

MOVEMENT PATTERNS AND THE RELATIVE IMPORTANCE OF CONSTRUCTED
AND NATURAL WETLANDS TO GREAT EGRETS IN THE SOUTHEASTERN U.S.

By

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To my parents, for everything.

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Abstract of Thesis Presented to the Graduate School
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AND NATURAL WETLANDS TO GREAT EGRETS IN THE SOUTHEASTERN U.S.

By

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I studied the movements and habitat selection of great egrets (*Ardea alba*) in the southeastern U.S. and compared selection of human-constructed wetlands to natural wetlands. Adult great egrets in Louisiana and South Carolina were tracked using satellite transmitters for up to one year. I analyzed habitat selection of home ranges and selection of specific wetland types used for foraging. I also compared use of agricultural and natural wetlands through aerial surveys at a Louisiana location where both wetland types were abundant.

I observed significant differences between selection of constructed and natural wetlands as foraging sites in SC, where constructed ponds were selected over all other habitat types ($P < 0.001$). Crayfish aquaculture ponds were selected over natural wetlands in Louisiana, especially when ponds were being drained. Rice fields were selected over natural wetlands when the crop was short but had been flooded for at least a month. Overall, agricultural wetlands and constructed ponds provided attractive foraging opportunities for local populations but did not appear to influence broad scale

movements of tagged birds. Depth, vegetation, and timing of inundation may limit use of these foraging sites.

Within populations, different individuals used migratory, nomadic, and sedentary movement strategies. Small patches of habitat could support individuals year round, while others conducted long distance movements, traveling up to 877 km/day at speeds reaching 79.9 km/h. Travel was usually at night, in a roughly straight line fashion, and often over large bodies of water far from sight of any landmarks, suggesting a target destination and true navigational abilities.

CHAPTER 1 INTRODUCTION

Habitat selection is a behavioral response resulting in a disproportional use of resources in order to influence the survival and fitness of an individual (Jones 2001). Therefore, determining selection is important for understanding the biological requirements of animals and the strategies they use to fulfill their needs for survival (Manly et al. 2002). Movement is one mechanism by which individuals can choose among available habitats, and habitat selection and movement processes are intimately related; movement is partly driven by habitat selection, whereas habitat selection is a process that is the consequence of movements (Martin 2009). Mobile species can remain within suitable habitat or, if they have the ability, they can relocate as habitat conditions or their needs change. High proportions of species that have evolved within the continuous vegetative cover of forest biomes are notoriously ill-adapted for relocation as habitat destruction and conversion spreads (Bierregaard et al.1992; Sieving et al.1996; Moore et al.2008). However, animal species of open habitats, such as large wetlands and grasslands, are quite often highly adapted for long distance movements allowing them to search for optimal resource conditions (Weller 1999; Dodman and Diagana 2007). Therefore, while habitat selection is a key process determining the demography and success of any species, animals of open habitats with high mobility are likely to locate isolated habitat patches that have been fragmented as a result of human development and provide information regarding the relative suitability of these patches to others within the landscape.

Wetland ecosystems have been greatly modified by human activities over the past century (Dahl 2006). While many wetlands have been destroyed or degraded, new

human-constructed wetlands have also been created (see Chapter 2). These include ponds, reservoirs, impoundments, and flooded agricultural wetlands; and comprise a rising percentage of the wetland area in the U.S. With these widespread changes in the wetland landscape, there is a need to understand the ability of constructed wetlands to fill the ecological roles provided by natural wetlands, particularly in regards to providing habitat for wetland obligate species.

Many wetland environments are naturally variable in both space and time, and wetland species have evolved a multitude of ways of surviving these dynamic conditions. Some amphibians use drying as a cue to undergo metamorphosis into terrestrial forms (Denver 1997), lungfish can remain underground in aestivation for years (Fishman et al. 1992), and bird species conduct incredible movements between usable wetland patches in response to wetland conditions. Waterbirds are particularly adapted to make movements in response to habitat: bar-tailed godwits (*Limosa lapponica*) fly non-stop across the Pacific (Gill et al. 2005), bar-headed geese (*Anser indicus*) are the world's highest altitude flyers (Scott et al. 2009), and arctic terns (*Sterna paradisaea*) travel from pole-to-pole twice each year (Hatch 2002). These movements are thought to be primarily undertaken in response to changing foraging conditions (Pineau 2000; Dodman and Diagna 2007). Their prey resources are patchily distributed and this increases the complexity of understanding successful foraging behavior. Prey availability for such mobile species is influenced by global climate, ocean currents, and variation in local factors including hydrology, rainfall, vegetation, and temperature (Kushlan and Hafner 2000). Wading birds (Ciconiiformes: egrets, herons, bitterns, storks, spoonbills, and ibises) in particular, are sensitive to prey availability

(Kushlan and Hafner 2000; Crozier and Gawlik 2003; Frederick et al. 2009) which appears to be the primary driver of both breeding success (Frederick and Collopy 1989; Maddock and Baxter 1991; Hafner et al. 1993) and over-winter survival (Butler 1994; Cezilly 1997). Therefore, they are dependent upon their ability to locate and exploit patches of prey year round (Frederick and Spalding 1994) and their movement strategies have evolved to cope with this challenge (Kushlan 1986; Frederick and Ogden 1997). However, many details regarding the annual movements remain unknown because we have lacked ways to study movements of many species across broad scales.

Great egrets (*Ardea alba*) are a widespread ciconiiform species common in both temperate and tropical wetlands. Their large distribution, abundance, size, and colonial behavior have made them relatively easy to study and much is already known about their microhabitat selection, foraging habits, and breeding ecology (McCrimmon et al. 2011). They are a suitable species for studies of habitat selection and movement as they are wetland generalist able to exploit a variety of wetland types (Chapman and Howard 1984; McCrimmon et al. 2011) and individuals are known to conduct long distance movements (Coffey 1943; Coffey 1948; Byrd 1978; Mikuska et al. 1998; Melvin et al. 1999). Thus they should provide insight into the relative attractiveness of many different wetland habitats across a broad area.

My research focused on the habitat selection and movements of great egrets using satellite tracking of individuals from two wintering populations in the southeastern U.S. Satellite tracking provided me with the ability to collect unbiased location data on great egrets on a daily basis. In Chapter 2, I report on habitat selection and compare

relative use of constructed and natural wetlands by individuals at multiple scales using data from marked individuals. Since these animals were marked in relatively small areas that did not necessarily contain high proportions of constructed wetlands, or constructed wetlands of all types, I also examined habitat selection by a breeding population of great egrets in a landscape where both natural and agricultural wetlands were abundant. While use of various agricultural wetlands by wading birds has been documented (Martin 1985; Fasola and Ruiz 1996; Elphick 2000; Czech and Parsons 2002; Huner et al. 2002; Ma et al. 2004; Stafford et al. 2010), use alone provides only limited information regarding the importance of these habitats. Information regarding the relative selection of these constructed wetlands compared to natural wetlands is needed in order to understand whether these wetlands are of similar quality and supporting individuals within the population. Determining how species' habitat decisions are influenced by the availability of these wetlands will allow us to make predictions as human-modification of wetland landscapes increases.

Birds can utilize a variety of movement strategies in response to changing environmental conditions. Some birds are sedentary, while others conduct nomadic or migratory movements. Identification of these different strategies inform us of the ecology of these species and enable us to understand regional population trends, and each of these different movement patterns present different challenges for species management and conservation (Boyd et al. 2008). Unfortunately, we have only limited information regarding the broad scale movement patterns used by most wading bird species. In Chapter 3, I describe the movement patterns employed by marked individuals over an annual time period. I present detailed data regarding long-distance

movements that were conducted during the study, which provides new information regarding the speed and timing of flights by this species.

CHAPTER 2 SELECTION OF CONSTRUCTED AND NATURAL WETLANDS BY FORAGING GREAT EGRETS AT MULTIPLE GEOGRAPHIC SCALES

Background

While wetland loss remains a conservation concern, the rate of loss in the U.S. has slowed in recent decades and the latest censuses show marginal increases in wetland area due in part to the construction and management of wetlands by humans (Dahl 2006, 2011). Constructed wetlands are aquatic features in which the depth and inundation period are controlled by human design. These include ponds, reservoirs, impoundments, and flooded agricultural wetlands; and comprise a rising percentage of the wetland area in the U.S. For example, nearly 282,000 ha (12.6% increase) of freshwater ponds were created in the contiguous USA between 1998 and 2004 (Dahl 2006). With these widespread changes in the wetland landscape, there is a need to understand the ability of human-constructed wetlands to fill the ecological roles provided by natural wetlands.

Here, I explore the importance of constructed wetlands to wading birds. Wading birds (egrets, herons, bitterns, storks, spoonbills, and ibises) forage and breed in wetlands and are a predatory group feeding on a variety of aquatic invertebrates, fish, and amphibians, with larger species opportunistically taking reptiles, birds, and small mammals. They are sensitive to prey availability (Kushlan and Hafner 2000; Crozier and Gawlik 2003; Frederick et al. 2009), which appears to be the primary driver of their breeding success (Frederick and Collopy 1989; Maddock and Baxter 1991; Hafner et al. 1993) and over-winter survival (Butler 1994; Cezilly 1997). Prey availability is dependent upon both the density and accessibility of prey, which are influenced by various factors. Hydroperiod (duration of surface water) influences species composition (Kushlan and

Hafner 2000; Lawler 2001), prey density, and the type of predators present (Batzer and Wissinger 1996) in wetland communities. Following inundation, species richness and density of the invertebrate community generally increase up to 6 months before leveling off (Batzer and Wissinger 1996), and perennially flooded wetlands are more likely to support fish populations (DeAngelis et al. 1997). Vegetation provides food and refuge for many prey species (Crowder and Cooper 1982), but emergent and submergent vegetation can obstruct access to wading birds (Pierce and Gawlik 2010; Lantz et al. 2010, 2011). Increasing water depth also reduces access to habitat by wading birds which are limited by leg length (Powell 1987). Season, water temperature, oxygen, trophic status, and substrate are additional factors which can influence prey availability for wading birds. Also, the establishment and maintenance of some prey populations depends upon landscape variables such as the distance between wetlands and the permeability of the matrix between them (Joly et al. 2001). Constructed wetlands are a broad mix of these features, and wading birds may not be attracted to all constructed wetland types. In general, however, it is unclear how constructed wetlands function by comparison to mosaics of natural wetlands.

Wading birds are known to use fields flooded for rice (*Oryza sativa*) production (Fasola and Ruiz 1996; Elphick 2000; Czech and Parsons 2002; Stafford et al. 2010), various aquaculture sites (Glahn et al. 2002; Huner et al. 2002; Ma et al. 2004; Cheek 2009), and constructed ponds (Edelson and Collopy 1990; White 2003). However, most of these studies did not compare use to availability (Johnson 1980; Manly et al. 2002), or came from situations in which non-constructed wetlands were not readily available.

Most wading birds do not nest in rice fields, but forage in them during the breeding season (Pierluissi 2010) when energetic needs are 2 – 3 times those in the non-breeding season (Kushlan and Hafner 2000). In regions where natural wetlands have been lost, populations of wading birds are dependent upon rice fields for foraging (Fasola et al. 1996; Fasola and Ruiz 1996), but whether rice fields provide foraging habitat comparable to natural wetlands is unclear. Wading birds often prefer natural wetlands over nearby foraging sites (Tourenq et al. 2001; Sundar 2006; Bellio et al. 2009). However, caloric intake by wading birds foraging in rice fields may be insufficient (Sizemore 2009), in which case they may be serving as ecological traps (Dwernychuk and Boag 1971). Thus the question remains whether rice fields are functionally equivalent to natural wetlands as adequate foraging sites.

