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Foraging Behavior and Success of Herons and Egrets in Natural and Artificial Wetlands

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FORAGING BEHAVIOR AND SUCCESS OF HERONS AND EGRETS IN NATURAL AND ARTIFICIAL WETLANDS

by

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(Under the Direction of C. Ray Chandler)

ABSTRACT

The southeastern United States has approximately 13.2 million hectares of wetland habitat, but these sensitive areas are subject to loss and degradation from draining and development. The effects, both positive and negative, that manipulation of these wetlands have on wildlife is still under study. In particular, there is a need to know whether artificial (mitigated) wetlands can serve as an appropriate substitute for the loss of natural wetlands. Therefore, I quantified the foraging behavior of herons and egrets (species that are dependent on wetlands for food) in natural and artificial wetlands in southeastern coastal Georgia and southern coastal South Carolina. I tested the hypothesis that wading birds would show similar foraging behavior and success in artificial (ponds and impoundments) and natural (rivers and estuaries) wetlands. I found that these birds use artificial wetlands without a shift in behavior and with similar success (captures/strike) in comparison to natural habitats. All species exhibited about a 70% strike success over all habitats. The only exception was the Great Egret, which foraged with lower success but captured larger prey in artificial wetlands. My results show that artificial wetlands are viable foraging habitats for herons and egrets.

INDEX WORDS: Behavior, Egrets, Foraging, Herons, Mitigation, Wetlands

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DEDICATION

I dedicate this body of work to all those individuals who have been and continue to be ecologically responsible and aware so that those who come after us will have a world left to experience and enjoy as we have.

In memory of Mr. Charlie Pitts

(1919-2006)

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CHAPTER 1
INTRODUCTION

The southern United States, with approximately 13.2 million hectares of forested wetland in ten states, is home to the majority (64%) of wetland habitat in the contiguous United States (Weir and Greis 2002). A precise definition of the term "wetland" is difficult because of the many characteristics that distinguish wetlands from other habitat types. Also, it is also difficult to establish a consensus for defining a wetland because the definition depends on the user's purpose (Mitsch and Gosselink 1993). According to Cowardin et al. (1979), the U.S. Fish and Wildlife Service, defines a wetland as "lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water". Regardless of definition, beneficial functions of wetlands range from moderating stream flow and settling out sediment to improving the quality of surface water. Southern wetlands also support a high diversity of both terrestrial and aquatic organisms (Selcraig 1996).

In the late 1800s and early 1900s, wetlands were subjected to activities such as draining, logging, and destructive farming practices. By the mid-twentieth century, U.S. wetlands were being lost at a rate of more than 185,000 hectares per year (Greis 2002). As a result of the passage of the Clean Water Act in 1972, loss of wetlands slowed dramatically. However, the U.S. still loses more than 40,485 hectares of wetland habitat annually (Yaich 2003). Current impacts include commercial and residential development, fire suppression, and agricultural runoff (Trani 2002). Other impacts include mining, waste disposal, and various types of pollution. Regardless of impact, there is increasing need to mitigate wetland loss and degradation, and to manage remaining wetlands for multiple use. Multiple uses and their effects create the potential for conflict between the needs of humans and those of the wildlife. This exploitation of resources has perhaps had a negative impact on the quality of wetland habitat. Persistent problems, such as the certainty of human population increase and the problems associated with this, guarantee there will be an ever-increasing strain on natural resources including wetlands. Thus, there is a need for the implementation of appropriate management practices, and these practices must benefit both wildlife and humans (Bouton and Frederick 2003).

On the coastal plain of the Southeastern U.S., natural wetlands often take the forms of rivers and estuaries. Due to activities such as stream flow manipulation and development, these areas are constantly being degraded and in some cases destroyed in terms of their biological and hydrological functions. Many river channels are straightened by cutting across a meander with the stream flow resulting in the premature formation of an oxbow lake. Also, there has been recent development along riverbanks. With the recent surge in development along the coast, estuaries have been destroyed and/or altered. The waterscape of an estuary is determined by a variety of factors, including tides, precipitation, and the area and shape of the estuary (Gordon et al. 1989). Plant species composition in these habitats is influenced primarily by salinity and length and frequency of inundation (Gordon et al. 1989).

