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Source: The Condor, 118(1) : 46-56

Published By: American Ornithological Society

URL: https://doi.org/10.1650/CONDOR-14-117.1

THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 118, 2016, pp. 46–56
DOI: 10.1650/CONDOR-14-117.1

RESEARCH ARTICLE

Selection of human-influenced and natural wetlands by Great Egrets at multiple scales in the southeastern USA

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Submitted July 26, 2015; Accepted September 17, 2015; Published November 18, 2015

ABSTRACT

Wetlands constructed or modified by humans (human-influenced wetlands [HIW]) constitute an increasing proportion of wetland habitat in the USA. It is unclear to what extent HIW (e.g., ponds, reservoirs, impoundments, aquaculture sites, and flooded agricultural fields) provide equivalent habitat for wading birds compared with the natural wetlands they are replacing or augmenting. We compared selection of HIW with natural wetlands by Great Egrets (*Ardea alba*) in 2 regions containing high proportions of wetlands (73% Louisiana [LA], 39% South Carolina [SC]) and similar proportions of HIW (4.3% LA, 4.5% SC). Great Egrets in LA ($n = 11$) and SC ($n = 19$) were tracked using satellite transmitters for up to 1 year to assess selection of home ranges and foraging sites. We also compared selection of flooded agricultural fields vs. natural wetlands as foraging sites from aerial surveys of untagged egrets in LA. In SC, tagged birds showed stronger selection for HIW than natural wetlands as foraging sites, driven by use of small man-made ponds (39.9% of foraging observations), but home ranges did not contain a disproportionate area of ponds. In LA, tagged birds showed no overall selection of HIW at either scale, but unmarked egrets showed strong selection for crayfish aquaculture ponds, especially during drawdown. Rice fields provided only a short window of opportunity for foraging Great Egrets and were not selected over nearby natural sites. Despite widespread availability of HIW in the southeastern USA, our results show that natural wetlands continue to provide the majority of foraging habitat for Great Egrets; however, some HIW types (aquaculture and small ponds) may be strongly selected.

Keywords: artificial wetland, agricultural wetland, habitat selection, rice, crayfish, ponds, Great Egret, *Ardea alba*

Selección por parte de *Ardea alba* de humedales con influencia humana y naturales a múltiples escalas en el sudeste de EEUU

RESUMEN

Los humedales construidos o modificados por los humanos (Humedales con Influencia Humana, HIH) constituyen una proporción creciente del hábitat de humedal en los EEUU. No está claro en qué medida los HIH (*e.g.*, estanques, diques, embalses, sitios de acuicultura y campos de cultivo inundados) brindan un hábitat equivalente para las aves zancudas comparados con los humedales naturales que están reemplazando o aumentando. Comparamos la selección de HIH con humedales naturales por parte de *Ardea alba* en dos regiones con una alta proporción de humedales (73% Luisiana [LA], 39% Carolina del Sur [CS]) y con una proporción similar de HIH (4.3% LA, 4.5% CS). Seguimos individuos de *A. alba* en LA ($n = 11$) y CS ($n = 19$) mediante el uso de transmisores satelitales hasta por un año para evaluar la selección de los ámbitos de hogar y de los sitios de forrajeo. También comparamos la selección de los campos de cultivo inundados versus los humedales naturales como sitios de forrajeo a partir de muestreos aéreos de individuos no marcados en LA. En CS, las aves marcadas mostraron una selección más fuerte de HIH que de humedales naturales como sitios de forrajeo, impulsada por el uso de pequeños estanques antrópicos (39.9% de las observaciones de forrajeo), pero los ámbitos de hogar no presentaron una superficie desproporcionada de estanques. En LA, las aves marcadas no mostraron una selección global de HIH a cualquier escala, pero los individuos no marcados mostraron una fuerte selección de estanques de acuicultura de cangrejos de río, especialmente durante el descenso en el nivel de agua. Los campos de arroz brindaron solo una corta ventana de oportunidad para los individuos que forrajeaban y no fueron seleccionados por sobre sitios naturales cercanos. A pesar de la amplia disponibilidad de HIH en el sudeste de EEUU, nuestros resultados muestran que los humedales naturales continúan brindando la mayoría de los hábitats de forrajeo para *A. alba*. Sin embargo, algunos tipos de HIH (acuicultura y pequeños estanques) pueden ser fuertemente seleccionados.

Palabras clave: Ardea alba, arroz, cangrejo de río, estanques, humedal agrícola, humedal artificial, selección de hábitat

INTRODUCTION

Wetlands constructed *de novo* by humans and natural wetlands substantially modified by humans (human-influenced wetlands [HIW]) are aquatic features whose physical nature, hydrology, nutrient cycling, or biotic composition is directly controlled by human activity. These ponds, reservoirs, impoundments, aquaculture sites, and flooded agricultural fields comprise a rising percentage of the wetland area in the USA and worldwide (Dahl 2006, 2011, Ramsar Convention Secretariat 2010). Comparisons of hydrology, soil, water chemistry, and plant and animal assemblages have shown that HIW are rarely identical to natural wetlands. Restored sites may require >100 years to approach comparable ecological function (Campbell et al. 2002, Hartzell et al. 2007, Hossler and Bouchard 2010, Moreno-Mateos et al. 2012); however, colonization by some fauna, particularly wading birds (egrets, herons, bitterns, storks, spoonbills, and ibises), may be rapid (Brown and Smith 1998). It is unclear to what extent HIW provide habitat for these species equivalent to the natural wetlands they are replacing or augmenting. Knowing to what extent wading birds incorporate HIW in the selection of home ranges and foraging sites will provide insight into the value of HIW as habitat.

