

1 **Do birds of a feather flock together? Comparing habitat preferences of piscivorous**
2 **waterbirds in a lowland river catchment.**

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17 Running title: *Piscivorous bird habitat preferences*

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20 **Abstract**

21 Waterbirds can move into and exploit new areas of suitable habitat outside of their native
22 range. One such example is the little egret (*Egretta garzetta*), a piscivorous bird which has
23 colonized southern Britain within the last 30 years. Yet, habitat use by little egrets within
24 Britain, and how such patterns of habitat exploitation compare with native piscivores,
25 remains unknown. We examine overlap in habitat preferences within a river catchment
26 between the little egret and two native species, the grey heron (*Ardea cinera*) and great
27 cormorant (*Phalacrocorax carbo*). All species showed strong preferences for river habitat in
28 all seasons, with other habitat types used as auxiliary feeding areas. Seasonal use of multiple
29 habitat types is consistent with egret habitat use within its native range. We found strong
30 egret preference for aquatic habitats, in particular freshwaters, compared with pasture and
31 arable agricultural habitat. Egrets showed greater shared habitat preferences with herons, the
32 native species to which egrets are most morphologically and functionally similar. This is the
33 first study to quantify little egret habitat preferences outside of its native range.

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42 **Introduction**

43 The spread of species through human-facilitated introductions and natural range expansions
44 into new areas is a global driver of change in ecosystem structure, functioning and service
45 provision (Manchester & Bullock, 2000; Crowl et al., 2008). Such range shifts are
46 particularly prevalent for mobile taxa such as birds (La Sorte & Thompson, 2007).
47 Furthermore, interspecies differences in the rate of such range shifts can produce novel
48 species assemblages (Walther, 2010). A major challenge now facing ecologists is to
49 understand interactions between colonizing species and native species, in particular through
50 competition for shared habitat (Davis, 2003). In order to understand the effects of such range
51 shifts, both on avian biodiversity and on ecosystem structure, functioning and service
52 provision, we need to understand how colonizing species exploit habitat in new areas.

53 Piscivorous birds are highly mobile predators that show high plasticity in habitat use within a
54 landscape, exploiting a range of habitat types from river channels to flooded fields
55 (Kazantzidis & Goutner, 1996; Dimalexis et al., 1997). Piscivore foraging may reduce fish
56 populations and thus also affect fisheries and aquaculture (Kennedy & Greer, 1988; Feunteun
57 & Marion, 1994). Given these ecological and socioeconomic consequences of piscivores in
58 aquatic ecosystems, in order to manage and conserve such ecosystems it is vital to understand
59 how species will exploit aquatic habitats as they spread into new regions. Such understanding
60 is needed as range shifts have already been documented for a number of species of
61 piscivorous waterbirds (Lock & Cook, 1998). For example, the cattle egret (*Bulbulcus ibis*
62 L.), a species of wading bird from southern Europe and Africa, crossed the Atlantic and
63 became established in parts of the Americas during the 20th century (Burger, 1978; Arendt,
64 1988). A different example is provided by the white stork (*Ciconia ciconia* L.), which

65 following historical declines in range has begun to recolonize suitable habitat within Europe
66 (e.g. Denac, 2010).

67 Within temperate ecosystems species habitat preferences can vary over time due to changes
68 in environmental conditions. For example for birds within river catchments, seasonal changes
69 in river hydrology may alter habitat choice (Royan et al., 2013); for example, periodic
70 decreases in both water depth (Powell, 1987) and water velocity (Wood et al., 2013a) have
71 been found to promote use of lotic habitats for foraging by waterbirds. Consequently, patterns
72 of habitat preference and avoidance within a landscape are typically seasonal as birds switch
73 habitats to gain adequate food (Hafner & Britton, 1983; Voisin et al., 2005). Hence
74 piscivorous birds may be observed to use a range of habitat types within a landscape,
75 including rivers, lakes and flooded fields (Kazantzidis & Goutner, 1996; Dimalexis et al.,
76 1997).

77 In this study we examined habitat preferences of three species within an assemblage of
78 piscivorous birds in a lowland river catchment. The piscivore assemblage comprises two
79 native species, the great cormorant (*Phalacrocorax carbo* L.) and grey heron (*Ardea cinera*
80 L.), as well a recent coloniser, the little egret (*Egretta garzetta* L.). Little egrets in Britain
81 represent a natural colonisation event in its early stages, with the population increasing and
82 spreading northwards since arriving on the southern coast in the 1980s (Combridge & Parr,
83 1992; Lock & Cook, 1998; Musgrove, 2002). However, to date there has been no study
84 which has quantified the seasonal patterns of habitat use by little egrets within a colonised
85 area, nor how such patterns of habitat use compare with native piscivores.

86 Herein, we combine repeated field observations and statistical analyses to address two key
87 objectives regarding the habitat preferences of a piscivorous bird assemblage. These
88 objectives have been selected as they allow us to understand habitat use of the piscivorous

89 bird assemblage in both space and time. Such quantitative information is a prerequisite of
90 understanding both the ecological and socioeconomic consequences of little egret
91 colonization. Firstly, we quantified the habitat preferences of each species of piscivorous
92 bird. Secondly, we examined whether the habitat preferences of each species varied
93 seasonally.