In an attempt to restore wetland habitat, artificial or mitigated wetlands have been constructed to serve as surrogates for their natural counterparts. In fact, “mitigation banking” is becoming increasingly popular with farmers and developers (Selcraig 1996). This process allows destruction of natural wetlands in return for constructing artificial (mitigation) wetlands elsewhere. Many biologists remain skeptical of this process, because many times these artificial wetlands are not the functional equivalent of the original (Kaiser 2001). These areas are often created with no ecological objective in mind. They are simply replacements for those areas that were destroyed. They are often created by governmental agencies and other entities in areas such as along highways in the form of borrow pits that scarcely do more than physically hold water. Factors such as soil type, topography, and surrounding hydrology are often not considered. Furthermore, construction of these anthropogenic wetlands may impact the ecology of a variety of wildlife. As Dr. Joy Zedler, professor of Biology at San Diego State, and a member of the National Research Council committee that worked two years to define wetlands points out:

> [B]iodiversity almost certainly suffers with the increase of "created" wetlands. There is no evidence that a created wetland can match the richness of one that is destroyed, because it's virtually impossible to inventory every living thing in order to know what you've lost.
>
> (Selcraig 1996: 98)

Mitigated or artificial wetlands can take many forms. In the southeastern U.S., artificial wetlands are often designed as ponds and impoundments. Ponds, which are man-made concave earthen depressions filled with surface water or via wells, (e.g. water for livestock, fish, wildlife, erosion control) can be designed with various shapes and sizes and with specific objectives in mind. Pond depth can be readily managed by excavating to desired depths and by placing water control structures that allow maximum depth and flood control. Vegetation type and structure can be altered or managed to propagate wildlife.

Coastal impoundments are another form of artificial wetland. Impoundments retain water to create a new wetland habitat. While many impounded coastal wetlands were used for rice plantations in the Southeast during the 18th and 19th centuries, today's uses include providing habitat for non-game wildlife, fishing, and aesthetics along with the primary objective of waterfowl management (Gordon et al. 1989). Depth is controlled by overflow spillways or by "flashboards" or "stoplogs". Water control in impoundments is critical because the pattern of flooding determines the plant community within the impoundment (Hammer 1992). In addition, practices such as drawdown, which is complete drying for an extended period of time during the growing season, can be implemented. This practice allows for the production of waterfowl food and cover plants and the improvements of the interspersion of vegetation in wetlands (Lewis 1994). Drawdown of artificial impoundments during late winter in preparation for the next growing season usually benefits dabbling ducks, wading birds, and shorebirds because food becomes available during this time. Additionally, aquatic invertebrates are concentrated as water levels recede (Gordon et al.1989). This also allows specific vegetation to flourish. It is quite common to employ practices such as growing-season burns to promote the growth of new vegetation during drawdown.

Lakes and reservoirs, like ponds but far larger, are also examples of artificial wetlands. They are often manipulated for recreational use and/or have some facilitative function such as production of electricity. These are areas that are inundated with water with little or no preplanned notions regarding water depth or vegetation type or structure. Reservoirs can negatively impact native stream communities (Havel 2005), and they are characterized by a high degree of disturbance and eutrophication. Reservoirs are often viewed as stepping-stones for the dispersal of exotic species. Kent (1994) asserts that reconstructed and enhanced wetlands such as reservoirs often are "disadvantageous for non-target species. For example, creating feeding areas for Wood Storks (*Mycteria americana*) is necessarily detrimental to fish" (p.171).

