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

Kevin A. Wood & Richard A. Stillman

Faculty of Science & Technology, Bournemouth University, Dorset, BH12 5BB, United Kingdom.

Corresponding author: (+44)1202966782; kevinwoodecology@hotmail.co.uk

Key words: *Aquatic landscape; Avian colonization*; *Electivity index; Habitat selection; Ornitholimnology; Wading birds*

Running title: *Piscivorous bird habitat preferences*

Abstract

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

Introduction

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

Piscivorous birds are highly mobile predators that show high plasticity in habitat use within a landscape, exploiting a range of habitat types from river channels to flooded fields (Kazantzidis & Goutner, 1996; Dimalexis et al., 1997). Piscivore foraging may reduce fish populations and thus also affect fisheries and aquaculture (Kennedy & Greer, 1988; Feunteun & Marion, 1994). Given these ecological and socioeconomic consequences of piscivores in aquatic ecosystems, in order to manage and conserve such ecosystems it is vital to understand how species will exploit aquatic habitats as they spread into new regions. Such understanding is needed as range shifts have already been documented for a number of species of piscivorous waterbirds (Lock & Cook, 1998). For example, the cattle egret (*Bulbulcus ibis* L.), a species of wading bird from southern Europe and Africa, crossed the Atlantic and became established in parts of the Americas during the 20th century (Burger, 1978; Arendt, 1988). A different example is provided by the white stork (*Ciconia ciconia* L.), which following historical declines in range has begun to recolonize suitable habitat within Europe (e.g. Denac, 2010).

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

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

Herein, we combine repeated field observations and statistical analyses to address two key objectives regarding the habitat preferences of a piscivorous bird assemblage. These objectives have been selected as they allow us to understand habitat use of the piscivorous bird assemblage in both space and time. Such quantitative information is a prerequisite of understanding both the ecological and socioeconomic consequences of little egret colonization. Firstly, we quantified the habitat preferences of each species of piscivorous bird. Secondly, we examined whether the habitat preferences of each species varied seasonally.

Methods

Study system

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

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

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

Catchment surveys

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

Piscivore habitat preferences

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

Woodland. The spatial extent of each habitat was recorded onto Explorer Maps 117 and OL15 (Ordinance Survey, UK) from which the total area of each habitat was measured (± 0.001 km^2). The calculation of two-dimensional area is a standardised way of comparing the size different habitats available to foraging piscivorous birds (e.g. Chavez-Ramirez & Slack, 1995; Tourenq et al., 2001). Bird habitat preferences were examined by electivity analysis (Wood et al., 2013b). For each month for each habitat category, Ivlev's electivity index (*s*) was calculated as:

$$s = (a - b) / (a + b)$$

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

Statistical analyses

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

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

Results

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

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

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

Discussion

In this study we demonstrated strong overlap in habitat preferences of native and colonizing piscivorous birds in a lowland river catchment. Furthermore, this is the first study to quantify the habitat preferences of the little egret outside of its native range. Within the recently colonised River Frome little egrets displayed strong preferences for river habitat with some lesser seasonal preferences for lake, estuary, ditch and pasture. Such seasonal use of multiple habitat types has been reported for the little egret at lower latitudes within its native range (Kazantzidis & Goutner, 1996; Dimalexis et al., 1997; Lombardini et al., 2001). Our finding of strong egret preference for aquatic habitats, in particular freshwaters, compared with pasture and arable agricultural habitat was also consistent with observations from within the native range of the little egret (Kazantzidis & Goutner, 1996; Lombardini et al., 2001). The little egrets which have recently colonised the River Frome, and similar lowland river catchments in southern England, are primarily exploiting the prey resources available in river habitat, with other aquatic and terrestrial habitats of lesser importance. Given the continued northwards range expansion, knowledge of egret habitat preferences will aid in understanding their exploitation of newly-colonized landscapes (Lock & Cook, 1998; Musgrove, 2002). There is no evidence that the arrival and subsequent colonization of southern England by the little egret has had an effect on the grey heron. The UK grey heron population size has remained relatively constant over the period of little egret colonization (Austin et al., 2014).

