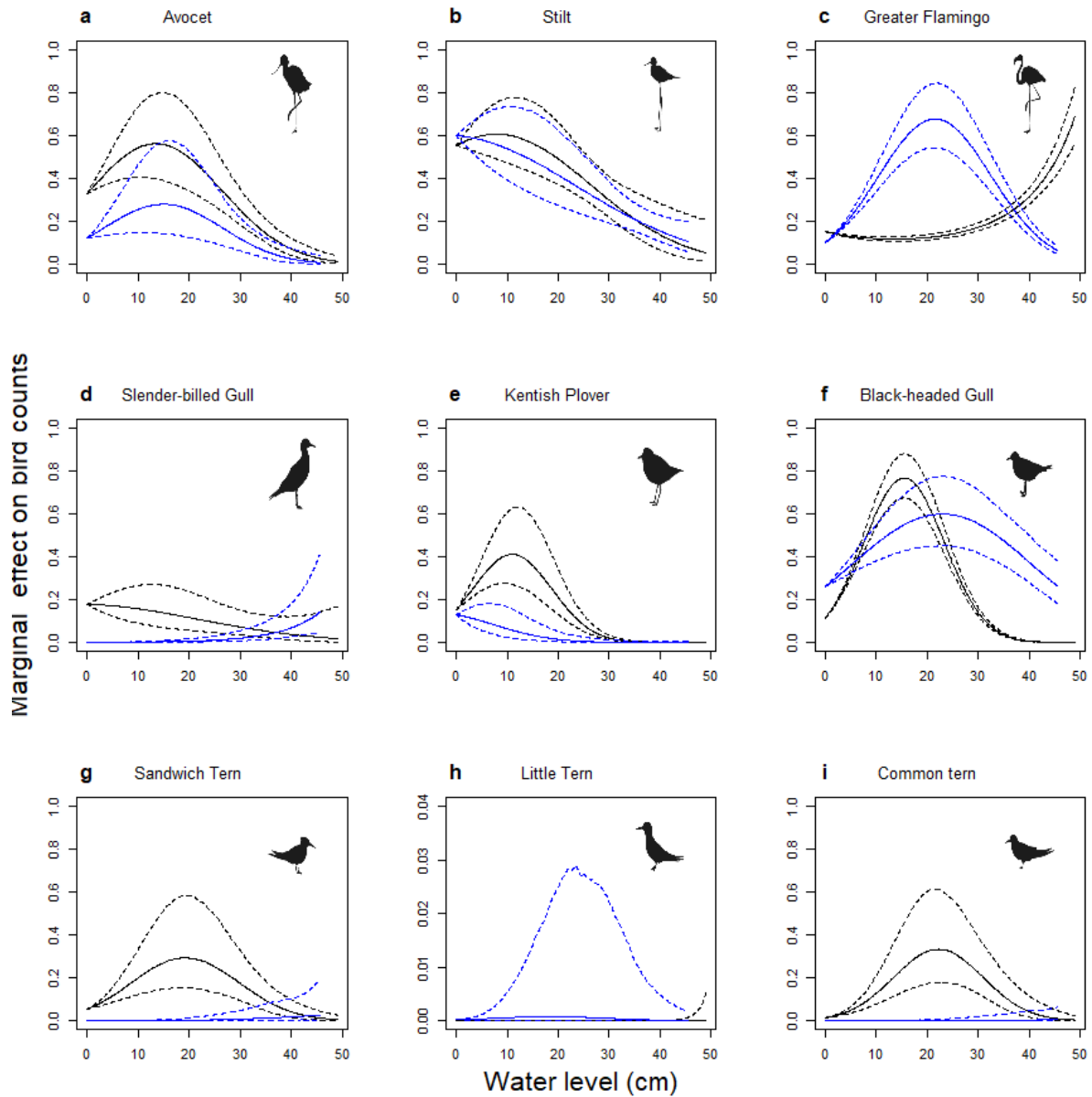


655

656 **Figure 1. Location and configuration of the study area.** The site is located on the French
 657 Mediterranean coast (a) and comprises two distinct saltpans located 3 km apart in a heavily
 658 urbanized seashore (b, urban areas in light blue). The two saltpans consist in mosaics of
 659 contiguous ponds that are connected together or to a belt canal (Pesquiers: c, Vieux Salins:
 660 d). The ponds included in the study are shown in dark blue, other ponds in grey. The white
 661 triangles indicate the location of the 14 measurement points for physico-chemical
 662 parameters and water levels.