At aquaculture sites, the high density of stock and other aquatic prey colonizing them may provide excellent foraging opportunities for wading birds. Rapidly increasing populations of several wading bird species in Louisiana during the 1970's and 80's corresponded with the expansion of crayfish aquaculture (Fleury and Sherry 1995), suggesting aquaculture may support larger populations. However, all aquaculture sites do not appear to be equal. Access to aquaculture ponds can be restricted to wading birds by pond depth (Powell 1987; Cheek 2009) or management practices employed to deter birds from using aquaculture sites. While Ma (2004) found similar abundances of wading birds in fish and crab aquaculture ponds as on natural tidelands, Cheek (2009) found that caloric intake by wading birds at shrimp farms in Ecuador was less than for birds foraging on natural mudflats. The inconsistencies regarding the benefits of rice fields and aquaculture ponds for wading birds suggest that further research is required

to determine when, where, and under what management practices bird populations benefit from agricultural wetlands.

Wading bird habitat selection is dependent upon the scale at which it is measured (Stolen et al. 2007). As selection is a hierarchical process, multiple scales are required to understand how species choose habitats (Johnson 1980; Aebischer 1993). Wading birds can select habitat over a broad area and individuals and populations are capable of responding to prey availability at regional scales (Frederick et al. 1996; Frederick and Ogden 1997). An *a priori* delineation of available habitat and study area boundaries can affect the results of selection analyses without a biological basis (Porter and Church 1987).

Great egrets (*Ardea alba*) are a cosmopolitan long-legged ciconiiform bird common throughout many temperate and tropical regions globally. As wide ranging wetland generalists, great egrets are able to exploit a variety of wetland types (Chapman and Howard 1984; McCrimmon et al. 2011) and they display plasticity in foraging tactics and prey consumption (Dimalexis and Provetsi 1997; Gawlick 2002). I selected this species, in part, because its behavioral flexibility and success in complex landscapes provided the opportunity to assess the relative attractiveness of different potential foraging habitats at local, landscape, and regional scales (see Chapter 3).

In this study, my objective was to quantify selection of foraging habitats by great egrets and specifically to compare the attractiveness of constructed wetlands to natural wetlands. Constructed wetlands have the potential to maintain water levels despite seasonal conditions and thus may provide an alternate source of food when natural wetlands are dry or too deep (Sundar 2004) and a stable hydroperiod may increase

densities of preferred prey (e.g. fish). Wading birds respond positively to the concentration of prey during drying of natural wetlands (Kushlan 1976). If management practices allow water levels in various constructed wetlands within a landscape to fluctuate asynchronously, they could create a patchwork of ephemeral, high quality foraging sites throughout the year. I hypothesized that constructed wetlands would provide attractive foraging opportunities for great egrets and would be selected over natural wetlands. I predicted that great egrets would show a significantly more positive selection of constructed wetlands than natural wetlands at the scale of home range selection and foraging site selection if this hypothesis was correct. I used free-ranging satellite-tagged egrets in two wetland dominated regions of the southeastern U.S. to test my hypothesis at scales defined by the movement patterns observed by individuals during both the winter and breeding season. I also determined selection within the breeding season across a landscape with approximately equal availability of both natural and agricultural wetlands.

Methods

I compared selection of constructed wetlands to natural wetlands by great egrets in two use-availability studies. Use information was collected both from satellite tagged great egrets, and from untagged breeding egrets surveyed systematically in a wetland landscape containing both agricultural and natural wetlands. Satellite telemetry allowed me to follow individuals in an unbounded geographic area and examine habitat selection based on movements of individuals. Survey of breeding individuals within an area of rice/crayfish culture allowed me to examine the relative importance of an agricultural system thought to be highly beneficial to birds.

Study Area

I studied birds in the coastal regions of Louisiana (LA) and South Carolina (SC) (Figure 2-1). These areas are important to wintering (Mikuska et al. 1998) and breeding populations of wading birds. Both regions have a humid subtropical climate and are centered on major river deltas and estuaries within the coastal plains. Both regions contain a large proportion of wetland area ranging from 73.3% (LA; Table 2-1) to 39.4% (SC; Table 2-2) and possess a concentrated area of impounded wetlands related to past or present agricultural practices. The LA study area included the major metropolitan areas of New Orleans and a portion of Baton Rouge, while SC included Charleston and Myrtle Beach, providing each with a similar portion of urbanized land cover (8-9%).

Agricultural Wetland Systems

Rice and crayfish production is often combined in a rotational manner in southern Louisiana. Rice fields typically are flooded in spring as rice is planted (March-May) and approximately 10cm of water is maintained in the field for weed control until draining and harvest (Aug-Sep). After the harvest, fields may be planted with soybeans or another terrestrial crop, or flooded to attract waterfowl over the winter and/or for crayfish production.

Crayfish production involves shallow flooding (30-40cm) in the fall (Sep-Oct), often following the rice crop, and drainage after the harvest the following May-Jun (McClain et al. 2007). A rotational system of rice-crayfish-fallow or rice-crayfish-soybean over a two year period is the most common method; accounting for ~70% of crayfish farming in Louisiana (McClain pers. comm. Jun 2011). Timing is often staggered so that there will

be crayfish fields available in one year to restock rice fields that will produce crayfish the next.

In South Carolina, many defunct rice fields from the 1800's remain along the tidal river floodplains. Many of these are now on wildlife refuges and game lands managed for a combination of waterbirds throughout the year. Water levels may be lowered in the spring and summer for migrant shorebirds and breeding wading birds, and raised in the fall to grow aquatic vegetation for waterfowl that use the flooded impoundments during the winter. Private landowners typically flood their impoundments for waterfowl in the winter and drain for planting corn or millet in the early spring. The timing and management of individual fields varies by manager, location, intent, and season and thus a landscape of deep and shallowly flooded, planted, and barren fields exist throughout the year.

Satellite Telemetry Study

I used satellite telemetry to study movements and habitat selection of individually marked adult Great egrets. From September 2010 through February 2011, great egrets were captured in coastal LA and SC at foraging and loafing locations using a pneumatic net gun fired from a moving automobile (Meyer et al. in prep). Solar powered GPS satellite transmitters (Model 22GPS, Northstar Science and Technology) were placed on adult great egrets using a Teflon ribbon backpack style harness. Total mass of the attachment (35 g) was kept to less than 4% of the bird's body mass.

The GPS transmitters were programmed to collect 2 locations per 24 hrs: 1 between 0800 and 0900 hrs local standard time, when birds were presumed to be foraging (Wiese 1975; Kushlan 1978) and a second from 0200 to 0300 hrs, when I presumed birds to be at roost sites. I used 1 foraging location per day to ensure independence

within locations (Gawlik 2002). Data collected from capture through August 15, 2011 was included in the analysis (maximum period of data collection of 11.5 months for any individual)

Classification of used and available wetland habitat

I adopted the Cowardin et al. (1979) definition of a wetland used in the National Wetland Inventory (NWI; USFWS 2011). Deepwater habitats such as lakes, rivers, and marine environments are not wetlands, but are still important aquatic features for wading birds included in this study and the NWI. I extended the definition to include the agricultural impoundments described more fully below. I use the term “natural” in reference to any wetland features that are not impounded, diked, or excavated; but acknowledge that wetlands identified as natural within the study may be impacted by human activity.

I used a geographic information system (ArcGIS v. 9.3; ESRI, Redlands, California) and the ABODE extension (Laver 2005) to calculate 90% fixed kernel home ranges for individuals for which >30 daytime locations were collected (Seaman et al. 1999) using a bandwidth determined by least squares cross validation (Worton 1989). I considered habitat as available to each individual if it was within a 20 km buffer around the center of each 90% kernel contour polygon. Twenty kilometers is a distance used previously to define habitat available to great egrets (Custer et al. 2004; Leberg et al. 2007) and was appropriate for this study as it approximately matched the maximum distance (22 km) traveled between roost and subsequent foraging site by any tagged egret and included all habitat within the kernel home ranges. If 2 or more disjointed polygons were created for an individual, buffers were created from each center point.

The buffers for all individuals within each of the 2 states (SC and LA) were merged to delineate my study areas.

I identified wetlands within the study area using the NWI. I reduced the NWI categories to 5 classes: emergent wetland, forest/scrub wetland, pond/lacustrine, riverine/canal, and unconsolidated shore. Each of these categories was further divided into one of the following categories: Constructed, Natural, and Riverine habitat. Wetlands categorized as impounded, diked, or excavated in the NWI were grouped as “constructed wetlands” while the remaining were grouped as “natural.” Riverine wetlands (including canals in LA) presented too many subtleties of modification to be classified cleanly as constructed or natural, and were retained as “riverine” habitat. Land cover not classified in a wetland category was lumped into a “terrestrial” habitat type.

I updated the NWI layer (based in part on 1980’s imagery) 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 (USDA 2010, 2011). I digitized any unclassified ponds $>1000\text{m}^2$ and canals $>10\text{m}$ wide. I also removed wetlands that had become occupied by urban and agricultural development. I assigned newly identified ponds to the sub-class of constructed wetlands, and canals to riverine habitat type. I identified wetlands surrounded by dikes or levees as constructed and confirmed or updated their status in the NWI layer. I identified these features by contrasting water depth or vegetation compared to their surroundings, visible levees and/or structures in place that could allow for depth manipulation.

Since great egrets can only utilize the shallow boundaries of deep water environments, I placed a 5 m buffer inside NWI wetlands originally classified as sub-

tidal estuarine/marine, riverine, pond, and lacustrine to better approximate the area available to egrets. This also effectively excluded open ocean from the study areas. Areas for each habitat were calculated using the USA contiguous Albers Equal Area Conic coordinate system.

Only daytime points with estimated accuracy error $\leq 100\text{m}$ and reported velocity $\leq 4\text{ m/s}$ were retained for analysis of foraging habitat use by the great egrets. In addition, daytime locations at known breeding sites were excluded. Points were assigned to the habitat class of the NWI wetland that they were located within, or the closest habitat within their reported margin of error. Points not within this proximity of wetlands were classified as terrestrial.

Analysis of habitat selection

I compared composition of home ranges to the proportions of habitat available within the study area. For each individual, I also compared the proportion of egret locations in each wetland type to the composition of the 20 km buffer around the home range center. I first tested for a difference between the selection of the broad categories of constructed and natural wetlands. If significant differences existed, I tested selection of specific wetland types to understand the pattern. To determine the effect of my classification of riverine/canal habitats, I reanalyzed the data including them with constructed habitats. I used compositional analysis to rank habitats and compare selection between habitat types (Aebischer et al. 1993). Data were analyzed in Program R using the `adehabitatHS` package (Calenge 2006), using Wilkes Lambda to test for overall selection and a randomization test with 1000 replicates to compare selection between habitat types ($\alpha = 0.05$).

Aerial Survey Study

I conducted aerial surveys of wading bird habitat use over a landscape of mixed agricultural wetlands and natural wetlands located outside of the geographic limits of the satellite telemetry study. This area included the southern portion of the crayfish and rice agricultural area in south-central LA and an expansive area of natural emergent wetlands to the south (Figure 2-3). On the boundary between these 2 primary land cover types were several great egret colonies, a situation I viewed as ideal for testing the prediction that great egrets prefer foraging in these highly productive agricultural wetlands.

I identified 4 colonies from 2008 that contained >100 great egrets (LNHP 2008) and that were located along the boundary of the agricultural region and southern marshes. I placed 30 km buffers around these colonies to delineate the study area boundary. This was typically the maximum distance that foraging great egrets travel from their colony locations to foraging sites (Custer and Osborn 1978; Smith 1995; Custer and Gali 2002). Survey flight transects were positioned at random distances north and south of the geographic center of the study area and oriented in an east-west direction. The length of each transect was also randomly determined, but were constrained by the boundary of the study site.