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96 **Methods**

97 *Study system*

98 The River Frome (Dorset, UK) is a mesotrophic chalk river that flows through a mixed
99 pastoral and arable agriculture landscape. The main river channel and associated side streams
100 are shallow (typically < 1.5 m depth), with water velocity which varies between 0.4 m s⁻¹ in
101 August and 1.1 m s⁻¹ in December (Wood et al., 2013a). The river channel is dominated by
102 the submerged macrophyte stream water crowfoot (*Ranunculus penicillatus ssp.*
103 *pseudofluitans* Webster) (Wood et al., 2012). The river is bordered by pasture grass fields
104 dominated by perennial ryegrass (*Lolium perenne* L.) which flood during winter, and a
105 smaller number of arable fields in which wheat (*Triticum* spp.), barley (*Hordeum vulgare* L.)
106 and maize (*Zea mays* L.) are grown (Bettey, 1999; Wood et al., 2013b). These fields are
107 intersected by a network of permanently wetted drainage ditches, typically < 2 m wide (Cook
108 et al., 2003). The catchment also contains numerous shallow lakes and small patches of damp
109 woodland comprised of black alder (*Alnus glutinosa* L.) and willow (*Salix* spp.). The River
110 Frome discharges into the western region Poole Harbour known as the Wareham Channel, an
111 estuarine habitat of intertidal mudflats and saltmarshes dominated by common cordgrass

112 (*Spartina anglica* Hubb), purple glasswort (*Salicornia ramosissima* Woods) and common
113 saltmarsh grass (*Puccinellia maritima* Parl.) (Hannaford et al., 2006).

114 The piscivorous bird assemblage of the River Frome catchment is dominated by great
115 cormorants, grey herons and little egrets; recent overwinter surveys of the Frome valley by
116 Liley et al. (2008) reported mean counts of 16 cormorants, 13 grey herons and 37 little egrets.
117 The two only other piscivorous species were common kingfisher (*Alcedo atthis* L.) and
118 goosander (*Mergus merganser* L.). They were not considered in our study as previous
119 surveys of the catchment had recorded < 5 individuals (Liley et al., 2008). The River Frome
120 supports a diverse and productive fish community dominated by Atlantic salmon (*Salmo*
121 *salar* L.), brown trout (*Salmo trutta* L.), Eurasian dace (*Leuciscus leuciscus* L.), Eurasian
122 minnow (*Phoxinus phoxinus* L.), European bullhead (*Cottus gobio* L.), stone loach
123 (*Barbatula barbatula* L.), European eel (*Anguilla anguilla* L.), northern pike (*Esox lucius* L.)
124 and brook lamprey (*Lampetra planeri* Bloch) (Mann, 1989). These fish can access the
125 network of drainage ditches that run through the fields, and during periods of high water
126 levels may also enter flooded fields (Masters et al., 2002). The fish communities of lakes
127 within the Frome catchment are typical of those of southern England, containing common
128 roach (*Rutilus rutilus* L.), common bream (*Abramis brama* L.), tench (*Tinca tinca* L.),
129 European perch (*Perca fluviatilis* L.) and northern pike (Gee, 1978). In addition to salmon,
130 trout and eels, the estuary contains European seabass (*Dicentrarchus labrax* L.), lesser sand
131 eel (*Ammodytes tobianus* L.), thicklip grey mullet (*Chelon labrosus* Risso) and European
132 flounder (*Platichthys flesus* L.) (Jensen et al., 2005).

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134 *Catchment surveys*

135 We carried out two surveys of the catchment during September and December 2009, and
136 monthly between February and November 2010. No surveys were carried out during October,
137 November, and January in order to balance the numbers of surveys carried out in each season
138 and thus allow us to test for between-season differences in habitat references. During each
139 survey we visited all habitats within 500 m of the main river channel from the Wareham
140 Channel estuary (50°43'N, 02°02'W) 56.5 km upstream to Maiden Newton (50°46'N,
141 02°34'W) on the River Frome, and 12.0 km to Warren Heath (50°43'N, 02°12'W) on the
142 River Piddle. We identified all birds with a tripod-mounted Swarovski STS 80HD (20 x 60)
143 telescope (Swarovski AG, Austria). For all individuals observed we recorded the category of
144 habitat in which the bird was present: pasture, river, lake, ditch, estuary, arable, woodland or
145 urban, representing all of the available habitat types. Each survey was only conducted during
146 daylight hours. To avoid weather-related biases, surveys were not conducted during heavy
147 rain. To reduce the risk of either double counting or missing birds, great care was taken not to
148 disturb individuals during the surveys: surveyors moved slowly, using cover where possible,
149 and remained ≥ 200 m from observed birds (Carney & Sydeman, 1999). Cooke (1987) found
150 that grey herons were disturbed by an approaching human at a mean (\pm SE) distance of $178 \pm$
151 13 m, which suggests that our surveys should not have been affected by disturbance to the
152 birds. Such survey methodology has previously been used to assess landscape-level habitat
153 use of piscivorous birds (Fasola, 1986; Lane & Fujioka, 1998).