Partly because of their extreme mobility and position high in aquatic food webs, wading birds are often identified as important functional components of wetlands and as indicators of wetland quality, particularly at larger spatial scales (Frederick and Ogden 2003, Stolen et al. 2005). Movement patterns of wading birds are largely responses to prey availability (Kushlan 1986, Frederick et al. 2009), suggesting that selection of habitat by wading birds should be indicative of abundant and accessible fish and invertebrate prey populations. Prey availability has important effects on wading birds through reproductive success (Maddock and Baxter 1991, Frederick et al. 2009) and overwinter survival (Butler 1994).

As a whole, HIW may offer enhanced foraging opportunities for wading birds because the majority of HIW receive nutrient subsidies in the form of agricultural fertilizer, field or lawn runoff, or wastewater, presumably leading to higher secondary productivity. HIW also tend to have shorelines and open water clear of dense vegetation that can deter foraging (Lantz et al. 2011, McCrimmon et al. 2011). In addition, HIW may be designed or managed in a way that fosters a more stable hydroperiod than natural wetlands, which in some cases allows them to act as refugia for wading birds and their prey.

Foraging by wading birds in HIW has been documented in ponds and impoundments (Edelson and Collopy 1990, Frederick and McGehee 1994, White and Main 2005), aquaculture sites (Glahn et al. 2002, Huner et al. 2002, Ma et al. 2004, Cheek 2009), and flooded rice fields (Elphick 2000, Elphick et al. 2010, Stafford et al. 2010). Rice fields are considered the most important HIW for wading birds worldwide, with many populations relying primarily on flooded rice for foraging (Czech and Parsons 2002). In the Mediterranean region, where 80–90% of natural wetlands have been lost, rice fields were determined to support 50–100% of wading birds during the breeding season (Fasola and Ruiz 1996). In China, traditional rice agriculture plays a critical role in Crested Ibis (*Nipponia nippon*) conservation (Wood et al. 2010), and large breeding populations of several wading birds are found in regions where rice agriculture is abundant (Fasola et al. 2004). In India, 6 species of wading bird, including Great Egrets (*Ardea alba*), are suspected to have undergone population or range increases due to the increasing extent of rice agriculture (Sundar and Subramanya 2010), and rice fields may play an important role in linking populations otherwise isolated by fragmented wetland landscapes (Sundar 2004).

It is less clear how important rice and aquaculture sites are when natural wetlands are also available within the landscape. In northwest Italy, wading birds in rice fields were found to be more abundant and have higher foraging rates than in riverine sites, and breeders captured 80% of their food in rice (Fasola et al. 1996, Fasola and Brangi 2010). Rice fields were selected positively as foraging habitat by wading bird species on a seasonal basis when natural wetlands may have been dry or too deep for foraging (Tourenq et al. 2001, Sundar 2004, 2006); however, Richardson et al. (2001) observed that conversion of natural wetlands to rice agriculture coincided with a decrease in Great Egret populations in southwest Australia. They found that foraging efficiency decreased as rice grew, which coincided with time of greatest food demands in the breeding season, making rice a poor substitute for natural wetlands in the area.

Aquaculture sites contain high densities of fish or crustacean stock that could be potential prey for wading birds; however, farmers may reduce prey availability by altering pond depth and shoreline access or by deterring foraging birds through hazing and lethal removal. Caloric intake by wading birds at shrimp farms in Ecuador was less than at seminatural coastal sites (Cheek 2009). Wading birds have been observed foraging in fish and crab aquaculture ponds and adjacent natural wetlands in equal densities (Ma et al. 2004). Rapidly increasing populations of several wading bird species in Louisiana during the 1970s and 1980s corresponded with an expansion of crayfish aquaculture (Fleury and Sherry 1995), suggesting increased local recruitment and/or immigration over hundreds of km as a result of increased area under crayfish aquaculture. For both aquaculture and flooded rice fields, these studies show that use by wading birds may depend on availability of other habitat types within the landscape as well as particular management practices.

The Great Egret is a widespread and common wetland species that feeds predominantly on fish, but they also take invertebrates, amphibians, reptiles, birds, and small mammals (McCrimmon et al. 2011). Great Egrets are able to exploit a variety of wetland types and are capable of moving hundreds of kilometers in a day to assess foraging and breeding site conditions (Fidorra 2012). Thus, selection of habitat by this species is predicted to reflect prey availability among multiple wetland types and across regional spatial scales.

Habitat selection is expressed by animals at multiple scales, including selection of home range from the larger landscape and selection of individual locations from within a home range (Johnson 1980). Objective evaluation of the selection of HIW by mobile wading birds should consider multiple scales, include a suitably large landscape that is considered available habitat, and offer clear comparisons between natural wetlands and HIW in reasonably close proximity.

We studied the selection of HIW including constructed ponds and impoundments, crayfish aquaculture, and flooded rice fields by Great Egrets at 2 study sites in the southeastern coastal plain of the USA. Using free-ranging satellite-tagged Great Egrets, we compared HIW selection with that of natural wetlands across both winter and breeding seasons. We also used systematic aerial surveys to determine how a breeding population of unmarked Great Egrets selected foraging habitat when both natural and HIW (flooded rice fields and aquaculture ponds) were widely available. We predicted Great Egrets would disproportionately use HIW compared to natural wetlands due to their potential for high productivity, stable hydroperiod, and open edges for foraging.