All species showed strong preferences for river habitat with some seasonal preferences for other feeding habitats, which suggests that river habitat was the preferred feeding habitat, with other habitat types used as auxiliary feeding areas. Egrets showed greater shared habitat preferences with herons, the native species to which egrets are most morphologically and functionally similar (Kushlan, 1981). We found no differences between egrets and herons in electivity for river, lake, ditch and pasture habitats. Egrets and cormorants exhibited no differences in electivity only for river and lake habitats. Non-native egrets and native herons both showed strong preferences for river habitat, with lesser seasonal preferences for lake and ditch habitat. In contrast, egrets showed the greatest differences in habitat preferences when compared to cormorants. As cormorants foraging strategy of pursuit-diving is better suited to open-water habitats, it is unsurprising that, unlike egrets and herons, cormorants did not show preferences for ditch or flooded pasture fields.

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

Birds can disperse within a landscape to take advantage of new areas of suitable habitat, potentially expanding beyond their native range (Burger, 1978; Arendt, 1988). In particular, climate change is facilitating the rapid northwards range shift of many avian species (Hitch & Leberg, 2007; Chen et al., 2011). In order to understand the effects of such range shifts, both on biodiversity and on ecosystem structure, functioning and service provision, we need to understand how colonising species exploit habitat in new areas. In this study we have demonstrated how an electivity index, informed by the types of data routinely collected for avian populations (e.g. Holt et al., 2012), can be used to quantify and compare the habitat preferences of different species.

Acknowledgements

We thank Lucy Mulholland for field assistance and the riparian landowners for access to the study area. Stuart Halse and two anonymous reviewers provided valuable feedback on an earlier version of this manuscript. We are grateful to the Freshwater Biological Association and the Centre for Ecology & Hydrology for logistical support.

References

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

TABLES

Table 1: The fit of linear models to the electivity data associated with each habitat. The model took the form *E* = Species + Season + Species*Season

Habitat	***F***	**d.f.**	***p***	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 %

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

Habitat	**Factor**	***F***	***p***
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