154

155 *Piscivore habitat preferences*

156 We estimated the spatial extent of each habitat category type within the study area (i.e.
157 habitat availability) via a visual assessment during a catchment survey (see Wood et al.,
158 2013b). We observed 8 habitat types; Arable, Ditch, Estuary, Lake, Pasture, River, Urban and

159 Woodland. The spatial extent of each habitat was recorded onto Explorer Maps 117 and
160 OL15 (Ordnance Survey, UK) from which the total area of each habitat was measured (\pm
161 0.001 km²). The calculation of two-dimensional area is a standardised way of comparing the
162 size different habitats available to foraging piscivorous birds (e.g. Chavez-Ramirez & Slack,
163 1995; Tourenq et al., 2001). Bird habitat preferences were examined by electivity analysis
164 (Wood et al., 2013b). For each month for each habitat category, Ivlev's electivity index (s)
165 was calculated as:

$$166 \quad s = (a - b) / (a + b)$$

167 where a was the percentage of the population using a given habitat, and b is the habitat area
168 as a percentage of the total available habitat area (Jacobs, 1974). Electivity values indicate
169 relative habitat use; values range between -1.0 (habitat never used) and +1.0 (habitat
170 exclusively used), with 0.0 representing habitat used in proportion with its availability (Ivlev,
171 1961). Hence positive and negative electivity values indicated habitat preference and
172 avoidance respectively. The monthly electivity values for a given habitat type were also
173 assigned to a season; spring (March, April), summer (May, June, July, August), autumn
174 (September, October), or winter (November, December, January, February). These seasons
175 reflected the annual changes in meteorological conditions within our study area (Wood et al.,
176 2013b).

177

178 *Statistical analyses*

179 For each habitat type we used linear models with Gaussian error structures to test the effects
180 of bird species, season, and the interaction between bird species and season, on electivity
181 values. We carried out all statistical analyses using R version 3.0.2 (R Development Core

182 Team, 2014), with data and residual exploration performed according to an established
183 protocol (Zuur et al., 2010), which confirmed that model assumptions were met. Electivity
184 values were rescaled between 0 and 1, then arcsine square root transformed to ensure model
185 residuals met the assumptions. Bird species was treated as a categorical variable consisting of
186 three levels: cormorant, heron and egret. Similarly, season was treated as a categorical
187 variable comprised of four levels: spring, summer, autumn and winter. Species were
188 considered to have a shared habitat preference if no significant effect of species on electivity
189 was detected. In contrast, where a significant effect of species on electivity values, these
190 species were judged not to share habitat preferences. For all comparisons a significant effect
191 was attributed where $p < 0.05$.

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194 **Results**

195 Over the study period we observed a mean (\pm 95 % CI) of 56 ± 19 piscivorous birds during
196 each survey (**Figure 1**). For each survey we recorded a mean (\pm 95 % CI) of 26 ± 12
197 cormorant, 12 ± 3 herons, and 18 ± 7 egrets. Cormorants, herons and egrets were observed to
198 use a mixture of river, lake, ditch, estuary and pasture habitats over the study period (**Figure**
199 **2**). The available habitat within the catchment was comprised of pasture fields (46.1 %),
200 estuary (10.3 %), river (4.5 %), ditch (3.4 %), and lake (1.0 %). The remainder (34.7 %) was
201 comprised of arable fields, woodland and urban areas, but these were never used by the birds
202 (i.e. electivity was -1.0 for all species in all months) and so were excluded from further
203 analyses.

204 For all three species our electivity values indicated both preferred and avoided habitats
205 (**Figure 3**). All three species showed strong preferences for river habitat in all four seasons,
206 with the strongest preference observed in spring for cormorants and egrets, and in summer for
207 herons. Our linear models, comprising species, and interactions between species and seasons,
208 explained the variance in electivity values well for all habitat types except lake (**Table 1**). We
209 found strong between-season differences in electivity for river habitat, with stronger
210 preferences detected in spring, summer and winter relative to autumn (**Table 2; Figure 3**).
211 Electivity for estuary habitat differed between seasons, with lower values in spring relative to
212 all other seasons, and lower values in winter relative to summer and autumn. We detected
213 significant between-species differences in estuary electivity, as cormorants and egrets showed
214 stronger preferences than herons which typically avoided the estuary (**Table 2; Figure 3**).
215 Furthermore, cormorants showed a stronger preference for estuarine habitat than egrets. We
216 also found significant effects of interactions between species and seasons on electivity values.
217 Herons in spring showed lower electivity for estuarine habitat compared with cormorants in
218 autumn and egrets in summer and autumn.