Avian Impacts

Wetland loss and conversion to artificial wetlands is likely to impact various terrestrial and aquatic species. Of these, "132 terrestrial vertebrate species are considered by Natural Heritage agencies to be of concern" in terms of their conservation status (Trani 2002:35). Various bird species use wetlands in the southeastern United States. Among the bird species most commonly associated with southeastern wetlands are the Great Blue Heron (*Ardea herodias*), Little Blue Heron (*Egretta caerula*), Snowy Egret (*Egretta thula*), Great Egret (*Ardea alba*), Tricolored Heron (*Egretta tricolo*r), and Green Heron (*Butorides virescens*). These species all feed similarly by striking at prey in or around water. As their name implies, wading birds are observed in varying types of wetland habitat. They use a range of habitats – from coastal marshes and estuaries to freshwater riverbanks and swamps –for foraging, breeding, nesting, and roosting.

Human encroachment on wetland habitats has a range of potential negative effects on herons and egrets. Several recent studies have shown that human activity near wading bird nesting sites can have a detrimental effects ranging from lower breeding success leading to population declines to alteration of nesting and breeding behaviors. (Rogers and Schwikert 2002; Bouton and Frederick 2003; Skegen et al. 2001). Perhaps most serious is the degradation or alteration of wetland habitats. Habitat loss and fragmentation, as well as increased disturbances, affect bird populations (Wear and Greis 2002). To persist in the face of wetland loss and conversion, wading birds such as herons and egrets must be flexible enough to occupy and use altered habitats, including artificial wetlands. In particular, the maintenance of waterbird diversity will depend on managing wetlands in a way that maintains an appropriate prey base. Ability to capture prey strongly influences the kinds and numbers of birds using an area. In fact, foraging behavior and/or foraging success are often used as indicators of survival rates in wading birds (Elphick 2000).

Diets of herons and egrets vary, but most of these birds prefer prey such as fish, amphibians, crustaceans, and aquatic insects, all of which are often found in or near water. These species exhibit a range of foraging behaviors from the "sit and wait" style commonly observed in Great Blue Herons to the more active foot-stirring and foot-raking of the Snowy Egret (Netherton 1994). The factors that influence foraging success and the role of these waders in the wetland ecosystem of the southeastern lower coastal plain have not been studied extensively. Possible differences in bird behavior and success between natural and artificial habitats have been studied even more rarely. Research has been conducted regarding activity patterns, water depth selection, diet, vegetation structure, diurnal rhythms, and flock constituents of various waterbirds in a range of areas from flooded rice fields to fish farms (Gawlik 1998, 2002; Ntiamoa-Baidu et al. 1998; Benedict and Hepp 2000).

To the best of my knowledge, however, no quantitative data exists for a specific comparison between natural and artificial wetlands with respect to the foraging behaviors within this group. Studies have been conducted on the opportunistic foraging of Great Blue Herons at catfish farms where they are perceived to be a problem, but experiments have failed to define the circumstances under which predation occurred (Glahn et al. 2002). Great Egrets as well as other species attained higher feeding efficiencies in seminatural wetlands than in flooded rice fields in California (Elphick 2000). Water depth selection has been studied globally with inconsistent results. Research in Ghana demonstrated that preferred water depth is correlated with bird tarsus length (Ntiamoa-Baidu et al. 1998). Great Egrets forage at various depths but they show a preference for the shallower depths by selecting them first (Gawlik 2002). Furthermore, the distribution of wading birds in the Everglades is closely linked to the distribution and depth of surface water (Gawlik and Rocque 1998). Past studies have indicated the importance of submergent aquatic plants to bird habitat quality. Foraging quality and aquatic plant diversity diminished greatly in Guntersville Reservoir, Alabama, with the introduction of grass carp (*Ctenopharyngodon idella*) (Benedict and Hepp 2000). This was perhaps due to water transparency.