METHODS

Study Area

The coastal plain of the southeastern USA contains extensive wetland mosaics, including large areas of both HIW and natural wetlands. We focused this study in 2 areas within the coastal plain: southern Louisiana (LA) and coastal South Carolina (SC; Figure 1). Both are important for wintering and breeding wading birds (Mikuska et al. 1998), have a humid subtropical climate, and are centered on high trophic-status river deltas and estuaries. These areas contain large amounts of natural palustrine and estuarine wetlands of various types and a concentrated area of HIW related to past or present agricultural practices. In LA, extensive rice and crayfish production is a dominant rotational agricultural practice (McClain et al. 2007). In coastal SC, extensive areas of abandoned rice fields from the 1800s remain as wetland impoundments along tidal river floodplains managed for a combination of crops and waterbirds, especially waterfowl. In both regions, management of water on individual fields varies by manager, location, intent, and season, and thus a landscape of deep and shallowly flooded, planted, and fallow fields exists throughout the year. Other kinds of HIW are also embedded within this landscape, including farm ponds and retention ponds for wastewater and storm runoff.

Satellite Telemetry Study

During fall and winter 2010–2011, we captured adult Great Egrets at foraging and loafing locations using a pneumatic net gun (Caudill et al. 2014). Solar-powered GPS satellite transmitters (Model 22GPS, Northstar Science and Technology, King George, VA, USA) were attached as backpacks with a Teflon ribbon harness to birds captured in LA ($n = 15$) and SC ($n = 23$). The total mass of the attachment (35 g) was $<4\%$ of the bird's body mass. The transmitters recorded one location at 0800–0900 hr local standard time each day, a time when egrets were likely to be foraging (Kushlan 1978), and a second location at 0200–0300 hr to identify nighttime roost/breeding sites. We only collected one foraging location per day to ensure independence within sampled locations (Gawlik 2002). Data collected from time of capture through August 15, 2011, were included in the analysis (maximum period of data collection was 11.5 months for any individual).

We used a geographic information system (GIS, ArcGIS 9.3, ESRI, Redlands, CA, USA) and the ABODE extension (Laver 2005) to calculate 90% fixed kernel home ranges using day and night locations for egrets that had >30 days of location data collected (Worton 1989, Seaman et al. 1999). We defined available habitat as being within a 20 km radius from the center of any individual's home range, a distance that approximately matched the maximum distance (22 km) traveled between roost and subsequent foraging site by any tagged egret in this study and was previously used to define habitat available to Great Egrets (Custer et al. 2004, Leberg et al. 2007). The boundaries of the 2 study areas were defined by the combination of all 20 km radii from that study area. Points collected from egrets that departed LA or SC were not included in this study.

We adopted the Cowardin et al. (1979) definition of a wetland used in the National Wetland Inventory (NWI; USFWS 2011) and extended it to include agricultural impoundments. Deepwater habitats such as lakes, rivers, and marine environments were not considered wetlands, but because their margins and islands are important aquatic features for wading birds, we included their edges. We use the term "natural" in reference to aquatic features that are not impounded, diked, or excavated; even so, we recognize that wetlands we identified as natural may sometimes be affected by human activity and water use.

We simplified the NWI classifications into 5 categories: emergent wetland, forest/scrub wetland, pond/lake, river-

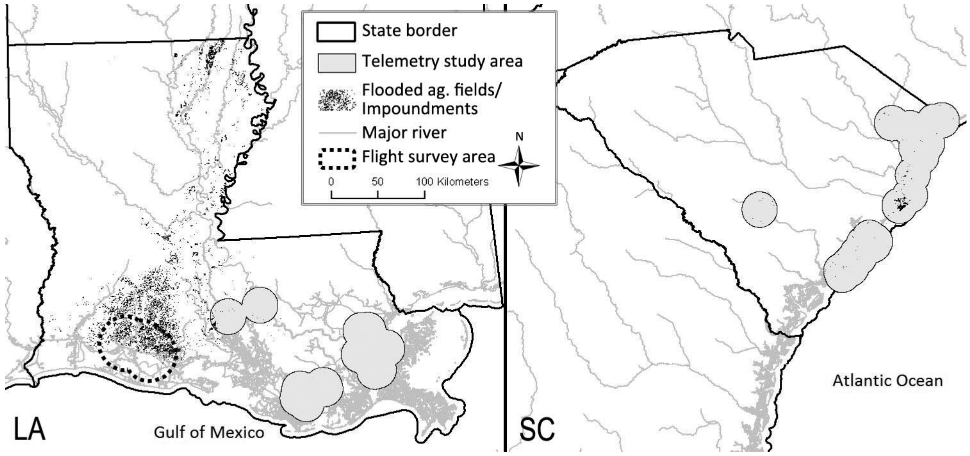

FIGURE 1. Study area extent as defined by 20 km radii around home range centers for Great Egrets tagged with satellite transmitters and general location of flight surveys. The rice and crayfish impoundments in Louisiana and abandoned rice plantations in South Carolina are identified as "Flooded Ag. Fields" in black.

ine, and unconsolidated shore. These categories were then subdivided into HIW and natural wetlands. Features categorized as impounded, diked, or excavated in the NWI were classified as HIW and all others were considered "natural." Riverine wetlands (including canals in LA) presented too many subtleties of modification to be classified cleanly as HIW or natural and were retained simply as "riverine" habitat in this study. Land cover not classified in a wetland category was grouped as "terrestrial" habitat.