219 Herons and egrets showed strong preferences for ditch habitat, in contrast to cormorants, and
220 hence we found strong between-species differences in ditch electivity. Summer electivity
221 values were significantly lower relative to autumn. We also detected interactions between
222 species and seasons, with cormorants in summer showing lower electivity than egrets in
223 spring and autumn. For pasture fields we found significant between-species differences, with
224 lower values of electivity for cormorants compared with herons and egrets. We also detected
225 lower values for summer and autumn relative to winter, and lower values for summer relative
226 to spring (**Table 2; Figure 3**).

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229 **Discussion**

230 In this study we demonstrated strong overlap in habitat preferences of native and colonizing
231 piscivorous birds in a lowland river catchment. Furthermore, this is the first study to quantify
232 the habitat preferences of the little egret outside of its native range. Within the recently
233 colonised River Frome little egrets displayed strong preferences for river habitat with some
234 lesser seasonal preferences for lake, estuary, ditch and pasture. Such seasonal use of multiple
235 habitat types has been reported for the little egret at lower latitudes within its native range
236 (Kazantzidis & Goutner, 1996; Dimalexis et al., 1997; Lombardini et al., 2001). Our finding
237 of strong egret preference for aquatic habitats, in particular freshwaters, compared with
238 pasture and arable agricultural habitat was also consistent with observations from within the
239 native range of the little egret (Kazantzidis & Goutner, 1996; Lombardini et al., 2001). The
240 little egrets which have recently colonised the River Frome, and similar lowland river
241 catchments in southern England, are primarily exploiting the prey resources available in river
242 habitat, with other aquatic and terrestrial habitats of lesser importance. Given the continued
243 northwards range expansion, knowledge of egret habitat preferences will aid in understanding
244 their exploitation of newly-colonized landscapes (Lock & Cook, 1998; Musgrove, 2002).
245 There is no evidence that the arrival and subsequent colonization of southern England by the
246 little egret has had an effect on the grey heron. The UK grey heron population size has
247 remained relatively constant over the period of little egret colonization (Austin et al., 2014).
248 All species showed strong preferences for river habitat with some seasonal preferences for
249 other feeding habitats, which suggests that river habitat was the preferred feeding habitat,
250 with other habitat types used as auxiliary feeding areas. Egrets showed greater shared habitat
251 preferences with herons, the native species to which egrets are most morphologically and

252 functionally similar (Kushlan, 1981). We found no differences between egrets and herons in
253 electivity for river, lake, ditch and pasture habitats. Egrets and cormorants exhibited no
254 differences in electivity only for river and lake habitats. Non-native egrets and native herons
255 both showed strong preferences for river habitat, with lesser seasonal preferences for lake and
256 ditch habitat. In contrast, egrets showed the greatest differences in habitat preferences when
257 compared to cormorants. As cormorants foraging strategy of pursuit-diving is better suited to
258 open-water habitats, it is unsurprising that, unlike egrets and herons, cormorants did not show
259 preferences for ditch or flooded pasture fields.

260 We found some evidence that the habitat preferences of piscivores varied seasonally.
261 Seasonal variations in electivity were detected for river, estuary, ditch and pasture habitats.
262 Such seasonal variations may reflect the seasonal changes in prey availability and hydrology
263 associated with the different habitat types and in particular the river as the principal feeding
264 habitat (Mann, 1989; Wood et al., 2013a). In particular, the greater use during winter of
265 pasture fields is probably due to these fields becoming partially submerged as the main river
266 floods, which creates a suitable feeding habitat for wading piscivores such as herons and
267 egrets (Kushlan, 1981). The lower electivity for river habitat in autumn may have resulted
268 from the arrival of large numbers of migrants which gather in the estuary in autumn before
269 dispersing to overwintering areas (Holt et al., 2012). Indeed, the decline in river electivity
270 was greatest for the two species, cormorants and egrets, which showed increased numbers in
271 the estuary. Unlike the ditches, estuary and flooded fields, the lakes were not directly
272 connected to the main river and so were not affected by such hydrological changes, which
273 may account for the lack of seasonal changes in electivity for lake habitat.

274 Birds can disperse within a landscape to take advantage of new areas of suitable habitat,
275 potentially expanding beyond their native range (Burger, 1978; Arendt, 1988). In particular,

276 climate change is facilitating the rapid northwards range shift of many avian species (Hitch &
277 Leberg, 2007; Chen et al., 2011). In order to understand the effects of such range shifts, both
278 on biodiversity and on ecosystem structure, functioning and service provision, we need to
279 understand how colonising species exploit habitat in new areas. In this study we have
280 demonstrated how an electivity index, informed by the types of data routinely collected for
281 avian populations (e.g. Holt et al., 2012), can be used to quantify and compare the habitat
282 preferences of different species.

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292 **References**

293 Arendt, W. J., 1988. Range expansion of the cattle egret (*Bubulcus ibis*) in the Greater
294 Caribbean Basin. Colonial Waterbirds 11: 252-262.