I counted birds on these transects from a Cessna 172 during the 2010 great egret breeding season on 27 March, 21 May, and 25 June. These time periods corresponded to periods of high food demands by nesting birds. Flights were conducted between 0800-1200 hrs with the same 2 observers and pilot conducting all 3 surveys, from an altitude of 500 feet and a ground speed of 120-145 km/h. Windows and wing struts were marked to delineate a 250m 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 habitat types were recorded. Habitat categories were rice paddy, crayfish pond, emergent, and other. The “other” category included all terrestrial land cover and forested wetlands. 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 nesting at colonies were not counted. Photographs were taken of aggregations >10 individuals to confirm number and species. The NWI and NAIP imagery were used to separate constructed emergent wetlands from natural wetlands. Selection ratios (Manly et al. 2002) comparing habitat used by great egrets to habitat available within the survey strips were created in Program R using the adehabitatHS package (Calenge 2006) and compared using Bonferroni confidence intervals.

Independent double observer counts (Nichols et al. 2000) were conducted within the study area during travel between transects but not during survey counts. Sightings were categorized by habitat type and size of foraging aggregation. Groups of 3 or more birds were analyzed separately from foraging pairs and individuals to account for potential differences in the detections of groups and individuals. Detection probabilities were estimated by habitat type, observer, and group size in the software program DOBSERVE and compared using AICc (Hines 2000).

Results

Satellite Telemetry

During the fall and winter of 2010-2011, 41 GPS equipped satellite transmitters were placed on great egrets, and >30 daytime location points were gathered for 30 individuals (LA=11, SC=19). The average number of foraging location points collected for each bird was 117.8 ± 12.7 SE. Eighty-three percent of the points retained for

analysis had reported accuracy error <26m, and 96% were collected between 0700 and 1100 hrs when wading birds are often foraging (Wiese 1975; Kushlan 1978).

The study areas defined by a 20 km radius around all home range centers in LA and SC (Fig 2-1) were 9,932 km² and 8,484 km² (excluding open ocean), respectively. Study area composition (Table 2-1 and 2-2) differed most between the 2 states in the proportion of terrestrial land cover and emergent wetland area. The total proportion of wetland area available to individuals was greater in LA than in SC. Constructed wetlands made up a similar percent of total wetland area within the LA (4.31%) and SC (4.47%) study areas.

Emergent wetlands were the most commonly used habitat in both study areas, followed closely by riverine/canal habitat in LA and constructed ponds in SC (Figure 2-2).

Use of constructed wetlands

All but two of the tagged egrets from Louisiana were recorded in constructed wetlands at least once. Louisiana egrets occupied constructed wetlands at 10.8% ± 5.2 SE of point locations. Constructed emergent wetlands were used by 6 of 11 egrets in Louisiana, and only 1 egret used constructed forest/scrub wetlands. Constructed ponds were used by 6 of the 11 egrets, but one of these individuals was recorded 146 times (56% of its locations) in constructed ponds within the New Orleans metropolitan area. Egrets in South Carolina used constructed habitats at 41.7% ± 8.0 SE of point locations. Four of the 19 egrets in SC used constructed wetlands >80% of the time, mostly occupying constructed ponds/lakes. Constructed emergent wetlands were used by 3 of the 19 SC egrets, and 1 bird made use of constructed forest/scrub wetlands.

The rare habitat classification of constructed unconsolidated shore was never occupied in either state.

None of the satellite tagged egrets in either state appeared to use functioning agricultural wetlands. However, these wetlands were mostly absent from the study areas. The historic but dysfunctional rice impoundments along the river floodplains in Georgetown County, SC were used 11 times by a single tagged egret over a 38 day period.

Selection of constructed wetlands

In LA, I failed to detect overall selection at the home range scale (Wilkes Lambda = 0.6236, $P=0.252$), or foraging site scale (Wilkes Lambda = 0.6288, $P=0.271$) and constructed wetlands were not selected over natural wetlands at either scale ($P=0.943$, $P=0.575$, respectively). The trial including riverine habitat within the constructed category produced similar results (Wilkes Lambda = 0.6384, $P=0.156$), with constructed wetlands not selected over natural wetlands ($P=0.098$).

In SC, habitat selection at the home range scale was detected (Wilkes Lambda = 0.3475, $P=0.002$). Constructed wetlands were selected over riverine habitat ($p<0.001$), but not over natural ($P=0.317$) or terrestrial ($P=0.891$) habitat at the home range scale. Overall selection of foraging sites within 20 km of each home range center was also detected (Wilkes Lambda = 0.0559, $P=0.001$), and constructed wetlands were selected over natural wetlands, riverine, and terrestrial habitats ($p<0.001$). Further investigation of foraging site selection in SC by comparisons of specific wetland types determined that constructed pond/lake habitat was selected more strongly than all other habitat types (Table 2-3; $p<0.001$). There was a significant difference in the selection of each of the 3 constructed habitat types where constructed ponds were selected greater than

constructed emergent ($p < 0.001$), which was selected over constructed forest/shrub wetlands ($P = 0.008$).

Aerial Surveys

The area within 30 km of great egret colonies in LA covered 4,974 km² (Figure 2-3). I surveyed approximately 137.5 km² of this area (2.76%) within the survey transect strips and recorded a total of 1333 foraging great egrets.

Analysis of great egret detection rates indicated that the null model incorporating no effect of observer or habitat was the best model for both group sizes. Competing models included evidence of observer effect ($\Delta AICc \sim 0.6$) and habitat effect ($\Delta AICc \sim 2$). However, the differences in detection estimates between these models and the null were considered non-biologically significant as estimates were all within 3-9% of each other. Therefore, no adjustments to the count data were made for observer or habitat effects.

Impoundments used for crayfish production were the only habitat type consistently selected more than natural emergent wetlands (Figure 2-4), and used more than expected given their availability in every survey. The selection of rice fields by great egrets changed over time: flooded rice fields were scarcely used in March, selected positively in May, and used in proportion to their availability in June. I did not detect a significant difference between the selection of natural emergent and constructed emergent wetlands in any month.

Discussion

Overall, I did not find evidence that great egrets favor constructed habitats over natural wetlands. Rather, the pattern of selection changed between study areas and by wetland type. Foraging site selection differed for each constructed wetland type in SC

(Table 2-3). Constructed ponds were highly selected as foraging sites there, but this pattern was not detected in LA, where I did not detect differences between the selection of constructed and natural wetlands.

In LA, “riverine” was the second most used habitat (Figure 2-2), but this category included aquatic features along a gradient of human control. Many birds foraged frequently along wide, navigable canals that didn’t fit neatly into constructed or natural categories. I ran the analyses comparing selection of constructed and natural wetlands again, this time including the riverine habitat class in the constructed category and observed the same results.

The low use of most constructed wetlands during the telemetry study (Figure 2-2) combined with the fact that these wetlands were generally uncommon (accounting for <5% of available wetland area in both study areas) suggests that most constructed wetlands are currently not very important to great egrets on a national scale. However, two constructed wetland types may be important for local populations: ponds and agricultural wetlands.

Ponds as Great Egret Foraging Habitat

Constructed ponds were abundant in the urbanized regions of both states. Egrets tagged in South Carolina selected constructed ponds more than any other habitat type, while in Louisiana, only the egret tagged within the New Orleans Metropolitan area utilized ponds extensively. Since great egrets were captured with net-guns fired from a slow moving vehicle, the majority of captures occurred at roadside canals and constructed ponds. Individuals captured may therefore have been more predisposed to forage in these habitats than a true random sample of the population. The fact that so many egrets used constructed ponds so frequently and throughout the duration of the

study indicates that constructed ponds provide important foraging opportunities for great egrets, particularly in urban environments. However, conclusions regarding the importance of these habitats for a typical great egret should be made with caution.

Many constructed ponds are deeper (1-15m on golf courses, White 2003) than the maximum depth accessible by great egrets (28cm, Powell 1987), which limits their foraging to pond edges. Edges may be ideal foraging locations for wading birds as prey fish seek shelter from aquatic deepwater predators in shallow water (Werner et al. 1983; Power et al. 1985) despite predation risk by wading birds (Crowder et al. 1997). Other studies have also found great egrets to be attracted to constructed ponds at golf courses (White 2003) and phosphate mines (Edelson and Collopy 1990). Constructed ponds may allow great egrets to coexist with urban development, although it's important to note that no birds were found exclusively in ponds. This suggests that compatibility with development is only likely where there are other habitats for roosting and feeding.

Agricultural Wetlands as Great Egret Foraging Habitat

This was the first study to quantify habitat selection by wading birds in a crayfish aquaculture system. In crayfish aquaculture, farmers mimic natural ecosystems by providing a community of plants and invertebrates for crayfish to eat. This community, in addition to the stocked crayfish, provides prey for larger predators which attract great egrets. Fleury (1996) found that crayfish ponds can rival natural wetlands in terms of the number of fish present and that great egrets had higher foraging success and took more preferred prey items in crayfish ponds. Strong selection of crayfish ponds in June was attributed to the draining of ponds. This reduction of water level provides an increasingly shallow environment of concentrated prey. During these drawdowns, crayfish ponds have significantly higher crayfish, fish, and total prey densities than natural wetlands

(Fleury 1996). This pulse of food availability coincides with the late nesting period for great egrets, a time when nestling death from starvation is usually high, and likely has abundant food likely has a significant impact on local reproductive success.

The selection of rice fields changed over the study period, which I attribute to a tradeoff between increasing prey density and decreasing accessibility. In rice fields, wading bird prey reaches maximum abundance during the late summer prior to harvest (Gonzalez-Soliz et al. 1996; Lane and Fujioka 1998; Sizemore 2009). Rice fields may offer little prey for great egrets soon after inundation, a prediction supported by nominal use of this habitat during March. Invertebrate densities in Louisiana rice fields during May (Hohman et al. 1996) are comparable to those of natural emergent wetlands in the state (Manley et al. 1992) and great egrets selected rice fields over natural wetlands in May. While some farmers in the region do stock to stock rice fields in late May and June with crayfish for harvest the following spring in rotational practices, they typically wait until rice stalks are large enough to avoid damage from foraging crayfish, provide shade for temperature regulation, and deter predatory birds (McClain pers. comm. June 2012), therefore, I do not believe that the stocking of crayfish was a major factor in attraction of egrets to these rice fields. Despite the presumed higher prey densities in June, selection of rice fields decreased from the May survey, probably because of the coverage and density of rice stalks that inhibits access (Lane and Fujioka 1998; Fujioka et al. 2001; Sizemore 2009).

Rice fields in southern LA do not appear to be as important as rice fields in other parts of the world for great egrets. At my study site, rice fields only provide suitable foraging habitat for a short part of the year (~2 months). Crayfish ponds and emergent

wetlands appear to be more important in supporting local great egret populations year round. However, as rice farming is usually an integral part of the crayfish production system, it is not possible to manage these habitats independently from a wildlife perspective.

I originally anticipated that egrets tagged in Louisiana would at some point make use of this region of dense agricultural wetlands 200 km to the west of their capture locations. This was not the case and agricultural wetlands were generally absent from the habitat considered available to the tagged birds. While the farthest foraging foray recorded during the study was 22 km, several individuals moved distances many times further than 200 km (Chapter 3). Similarly, the area of historic rice impoundments was geographically in the center of the SC study area and within 200 km of any of the tagged birds in that state, yet only 1 of the 19 egrets utilized these constructed wetlands. My observations therefore provide no evidence of attractiveness at a statewide scale by these constructed wetlands. I conclude that even when these constructed wetlands are at their most seasonally attractive, they are not *magnets* for egrets at a regional scale and are not responsible for supporting entire regional populations.

It is often assumed that a species will select resources that are best able to satisfy its life requirements, and that high quality resources will be selected over poor quality ones (Manly et al. 2002). However, there are situations in which selection may not reflect the quality of a habitat (Van Horne 1983). The relationship between habitat selection and fitness or reproductive success of great egrets was beyond the scope of this study and I have no evidence that these selected habitats function as ecological

traps. Exposure to structural hazards, disease, and toxins may be elevated in ponds and agricultural areas where pesticides, herbicides, and run-off are of concern and can affect wading bird health (Parsons et al.2010). My findings highlight the importance of future research into the relationship between both agricultural wetlands and constructed ponds to wading bird mortality and reproductive success.