The critical issue is whether wading birds can shift successfully from use of natural wetlands to managed artificial alternatives. Thus, the objective of my study is to determine whether herons and egrets are able to use both artificial and natural wetlands equally well in terms of their foraging ecology. I will address two questions. First, can herons and egrets shift from natural wetlands to artificial wetlands without a major alteration in their forging behaviors? Because the artificial habitats potentially differ in depth, prey density and vegetation, I might expect that for them to use the new habitat they would have to change aspects of their behavior to be able to use the new habitat. Second, are herons and egrets able to achieve the same foraging efficiency in artificial habitats as they do in natural habitats? Because artificial wetlands are often not designed necessarily as foraging habitat for wading birds, I predict that the foraging success of these birds will be lower in the artificial habitats compared to the natural habitat. I will use their feeding efficiency as an index of foraging performance in the habitats and measure variables that potentially affected the bird's feeding performance: prey size, water depth, mean emergent vegetation height, percent cover of water by surface vegetation, number of species of all other herons and egrets within 10 meters, and approximate distance bird traveled to the nearest m during a 5 min foraging bout (Elphick 2000).

CHAPTER 2

METHODS

I conducted fieldwork from July 2002 to July 2003 on the Atlantic coastal plain of southeastern Georgia and southernmost South Carolina (approximately 32ºN, 82ºW). I quantified the foraging behavior of herons and egrets in natural wetlands and in anthropogenic (artificial) waterways. In my study, natural wetland included rivers and estuaries. The artificial wetlands included coastal impoundments and artificial ponds.

Study Areas

Rivers

A natural river system was defined as a water stream of natural origin that consisted of headwater streams, tributary streams, and the mainstream and ended in a mouth (Lapedes 1971). All river systems used in this study were primary freshwater stream channels located within 125 km of the coast. These rivers include: Altamaha, Oconee, Ocmulgee, Ogeechee, Ohoopee, and Savannah. I searched for foraging herons and egrets along approximately 85 river kilometers. Although there are reservoirs far inland, no direct management strategies implemented along the rivers used in my study actively control for water depth and vegetation type or structure. Thus, water depth within these habitats is largely a function of rainfall. Within the river habitats, emergent vegetation was dominated by Dollarweed (*Centella asiatica*), Pickerelweed (*Pontederia cordata*) and Maidencane (*Panicum hemitomon*). Black willow *(Salix nigra)* was the dominant woody plant along the immediate shoreline.

I observed foraging behavior of birds using rivers either from the shoreline or from a boat. In areas that were accessible, I walked along the banks of the river until I encountered a bird. In less accessible areas, I used a boat to search the river for a wading bird. When I encountered a foraging bird along the shoreline, I tried to keep the bird from flushing by traveling upstream on the opposite side of the river from the bird and at a relatively fast speed, having found that it was less disturbing to the bird in question to travel at a faster speed rather than to drift slowly by (Stolen et al. 2003). I then stopped the engine and drifted downstream silently toward the bird while recording data. The bird would usually flush as I got closer depending on the species and its habituation to disturbance. This is also consistent with the findings of Stolen et al. (2003).

Estuaries

An estuary is a body of water that has a connection to both the sea and freshwater and where the freshwater substantially dilutes the saltwater (Northcote and Healey 2004). There are usually no active management practices that control for water depth or vegetation type or structure within these areas. I observed foraging behavior of herons and egrets in estuaries along the Georgia coast, ranging from Chatham County to the north to Camden County to the south. These include estuaries of: Altamaha, Ossabaw,St. Andrew and Wassaw Sounds. Emergent vegetation within the estuaries was dominated by Cordgrass (*Spartina spp*.). I made observations within the estuaries by walking along shorelines or choosing an observation point with a good field view. I also made observations from bridges, fishing piers and, to a lesser extent, from a boat.

Coastal impoundments

"Coastal impoundments are marsh dikes physically separating the wetlands from the estuary to allow for artificial flooding" (Poulakis et al. 2002:52). The coastal impoundments that I used for this study were Savannah Wildlife Refuge Complex, Jasper