295 Austin, G.E., W. J. Read, N. A. Calbrade, H. J. Mellan, A. J. Musgrove, W. Skellorn, R. D.
296 Hearn, D. A. Stroud, S. R. Wotton & C. A. Holt, 2014. Waterbirds in the UK 2011/12: The
297 Wetland Bird Survey. BTO/RSPB/JNCC, Thetford.

298 Bettey, J., 1999. The development of water meadows in the southern counties. In Cook, H. &
299 T. Williamson (eds), *Water Management in the English Landscape: Field, Marsh and*
300 *Meadow*. Edinburgh University Press, Edinburgh: 179-195.

301 Burger, J., 1978. Competition between cattle egrets and native North American herons, egrets
302 and ibises. *Condor* 80: 15-23.

303 Carney, K. M. & W. J. Sydeman, 1999. A review of human disturbance effects on nesting
304 colonial waterbirds. *Waterbirds* 22: 68-79.

305 Chavez-Ramirez, F. & R. D. Slack, 1995. Differential use of coastal marsh habitats by non-
306 breeding wading birds. *Colonial Waterbirds* 18: 166-171.

307 Chen, I. C., J. K. Hill, R. Ohlemüller, D. B. Roy & C. D. Thomas, 2011. Rapid range shifts of
308 species associated with high levels of climate warming. *Science* 333: 1024-1026.

309 Combridge, P. & C. Parr, 1992. Influx of little egrets in Britain and Ireland in 1989. *British*
310 *Birds* 85: 16-21.

311 Cook, A. S. 1987. Disturbance by anglers of birds at Grafham Water. In Maitland, P. S. & A.
312 K. Turner (eds), *Angling and Wildlife in Fresh Waters*. Institute of Terrestrial Ecology,
313 Cumbria: 15-22.

314 Cook, H., K. Stearne & T. Williamson, 2003. The origins of water meadows in England. *The*
315 *Agricultural History Review* 51: 155-162.

316 Crowl, T. A., T. O. Crist, R. R. Parmenter, G. Belovsky & A. E. Lugo, 2008. The spread of
317 invasive species and infectious disease as drivers of ecosystem change. *Frontiers in Ecology*
318 *& Environment* 6: 238-246.

319 Davis, M. A., 2003. Biotic globalisation: does competition from introduced species threaten
320 biodiversity? *Bioscience* 53: 481-489.

321 Denac, D., 2010. Population dynamics of the white stork *Ciconia ciconia* in Slovenia
322 between 1999 and 2010. *Acrocephalus* 31: 101-114.

323 Dimalexis A, M. Pyrovesti & S. Sgardelis, 1997. Foraging ecology of the grey heron (*Ardea*
324 *cinerea*), great egret (*Ardea alba*) and little egret (*Egretta garzetta*) in response to habitat, at
325 2 Greek wetlands. *Colonial Waterbirds* 20: 261-272.

326 Fasola, M., 1986. Resource use of foraging herons in agricultural and nonagricultural habitats
327 in Italy. *Colonial Waterbirds* 9: 139-148.

328 Feunteun, E. & L. Marion, 1994. Assessment of grey heron predation on fish communities:
329 the case of the largest European colony. *Hydrobiologia* 279/280: 327-344.

330 Gee, A. S., 1978. The distribution and growth of coarse fish in gravel-pit lakes in south-east
331 England. *Freshwater Biology* 8: 385-394.

332 Hafner, H. & R. H. Britton, 1983. Changes of foraging sites by nesting little egrets (*Egretta*
333 *garzetta* L.) in relation to food supply. *Colonial Waterbirds* 6: 24-30.

334 Hannaford, J., E. H. Pinn & A. Diaz, 2006. The impact of sika deer grazing on the vegetation
335 and infauna of Arne saltmarsh. *Marine Pollution Bulletin* 53: 56-62.

336 Hitch, A. T. & P. L. Leberg, 2007. Breeding distributions of North American bird species
337 moving north as a result of climate change. *Conservation Biology* 21: 534-539.

338 Holt, C., G. Austin, N. Calbrade, H. Mellan, R. Hearn, D. Stroud, S. Wotton & A. Musgrove,
339 2012. Waterbirds in the UK 2010/11: The Wetland Bird Survey. BTO/RSPB/JNCC,
340 Thetford.

341 Ivlev, V. S., 1961. Experimental ecology of the feeding of fishes. Yale University Press,
342 Connecticut.

343 Jacobs, J., 1974. Quantitative measurements of food selection. A modification of the forage
344 ratio and Ivlev's electivity index. *Oecologia* 14: 413-417.

345 Jensen, A., I. Carrier & N. Richardson, 2005. Marine fisheries of Poole Harbour. In
346 Humphreys, J. & V. May (eds), *The Ecology of Poole Harbour*. Elsevier, Amsterdam: 195-
347 203.

348 Kazantzidis, S. & V. Goutner, 1996. Foraging ecology and conservation of feeding habitats
349 of little egrets (*Egretta garzetta*) in the Axios River Delta, Macedonia, Greece. *Colonial*
350 *Waterbirds* 19: 115-121.