Summary

I observed strong selection at local scales for constructed ponds and agricultural wetlands by great egrets in comparison with natural wetlands. Selection of constructed ponds in SC coupled with consistent use indicated that the populations in this urbanized area might be supported to some significant extent by these features. In agricultural regions of LA, the pulse of food during the draining of crayfish ponds coinciding with the nestling period is likely important to the breeding success of local colonies. Rice fields, however, were positively selected during only a short portion of the breeding season. At broader spatial and time scales there was no indication that regional populations were reliant upon these agricultural wetlands.

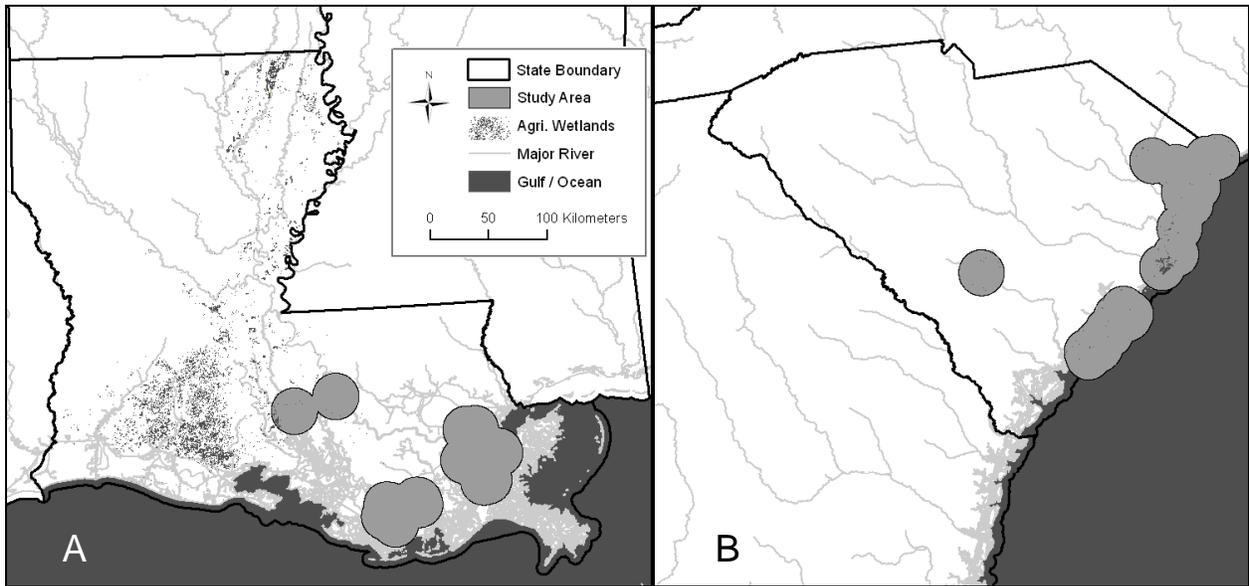


Figure 2-1. Study area extent defined by 20 km radii around home range centers for great egrets tagged with satellite transmitters. The rice and crayfish impoundments in Louisiana (A) and abandoned rice plantations in South Carolina (B) are identified.

Table 2-1. Proportions of habitat types available within the study area, home range, and 20 km radius circle used to define available habitat for individuals, and the proportion of satellite locations falling within each foraging habitat for great egrets in Louisiana, USA.

Habitat Type	Scale						
	Study Area	Home Range		20 km Radius		Point Locations	
	Percent	Percent	SE	Percent	SE	Percent	SE
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
Woody	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
Constructed – Emergent	1.47	1.01	0.52	2.18	0.34	3.28	2.35
Constructed - Forest/Scrub	1.58	1.42	0.89	1.94	0.77	2.41	1.62
Constructed - Pond/Lake	0.11	0.22	0.09	0.09	0.04	6.69	5.43
Constrcuted- Unconsol.Shore	0.01	0.00	0.00	0.01	0.01	0.00	0.00
Riverine/Canal	0.30	0.77	0.28	0.28	0.05	30.51	9.92

Table 2-2. Proportions of habitat types available within the study area, home range, and 20 km radius circle used to define available habitat for individuals, and the proportion of satellite locations falling within each foraging habitat for great egrets in South Carolina, USA.

Habitat Type	Scale						
	Study Area	Home Range		20 km Radius		Point Locations	
	Percent	Percent	SE	Percent	SE	Percent	SE
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
Constructed – Emergent	1.28	0.88	0.61	0.55	0.23	3.81	1.51
Constructed - Forest/Scrub	0.22	0.09	0.04	0.16	0.02	0.19	0.14
Constructed - Pond/Lake	0.26	1.09	0.15	0.32	0.03	39.90	8.15
Constructed- Unconsol.Shore	0.00	0.01	0.01	0.01	0.00	0.00	0.00
Riverine	0.13	0.06	0.03	0.30	0.08	0.41	0.41

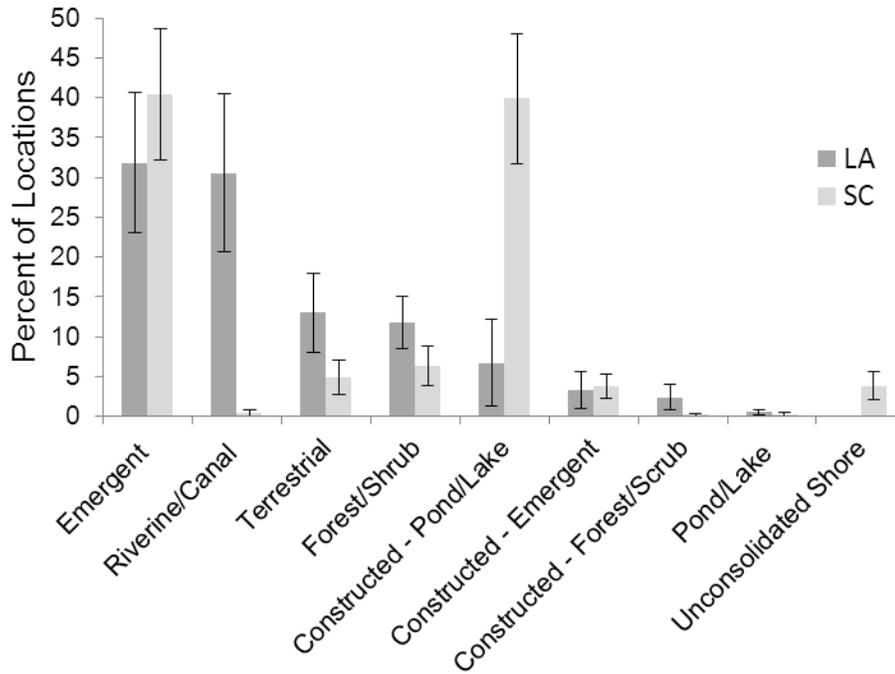


Figure 2-2. Average composition of habitat types used by great egrets tagged with satellite transmitters during daylight hours in Louisiana and South Carolina. Error bars indicate \pm SE.

Table 2-3. 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 selected. The sign indicates how selection of the row habitat differed from selection of column habitat type. Periods indicate no significant difference in selection.

Habitat Type	Rank	Significance of pairwise comparison of selection								
		PL*C	EM	EM*C	PL	FS	US	FS*C	RI	TER
Constructed - Pond/Lake (PL*C)	1	.	+	+	+	+	+	+	+	+
Emergent (EM)	2	-	.	.	+	+	+	+	+	+
Constructed Emergent - (EM*C)	3	-	+	+	+
Pond/Lake (PL)	4	-	-	+	+	+
Forest/Scrub (FS)	5	-	-
Unconsolidated Shore (US)	6	-	-
Constructed Forest/Scrub- (FS*C)	7	-	-	-	-
Riverine (RI)	8	-	-	-	-
Terrestrial (TER)	9	-	-	-	-

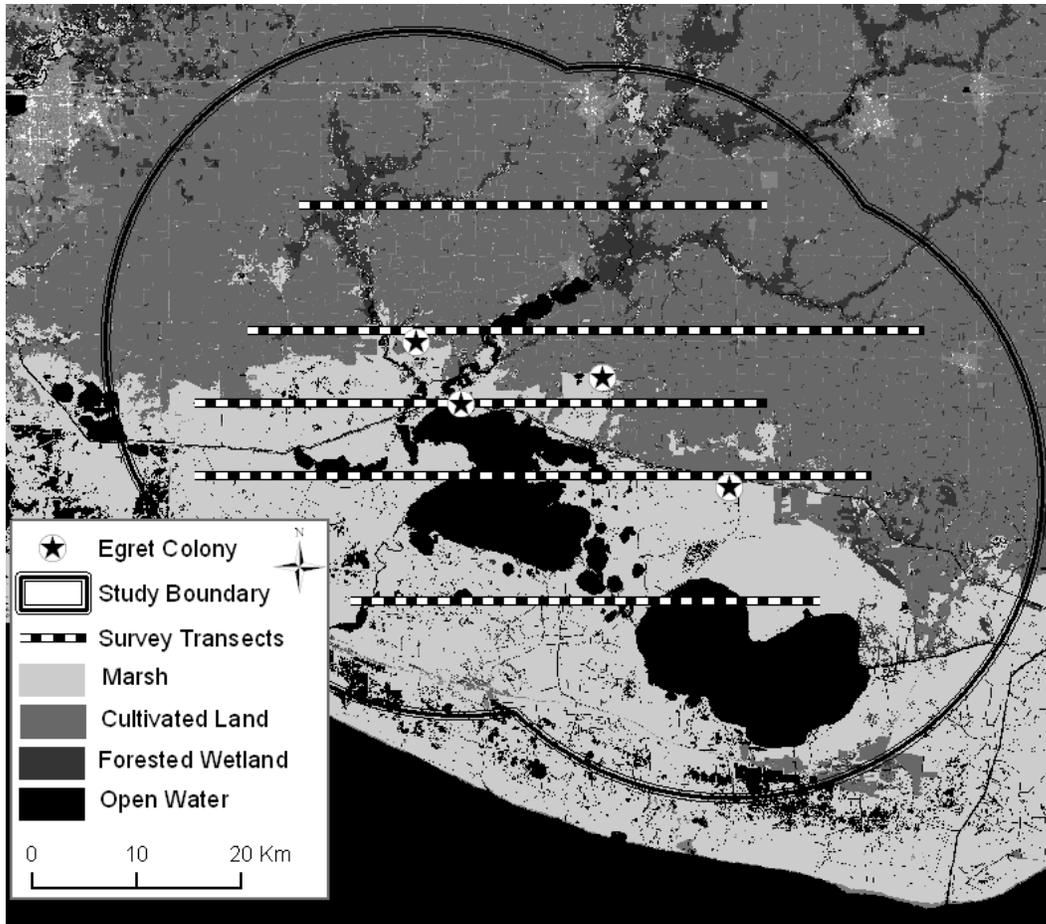


Figure 2-3. Flight transects and land cover map of area surveyed for great egrets in Louisiana, USA.