FIGURES

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

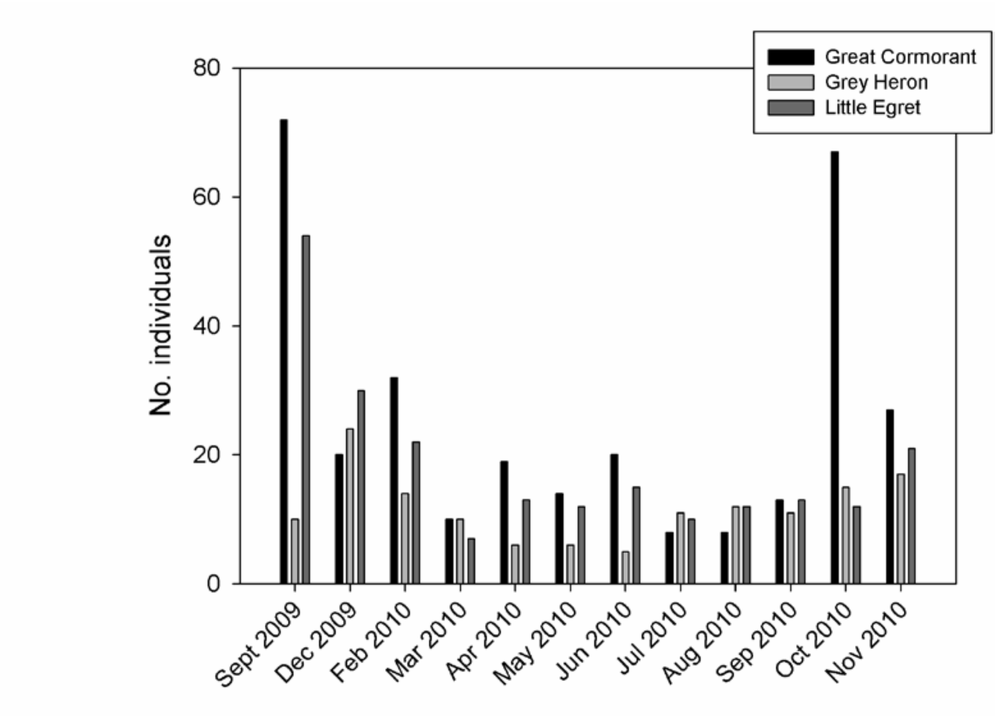

Figure 2: The percentage of the total numbers of (a) great cormorants, (b) grey herons, and (c) little egrets, observed on each habitat type during each season.

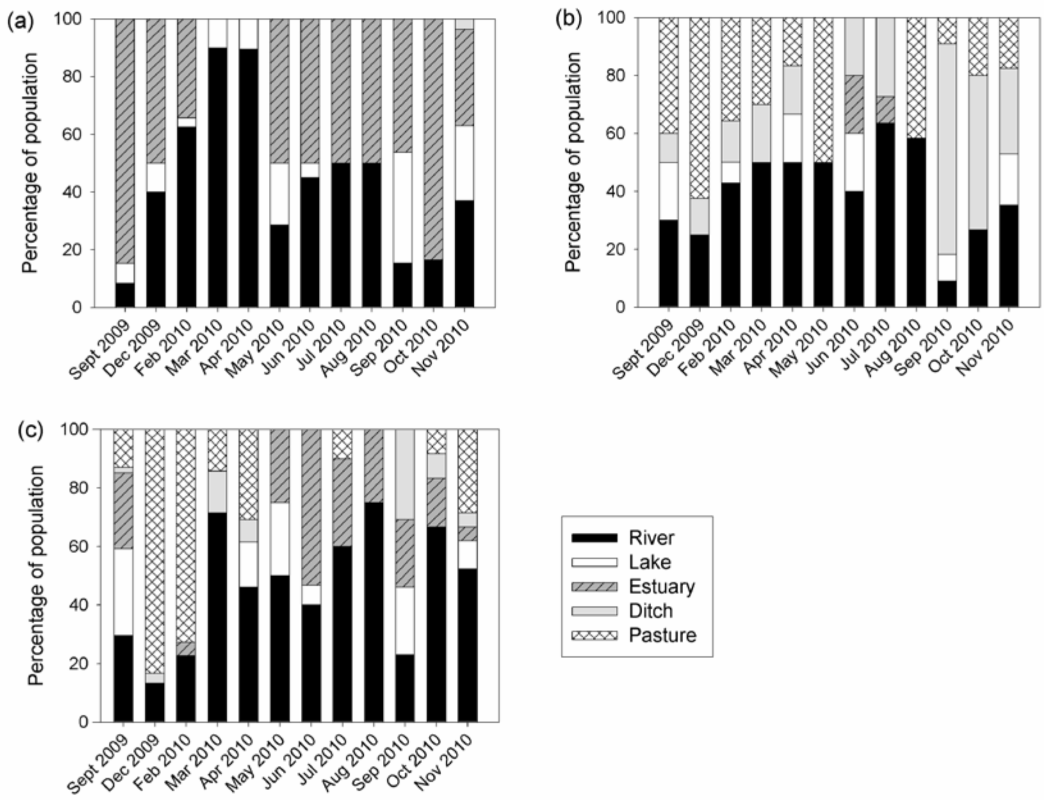

Figure 3: Seasonal comparisons of the mean (± se) habitat electivity (*s*) of great cormorants (black bars), grey herons (light grey bars) and little egrets (dark grey bars). Electivity values indicate relative habitat use; values range between -1.0 (habitat never used) and +1.0 (habitat exclusively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