County, South Carolina; Harris Neck National Wildlife Refuge, McIntosh County, Georgia; and the Altamaha Waterfowl Management Area, McIntosh County, Georgia. The Savannah National Wildlife Refuge is approximately 1,174 ha of former rice fields, comprised of 18 impoundments that are managed to benefit wetland flora and fauna, including about 25,000 ducks annually. Harris Neck National Wildlife Refuge consists of 1,143 ha, which were designated as a migratory bird refuge by the U.S. Fish and Wildlife Service in 1962. Its six freshwater impoundments provide an important rookery for the endangered Wood Stork as well as other migratory birds and waterfowl. The Altamaha Waterfowl Management Area (AWMA) has 1,310 ha of managed tidal freshwater and brackish impoundments, including 18 impoundments on three islands. Like its counterparts, the AWMA exists primarily to provide a high-quality habitat for wintering waterfowl. Emergent vegetation within the coastal impoundments was dominated by cattail (*Typha latifolia*), waterlillies (e.g., *Nymphaea, Nuphar, Nelumbo spp*.), duckweed (*Lemna minor*), pickerelweed, and sedges (*Cyperus sp*). Water hyacinth (*Eichhornia crassipes*) was occasionally present as well. Birds were observed from dikes and observation decks.

<u>*Ponds*</u>

Artificial ponds were defined as small, quiet bodies of standing water with rooted plants growing across them (Reid 1961). Most of the ponds that were used had a dam. I used a total of 36 ponds for this study. Ponds were located in the following counties: Bulloch, Effingham, Camden, Jenkins, Montgomery, Screven, and Toombs. These ponds ranged in size from <1 ha to approximately 25 ha. However, the most common ones were <8 ha. Most were <2 m deep. Emergent vegetation was dominated by cattail, duckweed, Giant Bulrush (*Scirpus tabernaemontani*), waterlillies, maidencane, and dollarweed. Woody stems were dominated by black willow. At ponds, I sometimes had a pre-planned observation point that served as both cover for me from the elements as well as a blind relative to the bird. This was an area from which most, if not all, of the shoreline was visible. If possible, I tried to position myself on the highest point available to allow reasonable assessment of surface vegetation cover. Observations were made from cars or along the shoreline.

Data collection

Behavior of actively foraging herons and egrets was quantified in both natural and artificial wetlands. I defined a bird to be actively foraging if it was standing or walking in or near the water while visibly searching for prey. The foraging bird's behavior involved stretching and sometimes rotation of the head and neck while staring into the water searching for prey items. I observed each foraging bird for 5 min. During the observation period, I measured variables that potentially affected the bird's feeding performance (Elphick 2000): prey size, water depth, mean emergent vegetation height, percent cover of water by surface vegetation, number of all other herons and egrets within 10 m, and approximate linear distance the bird traveled to the nearest 1.0 m during a foraging bout. In order to collect data rapidly, I recorded data using a handheld tape recorder. Observations were made using a 60-mm spotting scope (15-60X) and/or binoculars (7X50). To minimize the effect of temporal variations, observations were made at varying times of the day.

I defined a strike as any attempt to capture prey by rapidly projecting the head forward. I considered strikes to be a success (or capture) if (1) a prey item was physically seen in the bird's bill, or (2) movements of the gular region were consistent with swallowing, or (3) the bird showed evidence of prey transport by "head throwing" (Elphick 2000). Feeding efficiency was determined by the number of captures per number of strikes. During each strike I estimated vegetation height to the nearest 0.5 m within a 1-m radius of the foraging bird by comparing it to the known height of the bird species. I assigned the approximate water vegetation surface coverage a percentage score in 10% increments. Total surface coverage (100%) was not considered because it was assumed that if the bird struck at the prey item, the bird's view was not totally obstructed. I estimated water depth by observing to where on its legs the water came during the observation (Ntiamoa-Baidu et al. 1998; Elphick 2000). I estimated prey size by comparing to known bill lengths of species of birds I observed. If the prey item was too small to be detected, I considered the prey item to be <1 cm. I recorded the number and species of potential wading bird competitors within an approximate 10-m radius (and in the same body of water as) the bird in question. I also estimated the linear distance traveled to the nearest 1.0 m by the foraging bird during a foraging bout. For every strike I recorded all the variables. From that, for each 5 min period, I calculated strike rate and strike success and the modal characteristics of the habitat. If, during a foraging bout, the bird did not strike at all, I recorded habitat features at the end of the 5 min observation.