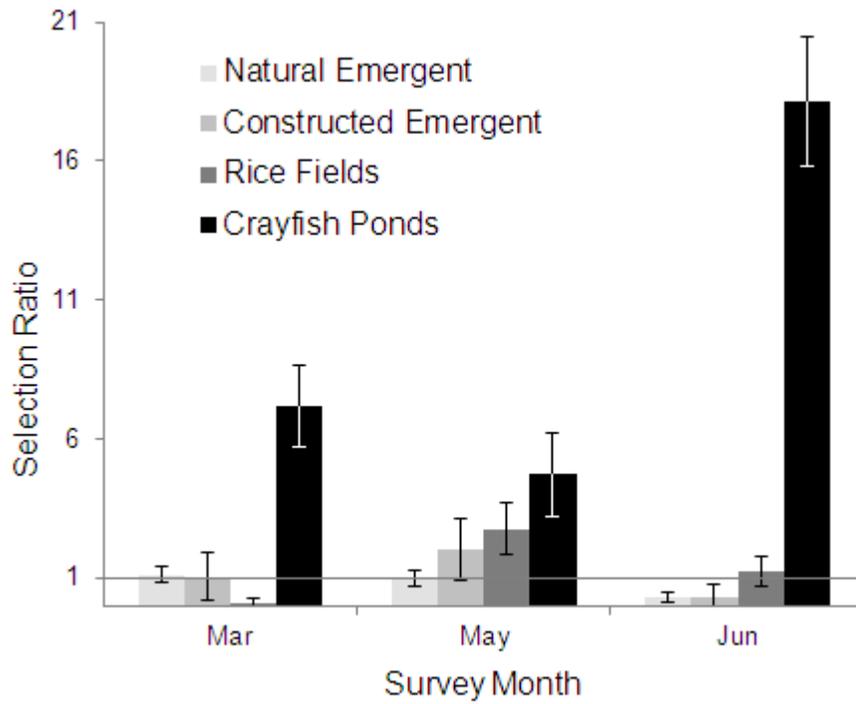


Figure 2-4. Selection ratios (+/- 95% CI) for habitat types used by foraging great egrets observed during aerial surveys near breeding colonies. A ratio >1 indicates habitats were selected more than expected given their availability. Note that the “other” land cover class which was used very rarely is not displayed.

CHAPTER 3 LOCAL AND LONG-DISTANCE MOVEMENT PATTERNS OF TWO GREAT EGRETS POPULATIONS

Background

Understanding movement patterns at various scales is essential for understanding of the ecology, life history, behavior, and conservation of most animals (Rubenstein and Hobson 2004). Few taxa possess the capacity for undertaking broad scale movements as far and rapid as birds, and no group of birds demonstrate this capability better than waterbirds: bar-tailed godwits (*Limosa lapponica*) fly non-stop across the Pacific (Gill et al. 2005), bar-headed geese (*Anser indicus*) are the world's highest altitude flyers (Scott et al. 2009), and arctic terns (*Sterna paradisaea*) travel from pole-to-pole twice each year (Hatch 2002).

Waterbirds evolved the ability to make such movements because the aquatic habitats they depend upon are highly dynamic. Particularly, food resources are patchily distributed in space and time, being influenced by global climate patterns, ocean currents, and local factors including hydrology, rainfall, and temperature (Kushlan and Hafner 2000). Thus, waterbird movements are primarily undertaken in response to foraging conditions (Pineau 2000; Dodman and Diagna 2007).

There are three general movement strategies used by birds for meeting their needs. Birds may be 1) migratory: conducting regular back-and-forth movements between two or more seasonal ranges, 2) nomadic: conducting irregular and unpredictable movements often in response to resources that are spatially and temporally unpredictable, or 3) sedentary: neither of the above (White and Garrott 1990; Dodman and Diagna 2007; Boyd et al. 2008). While these definitions are mutually exclusive, most species' use of them is not and subpopulations of the same species

may utilize different strategies (Boyd et al. 2008). In addition, dispersal is the movement of an individual away from the place of birth or population centers (Koford et al. 1994) and can describe certain movements of individuals that utilize any of the above strategies.

Wading birds (hereafter used in reference to the long legged waders including herons, egret, bitterns, storks, spoonbills, and ibises) are a group of waterbirds dependent upon shallow wetlands for foraging. Few other habitat types are as spatially and temporally dynamic, resulting in ephemeral food patches which are widely distributed (Hoffman et al. 1994). Wading birds are sensitive to prey availability (Kushlan and Hafner 2000; Crozier and Gawlik 2003; Frederick et al. 2009), which appears to be the primary driver of their breeding success (Frederick and Collopy 1988; Maddock and Baxter 1991; Hafner et al. 1993) and over-winter survival (Butler 1994; Cezilly 1997). Therefore, they are dependent upon their ability to locate and exploit patches of prey year round (Frederick and Spalding 1994), and their movement strategies have evolved to cope with this challenge (Kushlan 1986; Frederick and Ogden 1997). However, many details regarding the annual movements remain unknown because we have lacked a way to study movements across broad scales.

The great egret (*Ardea alba*) is a widespread species, common throughout many temperate and tropical regions of the world. They are wide ranging wetland generalists able to exploit a variety of wetland types (Chapman and Howard 1984; McCrimmon et al. 2011). Great egrets breed along both Pacific and Atlantic coasts from Washington and Maine south to Argentina and Chile, and also utilize scattered interior locations in the U.S., particularly within the Mississippi River Basin (McCrimmon et al. 2011). The

local movements of great egrets have been well studied during the breeding season. Studies of unmarked breeding individuals followed by plane have been useful in answering questions regarding local foraging flight distances, flight speeds, and habitat selection (Custer and Gali 1978, 2002; Thompson 1978; Smith 1995; Custer et al. 2004).

Band recovery studies have provided much of the current information regarding larger scale movements in North America (Coffey 1943; Coffey 1948; Byrd 1978; Mikuska et al. 1998; Melvin et al. 1999). Great egrets are considered migratory through much of North America, but some populations may be resident or disperse locally (Miccrimmon et al. 2011). However, large average dispersal distances (908 km) from natal sites to subsequent breeding sites, and a relatively low philopatry (24%) may indicate a more nomadic strategy (Melvin et al. 1999).

Important wintering areas of U.S. breeders include Florida and coasts of the Mid-Atlantic States, Gulf of Mexico, Central America, Bahamas, and Greater Antilles, although some move as far as Colombia (Mikuska et al. 1998). East-west movements are apparently uncommon, and populations breeding in Atlantic States appear to stay within the Atlantic Coast, Florida, and Caribbean, while banded birds from the Mississippi River Basin have been recovered mostly along the northern Gulf into Mexico, Central America, and western Cuba (Byrd 1978; Melvin et al. 1999). Banding data has provided information on the distances of movements over large periods of time (months or years) but have not provided details into the timing or frequency of these movements.

The annual pattern, types of movements, and number of movements made by great egrets is interesting from an ecological standpoint, as it provides previously unknown information about a common and widespread species. Little is known about this species's wintering movements and space use despite the critical role winter survival plays in driving wading bird population dynamics (Butler 1994; Cezilly 1997). Elucidating these details will allow for better interpretations of studies using wading birds as indicators of environmental change (Kushlan 1993; Erwin and Custer 2000) and increase our understanding of the interconnectedness of wading bird populations for the management and conservation of wading birds (Boyd et al. 2008).

This is the first broad scale study of any Ardeid using a robust sample of individuals tracked across seasons. My objective is to identify the movement strategies employed by great egret populations in the southeastern U.S. I provide details regarding long-distance movements, particularly the duration, timing, and speed of these flights. I also describe local movements and space use and make comparisons between winter and breeding-season ranges.

Methods

Capture and Tagging

I used satellite telemetry to study movements individually marked great egrets. The coastal regions of Louisiana and South Carolina were selected as capture sites. These regions are important areas for both wintering (Mikuska et al. 1998) and breeding populations. From September 2010 through February 2011, great egrets were captured at daytime foraging and loafing locations using a pneumatic net gun fired from a moving automobile (Meyer et al. in prep). Birds were aged by tail feather and scapular shape (Pyle 2008). Solar powered ARGOS platform transmitter terminals (Northstar Science

and Technology) were placed only on after-hatch-year birds (hereafter, adults) using a Teflon ribbon backpack style harness. Two styles of transmitters were used including ones equipped with a global positioning system (Model 22GPS: hereafter GPS) and traditional transmitters (Model 12GS: hereafter PTT) that collected locations by measuring the Doppler effect, which is the change in transmission frequency emitted by the PTT as detected by the moving satellite (Argos 2011).

Total attachment weight was kept to $\leq 4\%$ of the bird's body mass. Great egrets with a mass too low (< 875 g) to carry the 35 g GPS package were fitted with the PTT package (26 g) but some birds that could have carried a GPS were given a PTT based on availability of transmitters. Great egrets were released at their site of capture after a total processing time < 60 min.

The GPS transmitters were programmed to collect 2 locations per 24 hrs: 1 at 0800-0900 local time and a second from 0200-0300 hrs. PTT units were duty cycled to collect data over an 8 hour period each day which shifted by a few hours each cycle allowing operational hours to rotate through a 24 hr clock. PTT locations are less accurate (≤ 1000 m) than GPS points (≤ 100 m) so results from PTT egrets were excluded from fine scale analysis. Data collected from capture through August 15, 2011 was included in the analysis (maximum period of data collection of 11.5 months for any individual).

Eighty-two adult great egrets were fitted with satellite transmitters. LA transmitters ($n=41$) were deployed in Sep and Oct 2010, followed by SC ($n=41$) from December 2010 to February 2011. An equal number of GPS and PTT transmitters were deployed (41 each), but more GPS transmitters were deployed in SC than LA (23 vs. 15) due to the delivery schedule from the supplier.

Home Ranges and Flight Distances

I calculated home ranges and foraging flight distances of great egrets carrying GPS transmitters which reported ≥ 30 daytime locations (Seaman et al. 1999). Locations were entered into a geographic information system (ArcGIS 9.3, ESRI, Redlands, California). I used the ABODE extension (Laver 2005) to calculate 90% contours from fixed kernel densities of locations of each individual using a bandwidth determined by least squares cross validation (Worton 1989).

I found that long, one-way movements resulted in an over-smoothed kernel and home range sizes that were not biologically sensible. To remedy this, separate kernels were calculated for individuals that moved >50 km from its previous location during the study and generated >30 location points. This distance was selected as it was >2 times as far as any egret had flown in a foraging foray. Foraging flight distances were determined by calculating straight line distance from the night location to the foraging location collected the following day. Distances <30 m were excluded as I assumed the egret was attending the roost or breeding colony and not foraging.

When comparing flight distances and home ranges between seasons, winter was defined as Sept- 1 Mar and the breeding-season as 15 Apr-15 Aug. I omitted data collected between 1 March and 15 April when the populations were transitioning from winter to breeding season activities. I have no independent confirmation of breeding status for any egret so breeding-season simply applies to the period when great egret movements are most likely to have been influenced by breeding activity.

Both PTT and GPS locations were used to identify long distance movements. I defined movements >100 km based on geodesic distances as “long distance” movements. Trip speeds (km/d) were recorded by comparing distance covered between

the last point before a movement and the first point transmitted from the apparent destination. Flight speeds (km/h) were estimated for each movement step. Both of these speeds are minimum estimates based on direct paths between points. Local wind speed and direction was averaged over the time between locations from NOAA weather stations located near the origin of the flight path, unless otherwise noted.

Statistical Analyses

I tested for a difference between average winter foraging flight distances and breeding season flight distances using a student's t-test. I tested for a relationship between the number of locations collected and range size using a linear regression. I compared overall seasonal range sizes between both seasons using a student's t-test, and conducted a paired t-test to test for an effect of season on home range size for 11 great egrets tracked with GPS transmitters over both winter and breeding season.

Results

Capture and Telemetry Data Summary

Adequate samples for computing home ranges and daily flight distances (>30 daytime locations) were collected for 30 GPS tagged great egrets. Eighty-three percent of the points retained for analysis had reported accuracy error <26m. No minimum sampling period was needed to describe long distance movements, but data from 14 transmitters were received for <14 days and are excluded from the following results. On average, the remaining birds were tracked over 172 days ± 10.8 SE with locations transmitted on 76.9% of days.

Local Movements

I measured the distance from roosts to 2540 subsequent foraging locations for 30 GPS tagged great egrets. The longest distance between roost and foraging site

recorded by an egret that then returned to the same roost (i.e. was not en route to a new roost) was 22.1 km. For birds tagged in LA, birds foraged closer to roosts in winter (1.6 km) than in the breeding season (3.8 km, $P=0.005$; Figure 3-1), but there was no difference for the birds tagged in SC ($P=0.102$).