We updated and verified the NWI using digital scans with 1 m pixel resolution of 1:40000 scale aerial photographs taken in 2010 and 2011 for the National Agricultural Imagery Program (NAIP; USDA 2010, 2011). We confirmed our classification of wetlands as HIW by noting contrasting water depth or vegetation compared with their surroundings and/or visible levees or structures that could allow depth manipulation. We removed wetland from the NWI that had been converted to urban development and digitized any unclassified ponds/lakes >1000 m^2 and canals >10 m wide. We used an 8 ha benchmark to separate lakes from the smaller ponds (Cowardin et al. 1979), and although these habitats were lumped for analysis, we retained their identity for later discussion. We assigned newly identified ponds/lakes to the subclass of HIW and canals to riverine habitat type. Because Great Egrets typically forage in water depths <28 cm (Powell 1987), we placed a 5 m buffer inside deep water wetlands originally classified in the NWI as subtidal estuarine/marine, riverine, pond, and lacustrine to approximate the shallow edge foraging area available to egrets. Areas of each habitat type were calculated in GIS using the USA contiguous Albers Equal Area Conic coordinate system.

Daytime satellite locations of birds with a reported accuracy of ≤ 100 m and velocity ≤ 4 m s^{-1} were retained for analysis of habitat use. We discarded points that overlapped night locations, which we assumed were roost and nest sites. Points were assigned to the habitat class of the wetland that they were located within, or closest to if a wetland was within the reported margin of error (≤ 100 m).

We quantified 2 scales of habitat selection (Johnson 1980, Stolen et al. 2007). We compared habitat composition of home ranges with the composition within an entire study area (SC or LA), and for each bird we also compared the proportion of locations in each wetland type with the composition of land cover within the 20 km radii from home range centers. We used compositional analysis to rank habitats and compare selection between habitat types (Aebischer et al. 1993). Data were analyzed in Program R (R Development Core Team 2008) using the adehabitatHS package (Calenge 2006). We used the Wilkes lambda statistic to test for overall selection and a randomization test with 1000 replicates to compare selection between habitat types (alpha $= 0.05$). We tested for differences in selection among 4 broad categories of habitat: HIW, natural wetlands, riverine habitat, and terrestrial habitat. If significant differences existed, we also quantified selection of each of the wetland types. We also compared results of analyses in which riverine habitats were removed from the suite of habitats with a separate analysis in which riverine habitats were classified as HIW.

Aerial Survey Study

We conducted aerial surveys of unmarked foraging Great Egrets over an extensive landscape of mixed flooded agricultural fields and natural wetlands in LA during the 2011 breeding season (March–June). The survey area included the southern portion of the crayfish and rice agricultural area in south-central LA and an adjacent area of natural emergent wetlands (Figure 2). On the boundary between these primary land cover types were several Great Egret nesting colonies. This situation was viewed as ideal for examining the prediction that breeding Great Egrets select flooded agricultural fields for foraging.

We identified 4 recently active colonies that contained >100 Great Egrets along the boundary of the agricultural area and natural marsh wetlands (LNHP 2008). We placed 30 km buffers around these colonies to delineate the study area boundary because this is typically the maximum distance Great Egrets travel from their colony to foraging sites (Custer and Osborn 1978, Smith 1995, Custer and Galli 2002). Centered within this boundary, we placed 5 aerial survey transects oriented in an east–west direction with the spacing between transects and transect length randomly determined in 1 km increments.

We counted Great Egrets on these belt transects from a Cessna 172 during the 2011 breeding season on March 27, May 21, and June 25. Flights were conducted between 0800 and 1200 hr with the same 2 observers and pilot from an altitude of 152 m and a ground speed of 120–145 km hr^{-1}. Windows and wing struts were marked to delineate a 250 m wide strip of ground as viewed out both sides of the plane parallel to flight direction (Norton-Griffiths 1978). Within these strips, all foraging egrets and all habitat types were recorded. An egret was considered foraging if it was standing in an aquatic habitat or along the adjacent shore; birds in flight, perched in trees, or perched in colonies were not counted. Photographs were taken of aggregations >10 individuals to later confirm number and species. Habitat categories were rice field, crayfish pond, emergent wetlands, and "other," which included all terrestrial land cover and forested wetlands that could not be surveyed by plane due to poor visibility of egrets below the canopy. These wetlands comprised a relatively small proportion of the study area. Satellite-tagged birds showed low use of forested wetlands, so we are confident we overlooked few egrets in forested wetlands. Using a GIS, the flight line and survey transects were overlaid with the NWI and NAIP imagery to calculate areas of each habitat type and to help separate emergent HIW from natural emergent wetlands. Selection ratios (Manly et al. 2002) comparing habitat used by Great Egrets to habitat available within the survey strips were calculated in Program R using the adehabitatHS package and compared using Bonferroni confidence intervals.