351 Kennedy, G. J. A. & J. E. Greer, 1988. Predation by cormorants *Phalacrocorax carbo* (L) on
352 the salmonids populations of an Irish river. *Aquaculture Research* 19: 159-170.

353 Kushlan, J. A., 1981. Resource use strategies of wading birds. *Wilson Bulletin* 93: 145-163.

354 Lane, S. J. & M. Fujioka, 1998. The impact of changes in irrigation practices on the
355 distribution of forging egrets and herons (Ardeidae) in the rice fields of central Japan.
356 *Biological Conservation* 83: 221-230.

357 La Sorte, F. A. & F. R. Thompson, 2007. Poleward shifts in winter ranges of North American
358 birds. *Ecology* 88: 1803-1812.

359 Liley, D., J. Sharp & J. Baker, 2008. Wetland bird survey results for the Frome Valley: the
360 winter 2007–2008. *Footprint Ecology & Purbeck Keystone Project*, Dorset.

361 Lock, L. & K. Cook, 1998. The little egret in Britain: a successful colonist. *British Birds* 95:
362 273-280.

363 Lombardini, K., R. E. Bennetts & C. Tourenq, 2001. Foraging success and foraging habitat
364 use by cattle egrets and little egrets in the Camargue, France. *Condor* 103: 38-44.

365 Manchester, S. J. & J. M. Bullock, 2000. The impacts of non-native species on UK
366 biodiversity and the effectiveness of control. *Journal of Applied Ecology* 37: 845-864

367 Mann, R. H. K., 1989. Fish population dynamics in the River Frome, Dorset. *Regulated*
368 *Rivers: Research & Management* 4: 165-177.

369 Masters, J. E. G., J. S. Welton, W. R. C. Beaumont, K. H. Hodder, A. C. Pinder, R. E. Gozlan
370 & M. Ladle, 2002. Habitat utilisation by pike *Esox lucius* L. during winter floods in a
371 southern English chalk river. *Developments in Hydrobiology* 165: 185-191.

372 Musgrove, A. J., 2002. The non-breeding status of the little egret in Britain. *British Birds* 95:
373 62-80.

374 Powell, G. V. N., 1987. Habitat use by wading birds in a subtropical estuary: implications of
375 hydrography. *Auk* 104: 740-749.

376 R Development Core Team, 2014. R: a language and environment for statistical computing.
377 [3.0.2]. R Foundation for Statistical Computing.

378 Royan, A., D. M. Hannah, S. J. Reynolds, D. G. Noble & J. P. Sadler, 2013. Avian
379 community responses to variability in river hydrology. *PLoS ONE* 8: e83221.

380 Tourenq, C., R. E. Bennetts, H. Kowalski, E. Vialet, J. L. Lucchesi, Y. Kayser & P.
381 Isenmann, 2001. Are ricefields a good alternative to natural marshes for waterbird
382 communities in the Camargue, southern France? *Biological Conservation* 100: 335-343.

383 Voisin, C., J. Godin & A. Fleury, 2005. Status and behaviour of little egrets wintering in
384 western France. *British Birds* 98: 468-475.

385 Walther, G. R., 2010. Community and ecosystem responses to recent climate change.
386 Philosophical Transactions of the Royal Society B – Biological Sciences 365: 2019-2024

387 Wood, K. A., R. A. Stillman, R. T. Clarke, F. Daunt & M. T. O’Hare, 2012. Understanding
388 plant community responses to combinations of biotic and abiotic factors in different phases of
389 the plant growth cycle. PLoS ONE 7: e49824.

390 Wood, K. A., R. A. Stillman, D. Wheeler, S. Groves, C. Hambly, J. R. Speakman, F. Daunt &
391 M. T. O’Hare, 2013a. Go with the flow: water velocity regulates herbivore foraging decisions
392 in river catchments. Oikos 122: 1720-1729.

393 Wood, K. A., R. A. Stillman, T. Coombs, C. McDonald, F. Daunt & M. T. O’Hare, 2013b.
394 The role of season and social grouping on habitat use by mute swans (*Cygnus olor*) in a
395 lowland river catchment. Bird Study 60: 229-237.

396 Zuur, A. F., E. N. Ieno & C. S. Elphick, 2010. A protocol for data exploration to avoid
397 common statistical problems. Methods in Ecology and Evolution 1: 3-14.

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405 **TABLES**

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407 **Table 1:** The fit of linear models to the electivity data associated with each habitat. The
 408 model took the form $E = \text{Species} + \text{Season} + \text{Species}*\text{Season}$

Habitat	<i>F</i>	d.f.	<i>p</i>	R^2_{adj}
River	4.72	35	< 0.001	53.9 %
Lake	0.46	35	0.908	-20.3 %
Estuary	18.93	35	< 0.001	84.9 %
Ditch	7.04	35	< 0.001	65.5 %
Pasture	6.59	35	< 0.001	63.7 %

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420 **Table 2:** The influence of bird species, season and the species*season interaction on the
 421 electivity values for five habitat categories, as illustrated by linear models. Differences within
 422 factors are indicated by non-overlapping confidence intervals in Figure 3.