Home ranges averaged $53.6 \text{ km}^2 \pm 12.3 \text{ SE}$ (range = 0.67–225.1 km^2) and did not differ between LA and SC, $t(28)=1.86$, $P=0.073$. When broken down by season (Figure 3-2), variation was high, with the exception of the winter population in LA ($n=11$) which showed consistently small home ranges averaging $7.9 \text{ km}^2 \pm 2.6 \text{ SE}$. Seasonal ranges were generated from $140 \pm 11 \text{ SE}$ location points. The 3 smallest seasonal ranges ($<1 \text{ km}^2$) were of 2 egrets wintering in LA which appeared to forage almost exclusively along a stretch of canal, and of a sedentary egret in SC during the breeding season which foraged along a tidal creek in an estuary and occasionally nearby constructed ponds. The 2 largest seasonal ranges ($>200 \text{ km}^2$) were for egrets during the breeding season. One in North Carolina in the northern bays of the Albemarle Sound traveled over broad areas of open water between locations. The other was a wintering egret in SC which utilized 3 discrete activity centers 10-20 km apart and a 4th after a long distance movement south.

I could construct home ranges in both seasons for a total of 11 individuals from either state, but found no pattern in size change between seasons and no overall difference, $t(10)=1.35$, $P=0.206$. There was not a significant relationship between home range size and the number of points collected, $R^2= 0.005$, $F(32) = 0.162$, $P=0.69$.

Long Distance Movements

I combined GPS and PTT tagged great egret data to identify long distance movements by individuals. Within the non-breeding season (Sept–Feb), data was

collected for 63 great egrets for at least 2 weeks, with 41 individuals transmitting data on ≥ 30 days. Six individuals conducted movements >100 km: 4 birds moved to southern locations while 2 moved inland.

Two egrets from LA traveled south to Honduras (Figure 3-2). PTT#100097 was in LA on the afternoon of 4 Nov, but 26h 20m later was 925 km south on the Yucatan Peninsula. I received no locations over the Gulf, but the travel time was too short to allow for the >2700 km circum-gulf route (e.g. an unrealistic minimum flight speed of >103 km/h). Average winds (44 km/h NNW) at a weather station in the central Gulf supported the direct flight. The egret continued south and was recorded both over the Caribbean Sea in favorable winds (24 km/h NNW), and in Honduras at 6 Nov 2205 hrs. It remained in Honduras until its last transmission on 13 Nov. For the second egret, GPS#100022, an unusually long 30 day period without transmissions occurred from 23 Nov-22 Dec, during which the bird moved from LA to the La Miskitia region of Caribbean coastal Honduras, where it transmitted for 3 more days.

GPS#100237 (Figure 3-2) spent 7–27 Dec in SC before a location 360 km to the south and 77 km offshore over the Atlantic Ocean received at 0301 hrs on 28 Dec. A weather buoy reported NW crosswinds (32 km/h) relative to the bird's heading. The bird was recorded at Cape Canaveral, Florida the next morning through 8 Jan. The 4th southward movement was of GPS#100235, which moved 104 km down the SC coast on 21 Jan, where it stayed 8 days before continuing another 50 km.

Two birds moved >100 km inland during the winter. PTT#100104 remained in SC until 28 Dec. By 30 Dec it moved 70km to the southwest where it stayed >8.5 hrs before it continued 150 km, stopping in the interior coastal plain of Georgia by 1 Jan.

PTT#100070 moved from coastal LA on ~17 Jan to the Atchafalaya Basin. It moved up and down the basin over the next 16 days, traveling up to 155 km from its prior location on the coast.

Forty-one great egrets (LA = 13, SC = 28) were followed from the winter into the breeding season. Most of these individuals stayed within 40 km of their winter locations (Figure 3-3). However, 12 egrets (1 in LA, 11 in SC) relocated >100 km between the winter and breeding season. These movements were conducted 12 Mar-24 Apr (mean departure date = 26 Mar).

GPS#100015 from LA, traveled 127.9 km on 8 Apr to a location in the Atchafalaya Basin. Most of the 11 long distance migrants from SC moved to locations on the Atlantic coast (Figure 3-4), with the exception of 2: PTT#100317 moved 134 km to North Carolina where it settled 132 km from the coast; GPS#100240 which traveled 1574 km to Michigan (Figure 3-5). GPS#100240 was unique for many reasons: it traveled in an indirect route, made 2 prolonged stopovers (5 and 6 days), crossed the Appalachian Mountains in Pennsylvania, and spent a night on the South Shore of Lake Ontario before initiating a daytime flight westward across Southern Ontario to Michigan. Upon departure, winds on this westward leg were favorable (24 km/h NNE), but it likely faced headwinds during the second half (18 km/h SW).

In addition, 2 egrets conducted long distance flights early in the breeding season but quickly returned to their winter locations where they remained into the spring. GPS#100242 departed SC on 29 Mar and traveled overland 380 km to St. Augustine, FL, transmitting several moving points at night. It stayed no more than 40 hrs but visited a known active breeding colony before returning to SC by 2 Apr. PTT#10073 traveled

128 km from coastal LA on 27 Feb to a forested swamp on the banks of the Mississippi River where it remained for 1 to 3.8 days. Both birds returned to the same roost area they had used before their trips.

Minimum speeds estimated for long distance movements indicated that great egrets at times were traveling at ground speeds >79.9 km/h (Table 3-1). Most migrations were completed in under 2 days, exemplified by GPS#100250 and 100236 which traveled >700 km in <24 hrs. GPS#100240 and 100248, each made stops totaling 12 & 15 days, respectively. For egrets traveling >300 km, trip speeds averaged 405 km/d \pm 66 SE.

Of the 12 birds that conducted long distance movements between seasons, 2 individuals returned to their previous winter ranges before the end of the study. GPS#100015 returned on 1 Jun and GPS#100252 returned by 21 Jun. The remaining 10 were still on in the vicinity of their breeding season ranges as of 15 Aug.

Movement Strategies

Individuals from both LA and SC utilized migratory, nomadic, and sedentary movement strategies over the course of the study (Table 3-2). Of the 41 individuals tracked from winter into the breeding season, 19 (46.3%) displayed sedentary behavior, maintaining overlapping seasonal ranges in a relatively small area- 14 of these individuals were never recorded moving outside of a 15 km radius. Thirteen (31.7%) were migratory, and 9 (21.9%) were nomadic, moving between multiple distant, non-overlapping areas of activity within a season. This included 2 individuals, described above (GPS#100242, PTT#100073), which made long distance, exploratory movements at the onset of the breeding season but returned to their prior locations within 5 days.

Discussion

Local Movements

I found average foraging flight distances during the breeding season (~4 km) that were within the range of those reported at breeding colonies (2.8 km - 13.5 km; Thompson 1978; Smith 1995; Custer and Gali 2002; Custer et al. 2004). Flight distances in the winter in LA were shorter than breeding season. This could be explained by breeding egrets being more place-bound in terms of roost site, as they would have to travel further to foraging sites, rather than move roost locations in response to changing foraging conditions.

I know of no other study which has calculated individual ranges for great egrets in any season. Most previous methods of addressing space use for colonial wading birds have relied on flight distances to determine the area of foraging habitat required by colonies, as opposed to individuals (Gibbs et al. 1987; Custer et al. 2004). My seasonal range estimates were highly variable, but overall surprisingly small (0.67–220.2 km²). The large variances in my size estimates reflect differences in the underlying movement patterns utilized (see below). Large seasonal ranges were indicative of nomadic behavior associated with occasional shifts of activity centers within a season.

Several birds relied upon a few adjacent wetland features, indicating that some habitats may provide stable resources within a season. I could not identify a difference range between seasons, and across wading bird species there appears to be no consistent trend. Seasonal ranges for Black storks in France were similar between breeding and non-breeding adults (540 km², Jiguet and Villarubias 2004), while great bitterns in Brittan had larger home ranges in winter (0.33 km²) than during breeding season (0.15 km²; Gilbert et al. 2005).

Egrets wintering in LA had surprisingly small home ranges and foraging flight distances and generally did not make long distance migrations between seasons. This suggests that the quality of habitat is high in LA. These birds were in an area of abundant wetlands which accounted for >70% of land cover in the region (Chapter 2, Table 2-1), providing a variety of wetland habitats within a short distance. As temperatures in the region are rarely below freezing, this area can provide potential foraging year round (Frederick and Loftus 1993).

Long Distance Movements

Great egrets traveled up to 1500 km from their capture locations. While the capacity for such long distance movement has been known from band recovery programs (max = 3125 km; Melvin et al. 1999), the speed and directionality of flight was poorly understood. Generally, long distance movements were rapid, both in terms of the overall journey and ground speeds. Most flights were direct with locations received during travel in line with origin and destination, and based on time between departure and apparent arrival I infer that there were few instances of prolonged stop overs. Flights were usually occurred at night, and sometimes over great expanses of open water.

Hérons and egrets use flapping flight for long-distance migrations (Liechti & Schaller 1999; Kushlan and Hafner 2000). When ground speeds could be estimated, I determined velocities as high as >79 km/h based on time between locations (Table 3-1). Average flight speeds of great egrets over short distances have been recorded between 35.8 and 38.8 km/h, with a maximum of 45.1 km/h (Custer and Osborn 1978; Stolen et al. 2007). My reported trip speeds are indicative of assistance from tailwinds. Surface winds recorded during flights were typically favorable, but the altitude at which these

great egrets were flying was unknown. Similar flight speeds were reported for purple herons (max 80.0 km/h) which migrated on average at 700m altitude (van der Winden et al. 2010). Altitudes reported during the migration of medium sized herons in Israel found use of high altitude winds (>5000m) to maximize travel speed (Liechti & Schaller 1999). My speed estimates could have been reached with the support of surface winds, but these minimum estimates are based on straight line distances and I suspect that maximum speeds were much greater for portions of the flights. Great egret flight speeds have been shown to be influenced strongly by relative wind direction when compared with other wading birds (Maccarone et al. 2008), so selection of departure day based on wind direction would be advantageous.

Long distance movements were direct in terms of flight path— suggesting that the birds may have been there before or were traveling with others who had. Great egrets may migrate individually or in small groups which have been confirmed departing colonial roosts together (C. Weseloh, cited in Miccrimmon et al. 2011). The prolonged stopovers en route to breeding ranges made by 2 individuals (GPS#100240, GPS#100236) may have been visits to potential breeding sites or refueling stops.

Minimum trip speeds, including stop over time, averaged >400 km/d for movements >300 km. Due to long intervals between locations, determining when birds arrived or departed was often not possible within less than a 16 hr window, and therefore trip speeds are certainly underestimated for many individuals. These speeds are impressive when compared to other wading birds. Wood storks in Florida and Georgia moved between seasonal ranges at an average daily rate of 53 km/d (max 184 km/d; Hylton 2004), and storks migrating from LA to southern Mexico used a

circum-gulf route through coastal Mexico over a period of several weeks (Bryan et al. 2008). Similar migration speeds are used by white storks (*Ciconia ciconia*) in Europe and Asia (Van der Bossche et al. 2002; Pierre and Higuchi 2004), which took up to 2 months to complete their route. Storks are much heavier than egrets and use thermals to glide during migration, and thus would be unlikely to migrate at night or over open water (Kirby et al. 2008) and would be more dependent on weather conditions. Pilot studies of purple herons (*Ardea purpurea*) from Europe showed a rapid migration of individuals averaging >600 km/day (van der Winden 2010). These migrants crossed vast areas of inhospitable habitat in the Sahara, so the potential for making stopovers did not exist. In fact, many birds perished along the route in sandstorms, suggesting a proximate pressure for the adaption of rapid flight over the area. However, my great egrets traveled at a comparable rate over vast areas of suitable wetland habitat.