Independent double observer counts (Nichols et al. 2000) were also conducted during flights to assess detectability biases within the study area. Egret observations were categorized by habitat type and size of foraging aggregation. Groups of ≥3 individuals were analyzed separately from ≤2 egrets to test for potential differences in the detection of groups of various sizes. Detection probability was modeled using the software program DOBSERVE (Hines 2000). Models including observer,

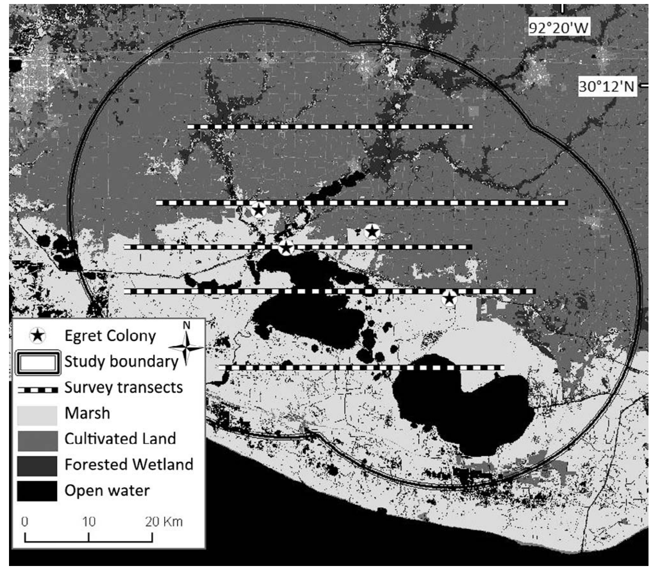

FIGURE 2. Flight transects and land cover map of area surveyed for Great Egrets in south-central Louisiana, USA.

habitat type, group size, observer*habitat, and observer*group size as factors were compared using AICc.

RESULTS

Satellite Telemetry Study

From September 2010 through February 2011, GPS equipped satellite transmitters were placed on 38 Great Egrets. For 19 individuals in SC and 11 in LA, we received >30 daytime locations with accuracy within 100 m (mean = 117.8 locations ± 12.7 SE). The remaining 8 egrets were excluded from this study.

The study areas defined by a 20 km radius around all home range centers in LA and SC were 9,932 and 8,484 km^2 (excluding open ocean), respectively (Figure 1). Both study areas contained a large proportion of wetland area: 39% in SC (Table 1) and 73% in LA (Table 2). HIW made up a similar proportion of the total wetland area in both LA (4.3%) and SC (4.5%) study areas.

Natural emergent wetlands were the most commonly used foraging habitat in both study areas, followed closely by riverine habitat in LA and HIW pond/lakes in SC (Figure 3). LA egrets on average used HIW at 10.8% ± 5.2 of point locations. Of the 11 tagged egrets in LA, 9 were recorded in HIW at least once: 6 used HIW emergent wetlands; 1 used HIW forest/scrub; and 6 used HIW ponds/lakes, with 1 individual recorded 146 times (56% of locations) in HIW ponds within the New Orleans metropolitan area. Great Egrets in SC used HIW at 41.7% ± 8.0 of point locations. HIW emergent wetlands were used by 3 of the egrets in SC, 1 used HIW forest/scrub wetlands, and all 19 were recorded in HIW ponds at

TABLE 1. Average proportion (±SE) of habitat types within the study area, home ranges, and 20 km radius circles used to define available habitat for individuals, and the proportion of Great Egret satellite locations within each habitat type in Louisiana, USA.

Habitat type	Study area	Home range	20 km radius	Egret locations
Terrestrial	26.69	38.15 (7.34)	21.82 (5.01)	12.98 (4.90)
Emergent	40.58	35.61 (8.28)	59.82 (6.96)	31.84 (8.77)
Forest/Scrub	29.05	22.72 (5.62)	13.65 (4.07)	11.78 (3.26)
Pond/Lake	0.14	0.05 (0.02)	0.11 (0.03)	0.50 (0.33)
Unconsolidated Shore	0.07	0.06 (0.04)	0.11 (0.04)	0.00 (0.00)
HIW - Emergent	1.47	1.01 (0.52)	2.18 (0.34)	3.28 (2.35)
HIW - Forest/Scrub	1.58	1.42 (0.89)	1.94 (0.77)	2.41 (1.62)
HIW - Pond/Lake	0.11	0.22 (0.09)	0.09 (0.04)	6.69 (5.43)
Riverine	0.30	0.77 (0.28)	0.28 (0.05)	30.51 (9.92)

least once. Four egrets used HIW at >80% of locations, mostly HIW ponds. Within the HIW ponds/lakes category in both study areas, 96.3% of foraging locations were in HIW ponds (<8 ha) vs. lakes, and thus we focus our discussion on these smaller HIW.

Satellite-tagged egrets were not observed using actively managed flooded agricultural fields in either study area. None of the egrets tagged in southeastern LA traveled to the region of concentrated flooded agricultural fields in south-central LA. The historic but now dysfunctional rice impoundments along the river floodplains in SC were only visited 11 times by a single egret over a 38-day period.

In LA, we did not find selection of any of the habitat categories at the home range scale (Wilkes lambda $= 0.62$, $P = 0.25$; Figure 4) or foraging site scale (Wilkes lambda $=$ 0.63, $P = 0.27$). This pattern held even when we included riverine habitats in the HIW category (Wilkes lambda $=$ 0.64, $P = 0.16$).