Habitat	Factor	<i>F</i>	<i>p</i>
River	Species	0.42	0.664
	Season	11.75	< 0.001
	Species*Season	2.65	0.108
Lake	Species	0.67	0.522
	Season	0.56	0.644
	Species*Season	0.34	0.906
Estuary	Species	48.95	< 0.001
	Season	26.00	< 0.001
	Species*Season	5.38	0.001
Ditch	Species	23.56	< 0.001
	Season	6.34	0.003
	Species*Season	1.88	0.125
Pasture	Species	22.75	< 0.001
	Season	5.05	0.007
	Species*Season	1.98	0.108

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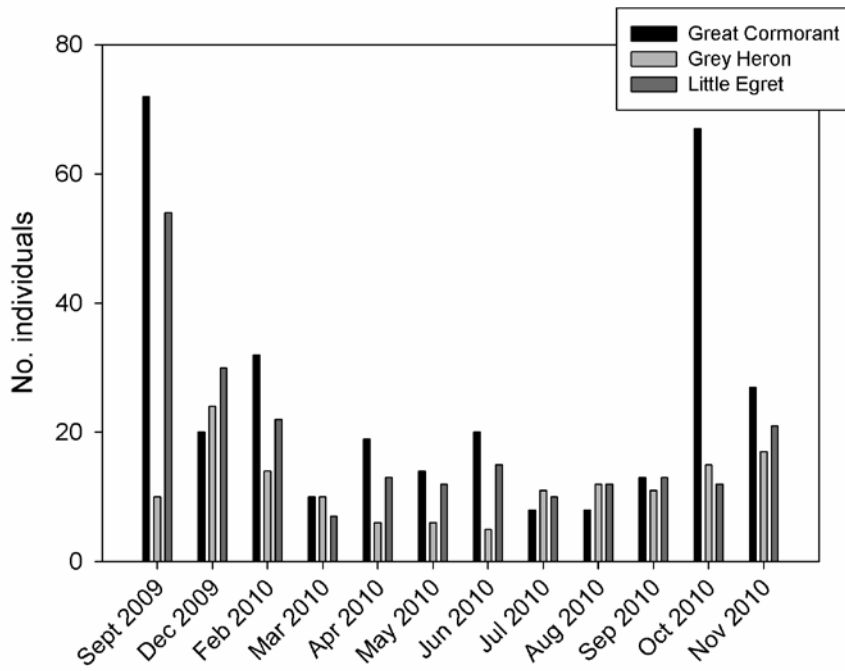
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429 **FIGURES**

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431 **Figure 1:** The numbers of individuals of three piscivorous birds recorded within the River
432 Frome catchment between September 2009 and November 2010.



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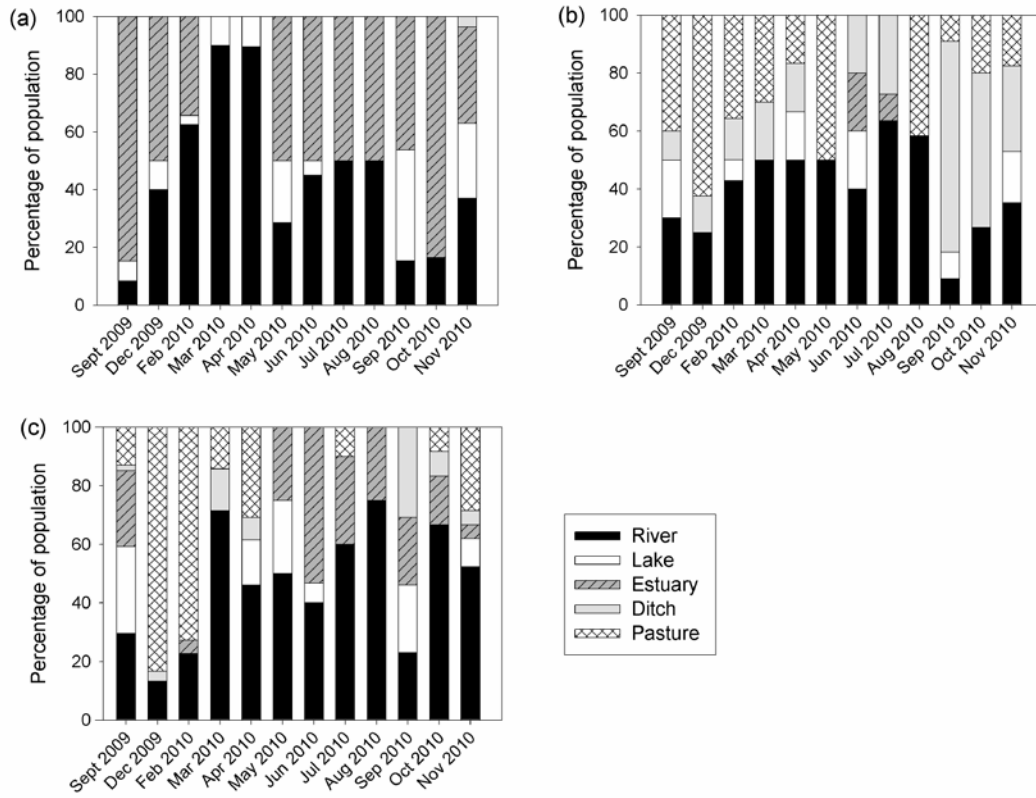
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442 **Figure 2:** The percentage of the total numbers of (a) great cormorants, (b) grey herons, and
443 (c) little egrets, observed on each habitat type during each season.