Many herons migrate at night (Liechti and Schaller 1999; del Hoyo et al. 1992; van der Winden 2010), but published reports of migrating great egrets are scarce. They had been considered diurnal migrants (McCrimmon et al. 2011), though nocturnal migrations were also reported (C. Weseloh, cited in Miccrimmon et al. 2011). In this study, long distance flights were typically conducted at night, but may have continued into the following morning, and segments were occasionally initiated during day (GPS#100240).

Great egrets were known to fly across open ocean based on band recoveries of continental birds on Caribbean islands (Coffey 1948; Mikuska et al. 1998; Melvin et al. 1999), and it was hypothesized that the birds may be arriving in the Caribbean via the circum-gulf route and shorter open water distance from the Yucatan (Coffey 1948; McCrimmon et al. 2011). This study confirmed at least one incident of a great egret

crossing the central Gulf of Mexico (>925 km). A second great egret was confirmed over the Atlantic making a direct flight between SC and Florida, cutting across 480 km of open-ocean. Movements by great egrets and other Ardeids over open ocean are not unusual off the Florida coast based on incidental sightings made from vessels 60 to 160 km off shore (M. Brothers, personal communication, May 2012). While this does not clarify the route taken to reach Caribbean islands, it certainly increases our understanding of the navigational and flight capabilities of this species.

Different bird species are believed to navigate through a variety of methods including landmark orientation, magnetic compass, solar compass, and celestial aids (Berthold 2001). Reliance on one method could restrict migration capabilities. For example, some nocturnal migrants use celestial navigational to migrate (Emlen 1967), which inhibits their ability to migrate during the day. Both nocturnal and diurnal migrants may use landmarks for navigation (Berthold 2001), but very few migratory birds appear to transition between nocturnal and diurnal migration (Liechti and Schaller 1999). An open water crossing of the Gulf of Mexico would exclude reliance upon visual landmarks, while a solar compass could not guide nocturnal flights. Coupled with the ability of great egrets to continue to navigate and even begin long distance flights in the day may suggest that the birds are guided by a magnetic compass or are not reliant on a single navigational aid.

Variety in Movement Strategies

Migratory, sedentary, and nomadic individuals existed within the tagged population. Despite the impressive flight capabilities I described above, many of the birds (46.3%) displayed sedentary behavior and remained within the same general location over the duration of the study. Most of the birds were not tracked long enough

to confirm whether the long distance movements observed were regular and round-trip, and thus migrations. However, 6 great egrets did return to their prior winter ranges before 15 Aug, suggesting that these movements at the onset of the breeding season are likely migrations. While southward migration of this species has typically been considered a response to lowering temperatures (Miccrimmon et al.2011), these southward returns during the warmest months of the year suggest that other motivations are involved. Nomadic behaviors, in this case indicated by movements between separate areas within a season, also suggest alternative factors motivating movement.

Most of the captures were conducted within a relatively small geographic area and many egrets used similar habitat types (Chapter 2). Why individuals within populations responded differently to local conditions is unknown. Individual variability in movement strategies in response to the same resources challenges the idea that movement patterns simply reflect underlying resources (Roshier 2008). One explanation could be that behavioral differences likely exist between non-breeders and breeders within seasons in my populations. I could not verify breeding status to confirm this, but based on roost locations it appeared that breeding attempts were not limited to birds using a single strategy.

I observed a striking difference between LA and SC egrets in terms of the distance traveled between winter and breeding season ranges. Even though migratory individuals existed within both populations, the distance traveled by LA birds was generally short. The farthest distance measured between winter and breeding sites for an egret in LA was ~130 km, while 39% of the birds in SC moved over 100 km and traveled up to 1574 km en route to breeding season locations. My study area in LA

contained a higher proportion of wetland habitat than SC, and its coastal wetlands comprise one of the most biologically productive ecosystems in the United States (Templett and Meyer-Arendt 1988). Coupled with a lower latitude and slightly warmer climate, LA could support a higher percentage of great egrets as year round residents than SC, as its wetlands may be more predictably higher quality. In addition, my observations may partly be explained by a bias towards capturing non-migratory residents in LA produced by a difference in capture dates between LA and SC. Southward fall migration can continue as late as November-December in northern states (Miccrimmon et al. 2011) and in LA, great egret numbers increase substantially from November to February (Martin 1985). By Oct 1, 31 of the LA transmitters (75%) were deployed, essentially prior to arrival of winter migrants. In contrast, SC captures were conducted Dec-Feb, thus exposing many more migrants to capture than in LA. Likewise, some birds from the breeding population in SC may have already departed for southern locations prior to trapping. Therefore, it is difficult to make generalizations about the proportions of these populations utilizing different movement strategies from my results.

Nesting populations of great egret can fluctuate between years by orders of magnitude in regions of the southeast U.S. (Frederick 1995). These changes are too rapid to be explained by local birth and death rates and thus emigration and immigration are likely responsible, but how wading birds gain information about conditions at distant locations is unknown. It's plausible that great egrets are able to cue in to climactic patterns to predict conditions elsewhere, or may move solely by chance once local conditions deteriorate. However, this study provides evidence that great egrets can

quickly scout distance sites to gain first-hand knowledge to inform breeding decision. GPS#100242 traveled to north Florida and visited a known colony before returning to SC; a 4.25 day round trip of 759 km. Similarly, PTT#100073 made a round trip of 256 km up the Mississippi River and back.

Summary

My findings illustrate the variety of spatial and temporal dynamics of movement behaviors utilized by a common and widespread Ardeid. I confirmed that great egrets can move great distances and do so rapidly. Flights were usually direct, timed with local wind conditions, and conducted at night. Open water did not appear to dictate movement paths. Great egrets can apparently explore distant locations rapidly, allowing them to make decisions about where to breed and winter based on empirical local information. Despite these capabilities, not all great egrets need to make long distance movements and relatively small areas of high quality habitat can support egrets year round.

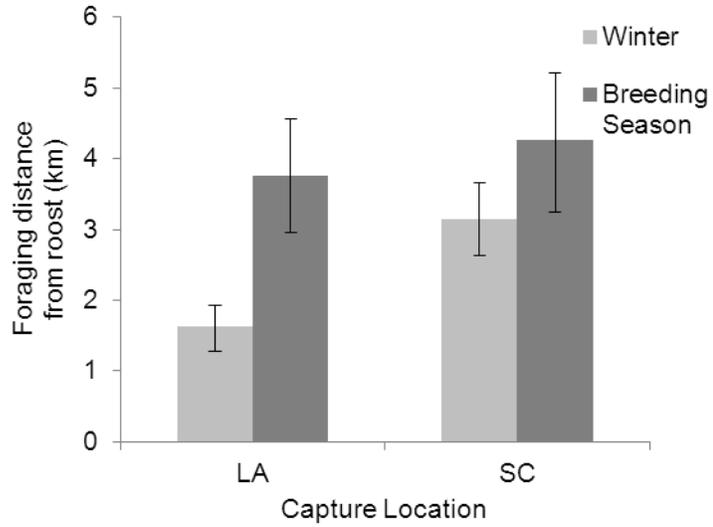


Figure 3-1. Average distance from nightly roost to subsequent foraging site for great egrets tagged with GPS transmitters in LA or SC. Winter distances were measured during Sep-Feb and breeding season from Apr-Jun. Error bars represent 95% CI.

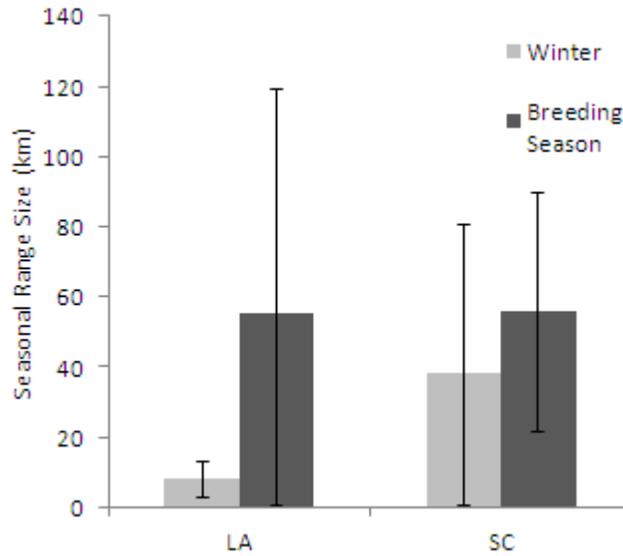


Figure 3-2. Comparison of 90% kernel ranges between seasons and capture location of great egrets tagged with GPS transmitters. Error bars represent 95% CL. Winter includes points collected Sep-Feb and breeding season from Apr-Jun.

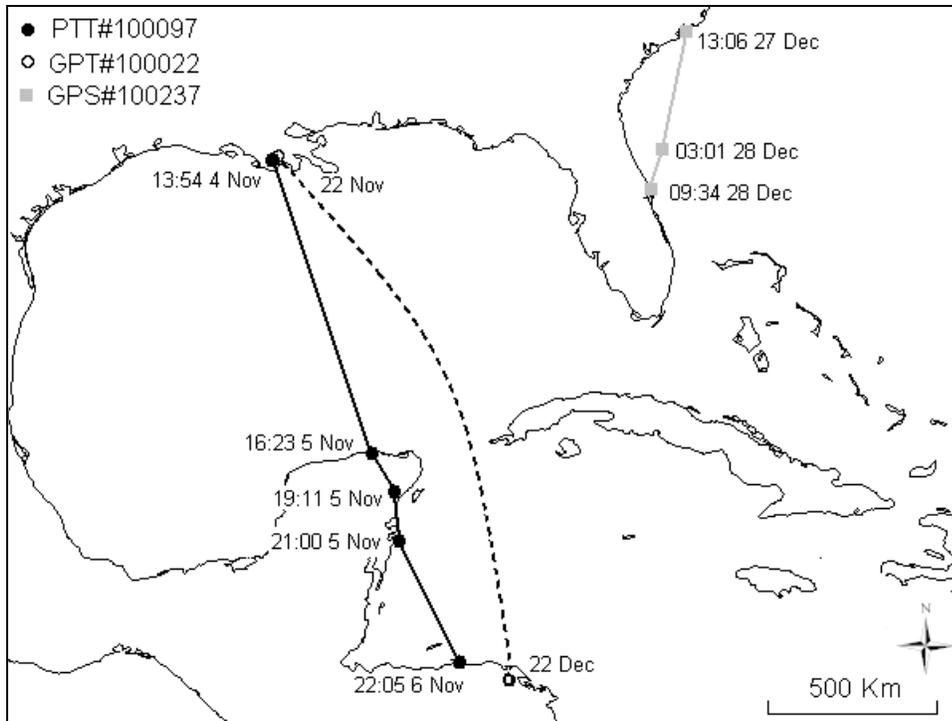


Figure 3-3. Southward long distance movements of 3 great egrets during the 2010-2011 winter. Dashed line represents hypothetical route during 1 month period of missing data.