In SC, birds selected habitat at the home range scale (Wilkes lambda $= 0.35$, $P = 0.002$; Figure 4). HIW were more strongly selected compared with riverine habitat ($P < 0.001$) but not compared with natural wetlands ($P =$ 0.32) or terrestrial habitat ($P = 0.89$). Selection at the scale of foraging sites was also detected (Wilkes lambda $= 0.06$, $P = 0.001$; Figure 4). Here, HIW were selected more strongly than natural wetlands, riverine, and terrestrial habitat categories ($P < 0.001$). Because a difference between selection of HIW and natural wetland was found in SC, we also compared selection between the different types of HIW and natural wetlands at this scale in SC. HIW pond/lake habitat was selected more strongly than all other habitat types ($P < 0.001$; Table 3). HIW emergent wetlands were not selected more strongly than natural emergent wetlands, and HIW forest/shrub wetlands were not selected more strongly than their natural counterpart.

Aerial Survey Study

The study area containing our flight surveys in LA covered 4,974 km^2 (Figure 2). Approximately 138 km^2 of this area (2.8%) fell within our observed transect strips during each survey. We recorded an average of 444 ± 183 unmarked Great Egrets during each of the 3 surveys. Habitat composition changed somewhat between surveys according to the flooding and draining of fields, but on average natural emergent wetlands accounted for 35% of the surveyed area, flooded agricultural fields comprised 14%, and emergent HIW comprised 6%, which were mainly large impounded wetlands with natural emergent vegetation managed for waterbirds. Additional land cover included 27% terrestrial, 12% deep open water, and 6% forested wetland.

The highest ranked model using double-observer methods suggested no effect of observer or habitat bias in detection of Great Egrets. Competing models included evidence of observer effect (ΔAICc ~0.6) and habitat effect (ΔAICc ~2); however, we considered the 3–9% difference

TABLE 2. Proportions (±SE) of habitat types within the study area, home ranges, and 20 km radius circles used to define available habitat for individuals, and the proportion of Great Egret satellite locations within each habitat type in South Carolina, USA.

Habitat type	Study area	Home range	20 km radius	Point locations
Terrestrial	60.64	65.31 (3.79)	59.91 (1.18)	4.94 (2.18)
Emergent	10.34	18.44 (3.54)	16.13 (2.89)	40.37 (8.22)
Forest/Scrub	25.87	10.69 (3.58)	20.16 (2.64)	6.31 (2.52)
Pond/Lake	0.02	0.01 (0.01)	0.01 (0.00)	0.26 (0.18)
Unconsolidated Shore	1.23	3.43 (0.92)	2.45 (0.45)	3.80 (1.76)
HIW - Emergent	1.28	0.88 (0.61)	0.55 (0.23)	3.81 (1.51)
HIW - Forest/Scrub	0.22	0.09 (0.04)	0.16 (0.02)	0.19 (0.14)
HIW - Pond/Lake	0.26	1.09 (0.15)	0.32 (0.03)	39.9 (8.15)
Riverine	0.13	0.06 (0.03)	0.30 (0.08)	0.41 (0.41)

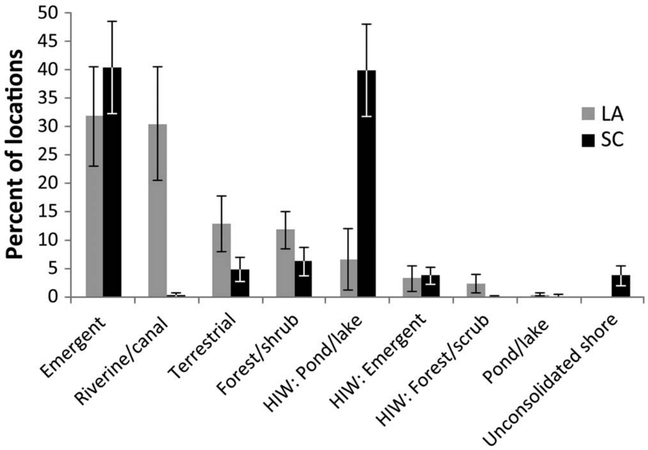

FIGURE 3. Average composition of habitat types used by Great Egrets tagged with satellite transmitters during daylight hours in Louisiana and South Carolina. Error bars indicate ±SE.

in detection probability between these models and the null (no observer or habitat effect) to be small enough that we did not need to adjust count data to account for observer or habitat effects on bird detection rates.

Impoundments used for crayfish production were the only HIW habitat type consistently used more in relation to availability than natural emergent wetlands based on aerial surveys (Figure 5 and 6). Crayfish impoundments were used significantly more than expected given their availability in every survey. Use of rice fields seemed to change during the growing season; flooded rice fields were scarcely used in March, had positive selection in May, and were used in proportion to their availability in June; however, rice fields were never selected more positively than natural wetlands. We did not detect a significant difference between the selection of natural emergent and HIW emergent wetlands in the aerial survey in any month.

DISCUSSION

Satellite telemetry provided observations of highly mobile birds over both wintering and breeding seasons across a landscape composed of natural and HIW in agricultural, urban, and natural settings. This allowed us to evaluate selection of HIW across a suitably large landscape with clear comparisons between natural wetlands and HIW in reasonably close proximity. We found that selection of HIW was not consistent between types of HIW and regions within the southeastern coastal plain. The lack of positive selection of HIW by egrets tagged in LA suggests that the absolute or relative habitat quality of HIW in LA is not better than natural wetlands for foraging. Some HIW, such as rice fields and crayfish aquaculture, seem to provide foraging opportunities, as indicated by our flight surveys, and may provide benefits for local populations, although foraging seems limited to some degree by depth (aquaculture) or dense vegetation during most of the agricultural cycle (rice).