In all habitats, I attempted to make observations from a concealed vantage point without disturbing the bird. These observations were made from land, automobile, boat, bridges, and observation decks. While my general methods for collecting data were the same for each habitat, slight habitat differences necessitated tailoring my approach to bird observations specific to each area. To ensure I visited each habitat type with relatively equal frequency, a log for visit frequency was kept.

I used ANOVA to compare foraging characteristics among species, and I used a priori linear contrasts to compare natural versus artificial habitats. For more general comparisons between individual habitat types (ponds, rivers, estuaries, or impoundments), I used a Tukey-Kramer test ($\alpha = 0.05$). Finally, I used Pearson's correlation coefficients to assess relationships among habitat variables and foraging variables.

CHAPTER 3
RESULTS

Species and Sample Sizes

I documented a total of 421 foraging bouts involving eight species during the study period (Table 1). Three species foraged across all four habitat types. Pooling across habitat types, the most abundant species were the Great Blue Heron (n=138) and the Great Egret (n=138). I observed 247 foraging bouts in artificial habitats (58.7% of the total) and 174 foraging bouts within natural waterways (rivers and estuaries, 41.3% of the total).

Within artificial habitats, the Great Blue Heron was the most abundant species (n=86, comprising 34.8% of the total number of individuals observed). The Great Blue Heron was also the most frequent species observed within ponds, and Great Egrets were the most abundant species observed within impoundments. In the natural habitats, the Great Egret was the most abundant species (n=61, comprising 35% of the total number of individuals observed). Within these habitats, the Great Blue Heron was the most abundant species observed in the rivers, while the Great Egret was most observed in the estuaries.

Only a single Black-crowned Night-Heron (*Nycticorax nycticorax*) and a single Yellow-crowned Night-Heron (*Nyctanassa violacea*) were observed actively foraging during my study. Other species that were observed actively foraging, but with a relatively small sample size, were the Green Heron and the Tricolored Heron. Therefore, comparison of habitats will only focus on Great Blue Heron, Great Egret, Little Blue Heron, and Snowy Egret (Table 1).

Habitat Comparison

Great Blue Heron – Great Blue Herons (Table 4) foraged with similar efficiency among the four habitats (Fig 1; F=2.42, df=3, 72, P=0.07), although there was a strong tendency for efficiency to be lower in artificial habitats. Great Blue Herons also showed no difference in strike rates (F=1.80, df=3,134, P=0.15), size of prey captured (F=1.69, df= 3, 55, P=0.18), distances moved (F=0.72, df=3, 134, P=0.54), or water depth (F=1.39, df=3, 134, P=0.25) across the four habitats. The number of potential competitors around Great Blue Herons did not differ among habitats (F=2.42, df=3, 72, P=0.07)

Given the lack of significant differences in behavior, a priori contrasts identified no differences in foraging behavior for Great Blue Herons between artificial and natural habitats (P>0.05). The only exception was prey size. Great Blue Herons caught larger prey in natural habitats (F=3.84, df=1,55, P=0.05). Prey averaged about 8.50cm ($\bar{x}$ = 8.59±0.69, n=28) in the natural habitats and averaged about 6.75cm ($\bar{x}$ = 6.73±0.62, n=31) in the artificial habitats.

Although Great Blue Herons foraged similarly among habitats, the habitats did not have identical structure. Vegetation height (F=2.90, df=3, 134, P=0.04) and vegetation cover (F=5.76, df=3, 134, P=0.00) varied among habitats, and were greater in impoundments and estuaries than in rivers and ponds (Tukey-Kramer).

Great Blue Herons tended to capture larger prey at higher efficiency (r =0.31, P=0.02), in areas with taller vegetation (r =0.31, P=0.02) and in deeper water (r =0.35, P=0.01) (Table 8).