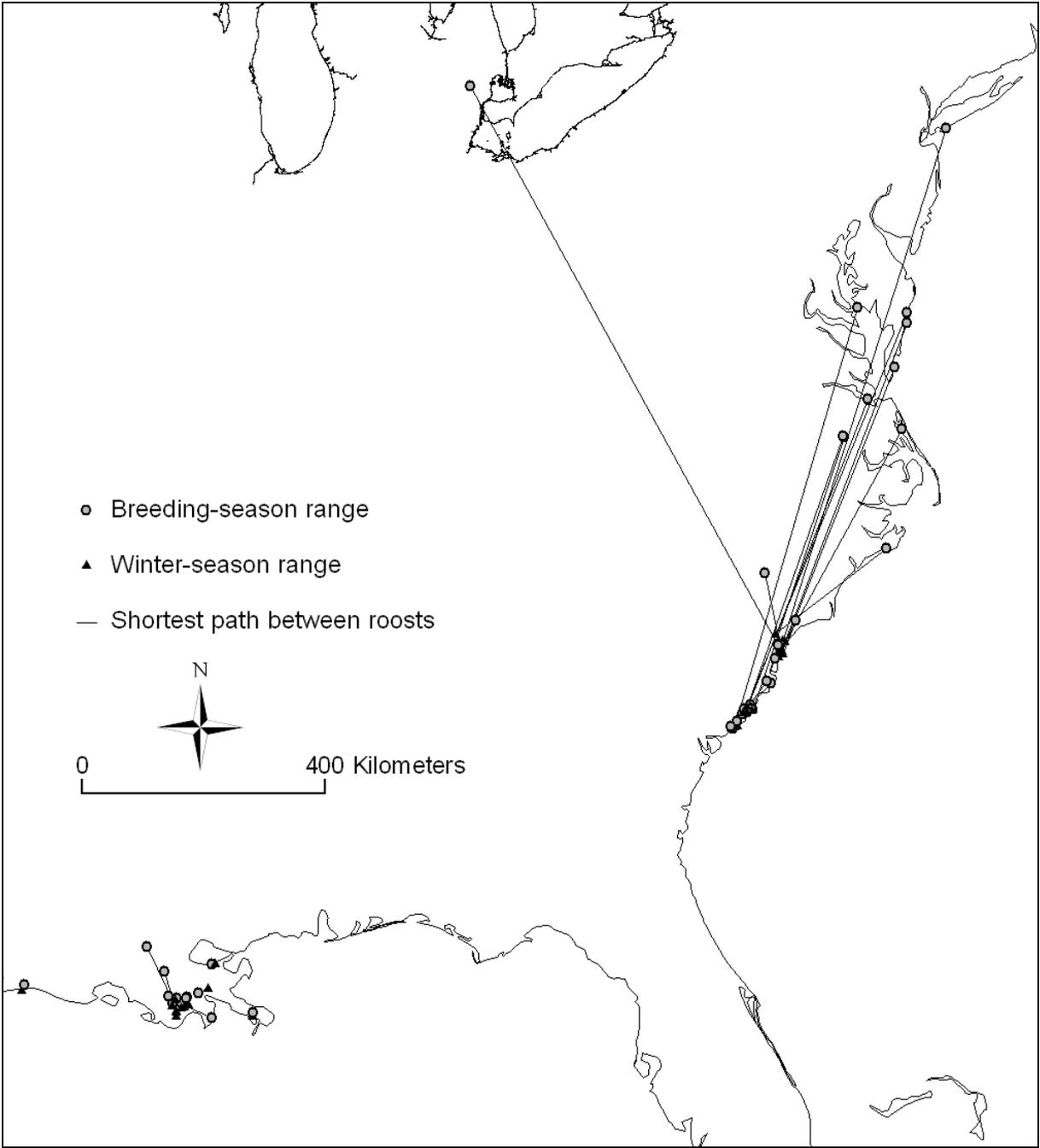


Figure 3-4. Distances between winter season and breeding season ranges for 41 great egrets tagged during winter in LA (n=13) and SC (n=28). Connecting lines are shortest distance paths, not flight paths.

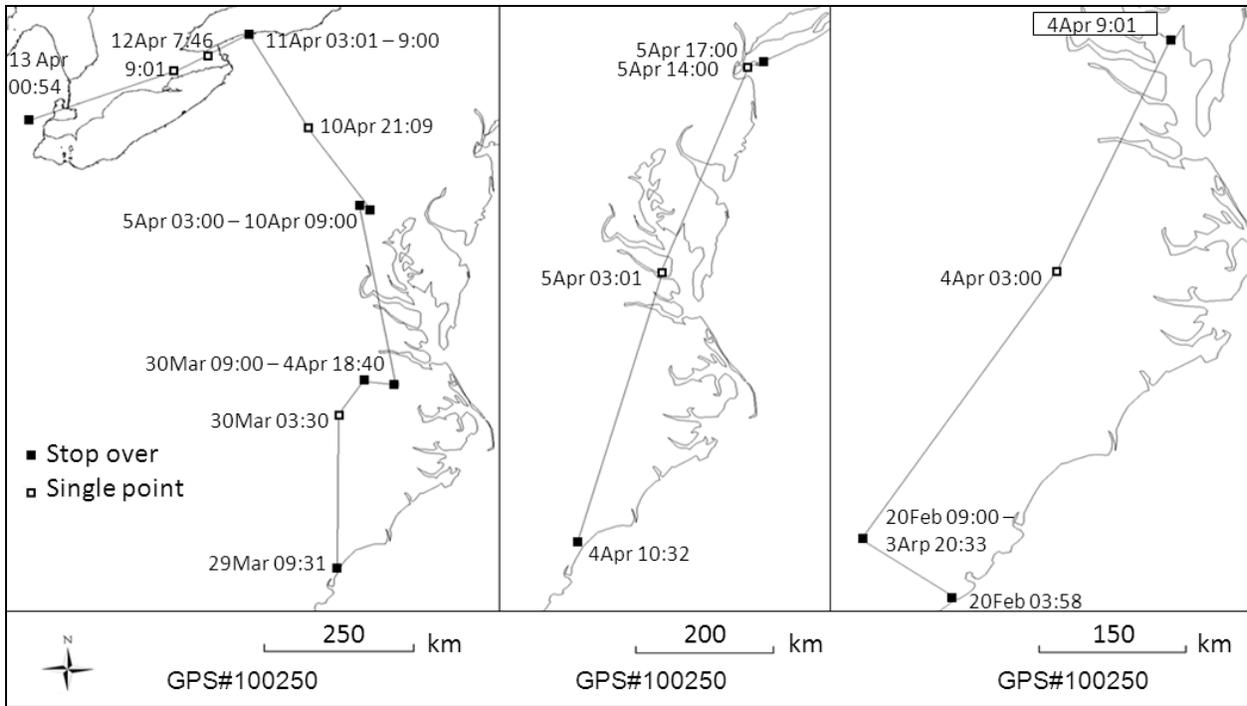
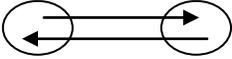
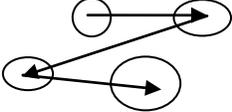


Figure 3-5. Long distance northward movements between winter and breeding season by three great egrets.

Table 3-1. Distance and speeds for long-distance flights (>300 km) of satellite tagged great egrets. Flights missing >1 day of data excluded. Travel Time is maximum duration of trip including stopovers, while speeds and distances are minimum estimates based on shortest geodesic distance between points. Segment Speed is the greatest speed calculated for movement steps on each trip, and winds data is for the same segment (NOAA). Note #100242 & 100252 conducted round trips.

Bird ID	Departure	Travel Time (days)	Travel Distance (km)	Trip Speed (km/d)	Segment Speed (km/h)	Wind Speed (km/h)	Relative Wind Type
PTT#100097	11/4/2010	2.34	1586.8	677.9	79.9	24.0	Tailwind
GPS#100240	3/29/2011	14.64	1574.3	107.5	50.6	24.2	Tailwind
GPS#100250	4/4/2011	0.94	876.8	876.8	64.5	32.2	Tailwind
GPS#100236	4/3/2011	0.52	708.9	708.9	61.2	7.6	Tailwind
PTT#100099	4/11/2011	1.11	685.3	614.8	25.6	16.4	Tailwind
GPS#100251	4/11/2011	2.04	612.5	299.8	43.3	20.3	Tailwind
PTT#100308	4/23/2011	1.17	503.5	431.5	18.0	11.4	Tailwind
GPS#100246	3/21/2011	3.14	476.9	152.1	19.5	15.1	Tailwind
GPS#100237	12/27/2010	0.85	474.2	474.2	25.9	34.8	Crosswind
GPS#100252	3/12/2011	0.30	427.3	427.3	59.5	13.2	Tailwind
GPS#100248	3/17/2011	17.98	423.8	23.6	30.7	2.4	Crosswind
GPS#100252	6/20/2011	0.54	383.6	383.6	29.4	7.4	Crosswind
GPS#100242	3/31/2010	2.00	379.7	189.8	56.0	3.2	Tailwind
GPS#100242	3/29/2011	1.25	379.1	303.2	44.6	17.7	Tailwind

Table 3-2. Movement strategies employed by great egrets followed over both the winter and breeding season and the proportion of the population utilizing each strategy.

Strategy	Definition	Observation	Prevalence (n)	Example
Sedentary	Remaining in a single area year-round	Overlapping seasonal ranges, never moved outside of a 30 km radius	46.3% (19)	
Migratory	Conducting regular, round-trip movements between seasonal ranges	Conducted round-trip movements between 2 seasonal ranges	31.7% (13)	
Nomadic	Conducting irregular and unpredictable movements	Moved between non-overlapping, separate areas within a season	21.9% (9)	

CHAPTER 4 CONCLUSION

In this study, I successfully followed individually marked great egrets using satellite tracking. This study demonstrated that satellite telemetry backpacks can be used on great egrets, and that this method is likely the only logistically feasible way to track this species throughout its annual movements, given the distances traveled by some individuals.

In Chapter 2, I found that some great egret populations were selecting constructed ponds and agricultural wetlands over natural habitat at local scales. These populations may be supported to a significant extent by these features, particularly in agricultural regions of LA where the pulse of food during the draining of crayfish ponds coincided with the nestling period. Current trends in land cover change will ultimately lead to more constructed wetlands and fewer functional natural wetlands. My findings, in addition to data from current populations of wading birds which persist in areas where natural wetlands have nearly all been lost (Fasola and Ruiz 1996; Fasola et al. 1996), indicate that some constructed wetlands can become important habitat and should be considered in future management planning. However, exposure to structural hazards, disease, and toxins may be elevated in ponds and agricultural areas as pesticides, herbicides, and run-off can affect wading bird health (Parsons et al.2010). The seriousness of these risks will vary depending upon land use and agricultural practices which can vary from region to region and farm to farm. This study indicates that there is a need for future research into the relationship between both agricultural wetlands and constructed ponds to wading bird mortality and reproductive success in the southeastern U.S.

There was no indication that national populations were currently reliant upon these constructed wetlands. Broad scale movements of satellite tagged birds did not appear to be influenced by the presence or absence of constructed habitats. Dense areas of agricultural wetlands exist not only in Louisiana, but in Florida, Texas, Arkansas, and to a lesser extent in other southeastern states, but these areas were not incorporated into the annual movements of any of the tracked egrets.

In Chapter 3, I identified large variation among individual movement strategies. Great egrets from the same wintering population appeared to utilize migratory, nomadic, and sedentary strategies. Great egrets proved capable of making extremely fast and direct flights of hundreds of kilometers both within and between winter and breeding seasons. On several instances, egrets returned to prior locations after traveling hundreds of km. Great egrets appear to have the ability not only to orient themselves for long distance flights but possess true navigational capabilities to arrive at predetermined destinations. Flights crossing the Gulf of Mexico and out over the Gulf Stream indicated that the birds were navigating in a manner other than landmark recognition. Despite this capacity for long distance flight, many individuals remained within surprisingly small areas of habitat throughout the study. This suggests that relatively small areas of high quality habitat can support great egrets year round. The different responses to similar conditions suggest that great egret may be conducting some long distance movements for proximate reasons other than food availability. Some great egrets likely leave suitable habitat at the onset of the breeding season to find suitable nesting sites or mates. Movements conducted during the winter may have

been in response to density dependent factors related to the arrival of egrets from northern regions resulting in increased competition.

These findings not only increase our understanding of the ecology of this species, but they provide some of the only detailed movement and habitat selection information for any heron or egret species at broad spatial and temporal scales. It provides us with knowledge regarding the range of movement strategies incorporated by a single species and should thus be informative for study designs and conservation actions focused on Ardeid populations.

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BIOGRAPHICAL SKETCH

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