In SC, overall use of HIW wetlands was considerably higher than in LA (41.7% of observations), and HIW ponds were highly selected, suggesting that some types of HIW may play an important role in supporting egret populations here, particularly near suburbanized areas where these features were abundant. In contrast to rice fields and aquaculture ponds, HIW ponds are much more stable in hydrology and offer shallow vegetated edges preferred by hunting Great Egrets (Stolen et al. 2007). Pond selection was considerably lower in LA than SC, suggesting either that pond quality was lower in LA or that there were important differences in quality of other available habitats between the 2 study sites. The LA study area was dominated by expansive emergent wetland (40.58% of study area compared with 10.34% in SC), a habitat traditionally considered ideal for foraging Great Egrets.

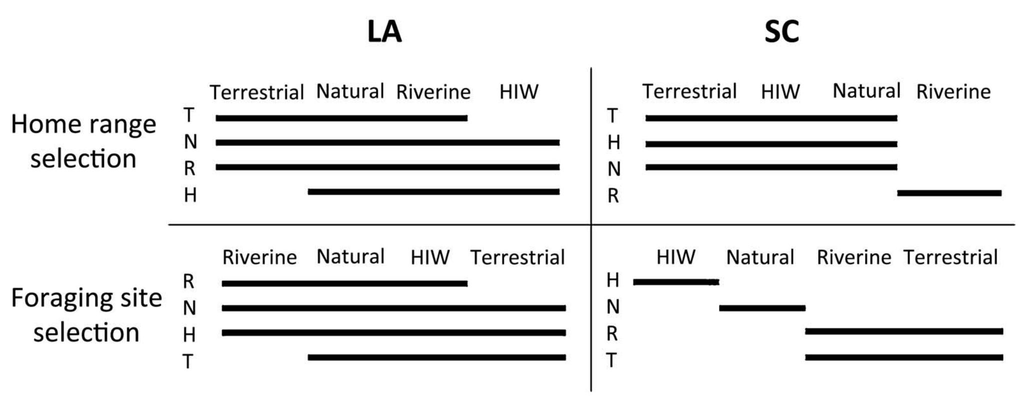

FIGURE 4. Comparison between the selection of HIW (H) and natural wetlands (N), Riverine (R), and Terrestrial (T) habitats in home ranges and as foraging sites by Great Egrets in Louisiana (LA) and South Carolina (SC). The black bar across each row indicates no difference in the selection between the habitat in that row and the habitat in each column; a cell lacking a bar indicates a significant difference was found in the compositional analysis randomization test. Columns are ordered with the most positively selected habitat on the left.

TABLE 3. Results of compositional analysis for the selection of foraging site habitat by Great Egrets in South Carolina. Rank indicates the relative selection of habitats, with smaller ranks being more highly used in relation to availability. The sign indicates how relative use of the row habitat differed from relative use of column habitat type. Bullets (•) indicate no significant difference in use/availability.

Habitat Type	Rank	HPL	EM	HEM	PL	FS	US	HFS	RI	TER
HPL (HIW Pond/Lake)	1	•	+	+	+	+	+	+	+	+
EM (Emergent)	2	–	•	•	+	+	+	+	+	+
HEM (HIW Emergent)	3	–	•	•	•	•	•	+	+	+
PL (Pond/Lake)	4	–	–	•	•	•	•	+	+	+
FS (Forest/Scrub)	5	–	–	•	•	•	•	•	•	•
US (Unconsolidated Shore)	6	–	–	•	•	•	•	•	•	•
HFS (HIW Forest/Scrub)	7	–	–	–	–	•	•	•	•	•
RI (Riverine)	8	–	–	–	–	•	•	•	•	•
TER (Terrestrial)	9	–	–	–	–	•	•	•	•	•

We interpret our results to mean that these natural wetlands continue to play a significant role in providing appropriate habitat for Great Egrets in LA. The differences found in the selection of HIW between study sites indicates that broad generalizations regarding the importance of particular HIW should be made with caution and must consider the wetland landscape of a specific region.

Flooded Rice Fields and Crayfish Ponds as Great Egret Foraging Habitat

Crayfish aquaculture impoundments can rival natural wetlands in densities of macroinvertebrates and fish (Fleury 1996). In crayfish aquaculture, farmers mimic natural ecosystems by fostering a rich community of plants and invertebrates for crayfish to eat, which also supports larger species of fishes and macroinvertebrates preyed upon by Great Egrets. Great Egrets have been shown to have higher foraging success rates and take more preferred prey items from crayfish ponds compared with natural wetlands (Fleury 1996). We attribute the increased selection of crayfish ponds that we saw in LA in June to the draining of ponds after harvest. This reduction in depth also increases access to areas previously too deep for foraging and provides a mechanism for concentrating prey in shallow water. These pulses of food availability are not entirely synchronous across the landscape due to slightly different schedules from farm to farm. This period of pulsed food availability coincides with the late nesting period for Great Egrets, a time when energy demands are high and when low food availability can result in brood reduction or nest failure (Frederick et al. 2009).