Great Egret – Foraging success of Great Egrets (Table 5) varied among habitats (Fig. 1; F=5.47, df=3, 119, P=0.002) as did strike rate (F=3.57, df=3, 134, P=0.02). Size of prey captured (F=1.51, df=3,113, P=0.22), distance traveled (F=1.48, df=3, 134, P=0.22), and water depth (F=2.31, df=3,134, P=0.08) were similar among habitats. There was no significant difference in the number of competitors among habitats (F=1.99, df=3, 134, P=0.12).

A priori contrasts indicated a significant difference in foraging efficiency, water depth, and size of prey between artificial and natural habitats. Great Egrets had higher foraging efficiency in the natural habitats (F=10.09, df=1,119, P=0.002). However, in the artificial habitats, they caught larger prey (F=4.33, df=1,113, P=0.04) at greater depths (F=6.35, df=1,134, P=0.01)

Habitats within which Great Egrets foraged also differed in structure. Estuaries had taller vegetation than rivers (F=3.55, df=3, 134, P=0.02) (Tukey-Kramer). Rivers have less vegetation cover than estuaries (F=3.69, df=3,134, P=0.01) (Tukey-Kramer).

Great Egrets also caught larger prey in deeper water (r =0.32, P=0.00) across all habitats. When the bird was more mobile, it struck at a greater rate (r = 0.17, P=0.04), although its efficiency decreased with the number of strikes (r =-0.27, P=0.00) (Table 9). Although Great Egrets have a lower capture efficiency in artificial habitats, they strike more often. Therefore, the net result is about the same total capture rate (20.12 prey/hour in natural habitats versus 19.12 prey/hour in artificial habitats).

<u>Little Blue Heron</u> –Foraging efficiency of Little Blue Herons (Table 6) did not differ among habitats (Fig 1; F=1.28, df=3, 55, P=0.29). Little Blue Herons also showed no difference in strike rates (F=0.35, df=3, 57, P=0.79), or size of prey captured (F=0.55, df=3, 51, P=0.65). Little Blue Herons traveled farther while foraging in rivers than in impoundments (F=3.65, df=3, 57, P=0.02) (Tukey-Kramer). This species showed no

significant difference in water depth among the habitats (F=0.19, df=3, 57, P=0.90). The number of potential competitors did not differ among habitats (F=1.62, df=3, 57, P=0.19).

A priori contrasts identified no differences in foraging behavior for Little Blue Herons between artificial and natural habitats (P>0.05).

Although the Little Blue Heron foraged similarly among habitats, the habitats differed in structure. Vegetation height was greater in the impoundments and estuaries than in the rivers (F=9.86, df=3, 57, P=0.00) (Tukey-Kramer). Vegetation cover was lower in rivers than in the impoundments (F=6.64, df=3, 57, P=0.00) (Tukey-Kramer).

Little Blue Herons tended to have a higher efficiency when they moved farther while foraging (r =0.36, P=0.01) (Table 10).

Snowy Egret –Snowy Egrets (Table 7) were only observed foraging in impoundments and estuaries, representing both artificial and natural habitats. They showed no significant difference in foraging efficiency between these habitats (Fig 1; F=1.98, df=1, 47, P=0.17). Regardless of habitat, Snowy Egrets had similar strike rates (F=0.00, df=1, 51, P=0.98), captured similar-sized prey (F=0.32, df=1, 44, P=0.57) moved similar distances during a foraging bout (F=0.03, df=1, 51, P=0.87), and foraged at similar depths (F=0.88, df=1, 51, P=0.35). There were more competitors for this species within the impoundments (F=7.59, df=1, 51, P=0.01) (Tukey-Kramer), and these were mostly conspecifics (F=7.88, df=1,51, P=0.01).

Unlike other species that I observed, Snowy Egrets foraged in structurally similar areas between habitats. Vegetation height within habitats was similar (F=2.60, df=1, 51, P=0.11). Likewise, vegetation cover was about the same among the habitats (F=0.45, df=1, 51, P=0.51).