663

664

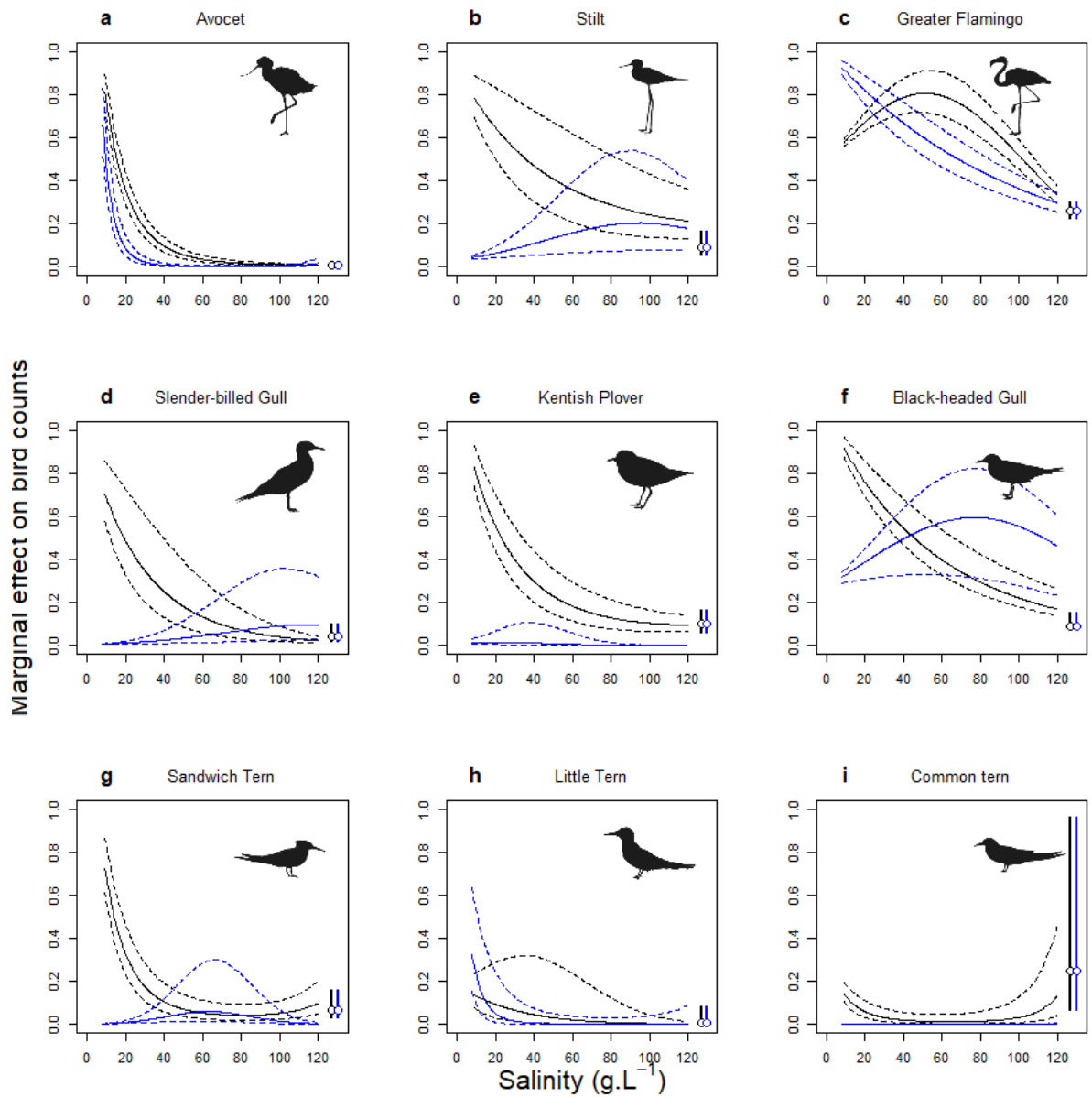


665

666 **Figure 2.** Waterbird responses to variations in water levels in Pesquiers (black) and Vieux
 667 Salins (blue). Curves depict marginal variations in species' counts on the two sites, as
 668 predicted by a hierarchical model, holding all other variables in the model constant.
 669 Responses are standardized by their maximum to ease comparisons (plain line = median,
 670 dashed line = 95% credible interval). Vertical scale magnified in h.