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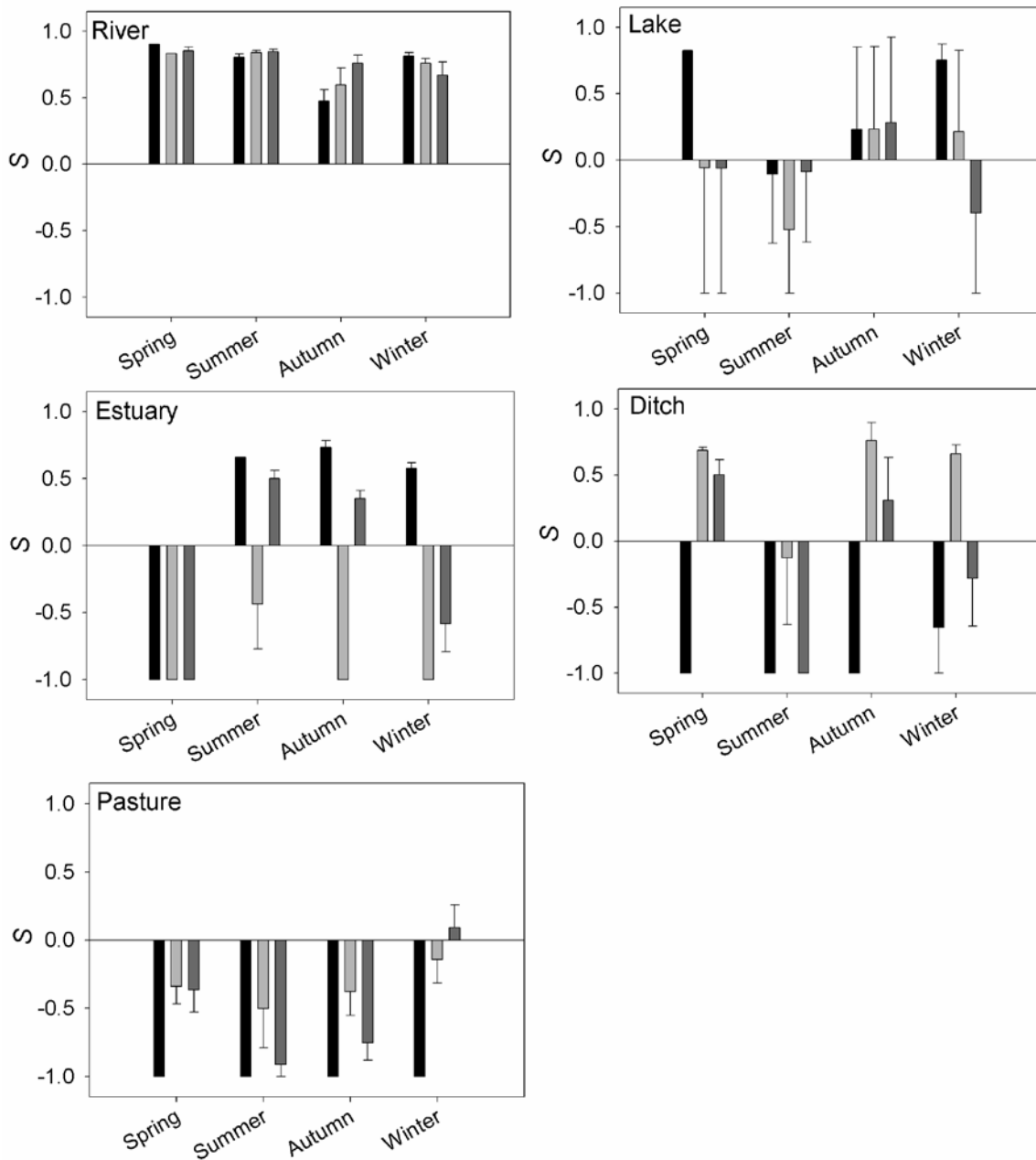
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452 **Figure 3:** Seasonal comparisons of the mean (\pm se) habitat electivity (s) of great cormorants
453 (black bars), grey herons (light grey bars) and little egrets (dark grey bars). Electivity values
454 indicate relative habitat use; values range between -1.0 (habitat never used) and +1.0 (habitat
455 exclusively used), with 0.0 representing habitat used in proportion with its availability.



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