We found a relatively short window of selection of LA rice fields in May. Prey abundance in rice fields is generally low initially following inundation (Gonzalez-Solis et al. 1996, Sizemore and Main 2012), and soon thereafter heavy growth of rice stalks and leaves makes foraging by egrets difficult (Fujioka et al. 2001, Richardson et al. 2001, Sizemore and Main 2012). Even when rice fields were most

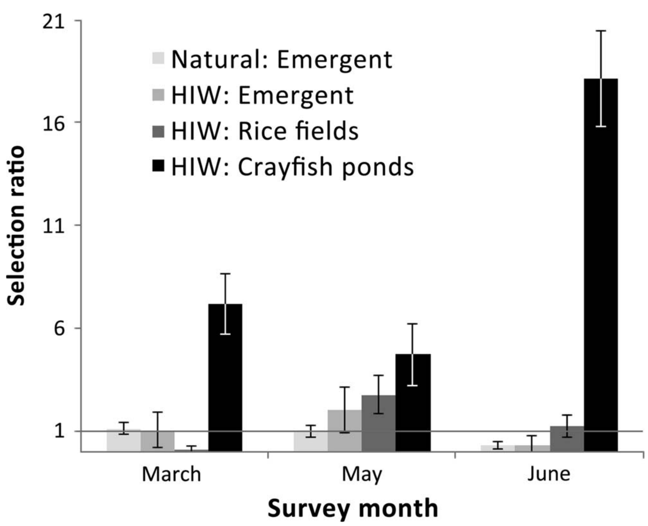

FIGURE 5. Selection ratios (±95% CI) for habitat types used by foraging Great Egrets observed during aerial surveys near breeding colonies. A value >1 indicates habitats were used more than expected given their availability. Note that the "other" land cover class, which was rarely used, is not displayed.

FIGURE 6. Photo of crayfish ponds divided by contour levees taken during March survey flight in south-central LA.

heavily used by egrets (May), they were not selected more strongly than the surrounding natural wetlands.

Rice fields in southern LA do not currently seem to be as important for wading birds as rice fields in other parts of the world where natural wetlands have been reduced or degraded. In contrast, the diverse matrix of natural wetlands, and especially crayfish ponds, seemed to dilute the relative importance of the rice-growing phase of rice/crayfish polyculture for wading bird populations in LA. In SC, the area of historic coastal rice impoundments was the geographical center of the study area, yet only 1 of the 19 egrets utilized these wetlands during this study. Our observations therefore provide little evidence of selective use by egrets of either active rice agriculture or former rice fields being managed for waterfowl. We conclude that in these 2 regions, rice impoundments play a negligible role in supporting regional populations of Great Egrets, suggesting that natural wetlands should continue to receive conservation attention in the US, and that populations of wading birds may benefit from increased natural wetland habitat in parts of the world where rice fields are the dominant wetland type.

Ponds as Great Egret Foraging Habitat

HIW ponds were abundant in the suburbanized regions of both study areas. In LA, only a single egret utilized ponds extensively; however, in SC the egrets selected ponds as foraging sites more strongly than any other habitat type and satisfied the general prediction that HIW would be used more than availability would suggest. HIW ponds included sewage treatment ponds, borrow pits, livestock watering ponds, and especially urban and golf course ponds created for beautification and storm water retention. Nationally, the area of HIW ponds has increased since 1998 by $>$17%, with a disproportionate number being built along the Gulf and Atlantic coastal plains of the southeastern USA (Dahl 2006, 2011).

Other studies have found Great Egrets to utilize ponds at golf courses (White and Main 2005) and phosphate mines (Edelson and Collopy 1990). Because many ponds are deeper (1–15 m on golf courses; White and Main 2005) than the maximum depth accessible by foraging Great Egrets (28 cm; Powell 1987), it seems likely that the egrets are utilizing narrow belts of shallow habitat on the edges of ponds. Edges may be ideal foraging locations for stalking wading birds because prey fish may be forced there by aquatic deep water predators (Crowder et al. 1997, Stolen et al. 2007).

Although Great Egrets clearly used ponds out of proportion to availability, it does not necessarily follow that those choices were adaptive or optimal. Many of these pond types (sewage treatment, urban or agricultural retention) may involve exposure of birds to structural hazards, disease, parasites, and toxins (Frederick et al. 1996, Parsons et al. 2010). Our findings highlight the importance of future research aimed at understanding the net effects of these HIW habitats on survival and reproduction.

ACKNOWLEDGMENTS

We are grateful to many individuals who provided assistance in this study including technicians M. G. Lemon, A. Mulligan, and D. Scott; J. Huner, R. McClain, R. Romaire, and J. Saichuk from the LSU Agricultural Center; J. Durand of Durand Farms; C. Jeske of the National Wetlands Research Center; and C. Hand and J. Rader from the SC Department of Natural Resources.

Funding statement: This work was supported by a grant from Biodiversity Research Institute and the U.S. Fish and Wildlife Service. None of our funders required approval of the final manuscript before publication.

Ethics statement: We followed the ethics protocols in line with the University of Florida/IFAS Animal Research Committee.

Author contributions: J.C.F. and P.C.F. conceived the idea, design, and experiment. J.C.F., D.C.E., and K.D.M. collected the data and conducted the research. J.C.F. and P.C.F. wrote the paper. J.C.F. and K.D.M. developed or designed the methods. J.C.F. analyzed the data. P.C.F., D.C.E., and K.D.M. contributed substantial materials, resources, or funding.

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