671

672



673

674 **Figure 3.** Waterbird responses to variations in salinity (censored at 120 g.L⁻¹) in Pesquiers
 675 (black) and Vieux Salins (blue). Curves depict marginal variations in species' counts on the
 676 two sites, as predicted by a hierarchical model, holding all other variables in the model
 677 constant. Responses are standardized by their maximum to ease comparisons (plain line =
 678 median, dashed line = 95% credible interval). The bars on the right indicate the estimate and

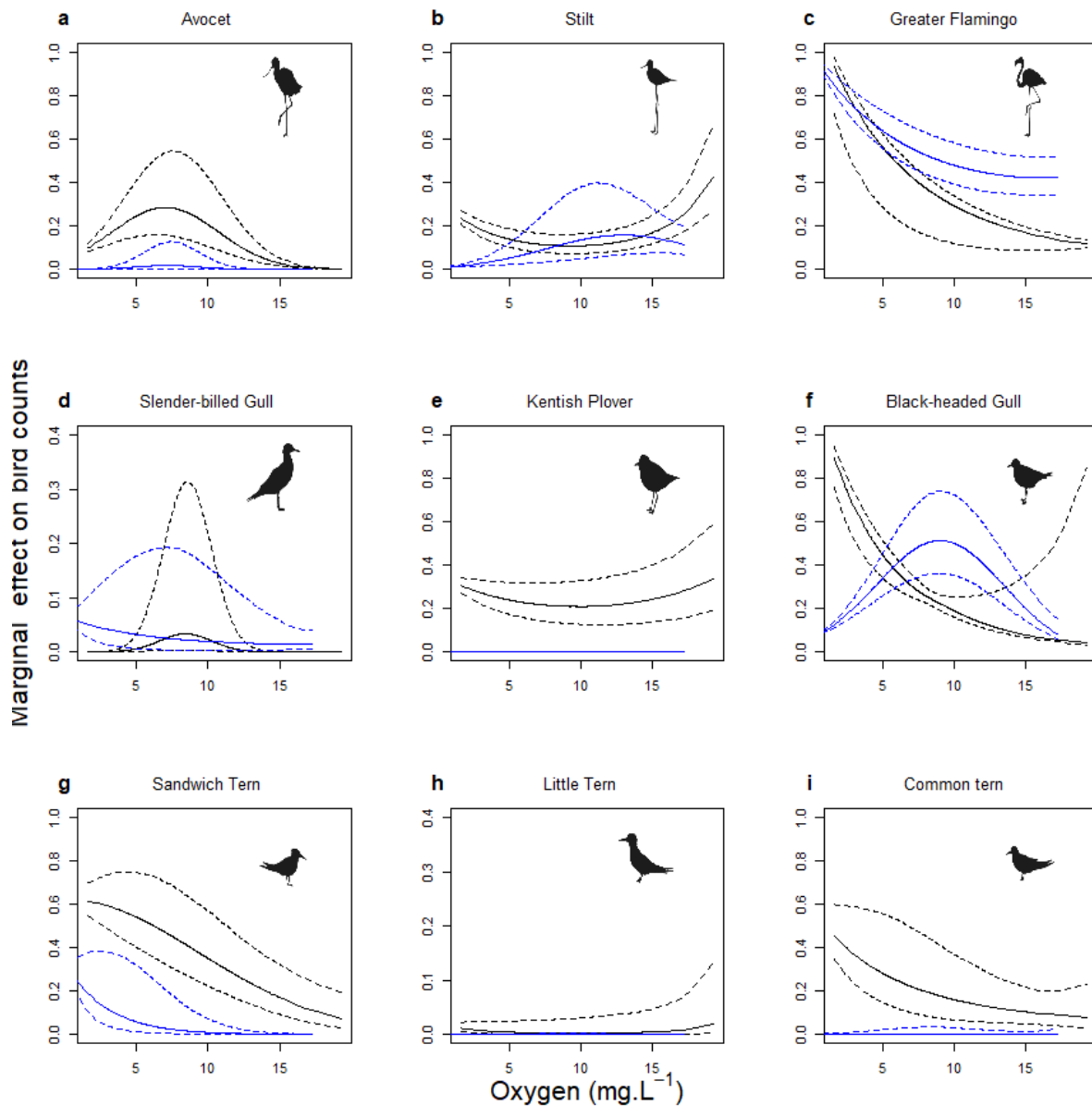
Waterbird responses to wetland management

679 95% credible interval of relative marginal species' abundance when salinity is above 120 g.L⁻¹

680 (α_{120} in equation 2).

681

682



683

684 **Figure 4.** Waterbird responses to variations in oxygen concentration (mg.L⁻¹) in Pesquiers

685 (black) and Vieux Salins (blue). Curves depict marginal variations in species' counts on the

Waterbird responses to wetland management

686 two sites, as predicted by a hierarchical model, holding all other variables in the model
687 constant. Responses are standardized by their maximum to ease comparisons (plain line =
688 median, dashed line = 95% credible interval). Vertical scale magnified in d and h.

689