Snowy Egrets tended to strike less often in taller vegetation (r =-0.28, P=0.04). Snowy Egrets had a higher strike rate when they were (a) more mobile (r =0.45, P=0.00) (b) in deeper water (r =0.32, 0.02) and (c) had others present (r =0.32, P=0.02) (Table 11).

Comparative Foraging Ecology

My results showed no pronounced habitat effects on the behavior of herons and egrets. With the possible exception of Great Egrets, each species implemented approximately the same behavior across habitats. However, there were fundamental differences among the species. They exhibited different foraging strategies.

Across all habitats, the birds I observed strike at different rates (F= 9.2, df=3, 386, P=0.00). They ranged from rapid strikers such as the Snowy Egret to the slower strikers like the Great Blue Heron (Tukey-Kramer). Surprisingly, however, all the species exhibited a similar efficiency rate of about 70% (F=0.17, df=3, 303, P=0.91). Strike rate was related to mobility. The species differed in the distance moved during foraging bouts (F=45.77, df=3, 386, P=0.00), with species moving long distances tending to strike more (Fig. 2). There were also interspecific differences in prey size (F=45.14, df=3, 273, P=0.00) (Tukey-Kramer), with slow movers (Great Blue Heron and Great Egret) catching larger prey than fast movers (Little Blue Heron and Snowy Egret) (Fig. 3; Tukey-Kramer). In terms of water depth, the Great Blue Heron and Great Egret forage in deeper water than do the Little Blue Heron and Snowy Egret (F=25.17, df=3, 386, P=0.00) (Tukey-Kramer).

The species showed no preference for height of the vegetation in the immediate foraging areas (F=0.10, df=3, 386, P=0.96). However, species did show a preference for vegetation cover in these areas (F= .65, df=3, 386, P=0.01). The Great Blue Heron was found in less vegetation cover than the Snowy Egret (Tukey-Kramer).

CHAPTER 4

DISCUSSION

I compared the foraging behavior of egrets and herons in artificial and natural wetland habitats on the coastal plain of the Southeastern United States. These habitats included estuaries, rivers, impoundments, and ponds. Herons did select slightly different structural elements within the habitats. Birds foraging in estuaries and impoundments were surrounded by taller vegetation and greater vegetation cover. Nevertheless, all herons are able to use artificial habitats with equal foraging success, achieving a foraging success around 70% in all habitats. The only exception to this is the Great Egret, which foraged with higher efficiency in the natural habitats. Although habitat had little effect on behavior, species differed considerably. Little Blue Herons consistently foraged at a faster rate (distance/time) than the other three species, and traveled farthest in rivers. The two smallest species—Snowy Egret and Little Blue Heron—consistently choose smaller prey than the larger species. Great Egrets and Snowy Egrets tended to forage in larger groups, usually with conspecifics. The two larger species prefer deeper water with less vegetation cover. Because the larger species can exploit deeper water, they have a potentially larger feeding area. However, they strike less often than the smaller species while maintaining the same efficiency. The smaller species strike more often in shallower water with more vegetation cover and travel farther than the larger birds, but they have the same foraging efficiency. The larger birds select prey from deeper water while the smaller birds choose prey from shallower water.

The most significant finding from my study is the fact that foraging efficiency (captures/strike) was generally not lower in the artificial habitats compared to the natural habitats. Great Blue Herons, Little Blue Herons, and Snowy Egrets all achieved a success rate of about 70%, regardless of habitat type (Table 2). These findings are consistent with the findings of a recent study that showed that Great Blue Herons, Great Egrets, and Little Blue Herons have nearly identical foraging efficiencies, with the Great Blue Heron exhibiting the highest foraging efficiency of about 73% (Werner et al. 2005). However, my study demonstrates that these similarities persist across artificial and natural habitats. This is good news for wildlife managers seeking to manipulate or restore wetland habitats.   Ma et al. (2004) also showed that while it is a better practice to conserve natural wetlands rather than to construct artificial ones, the artificial habitats are suitable foraging habitats for waterbirds.

There are some important points to note here. First, an important exception to the pattern described above was the Great Egret. Great Egrets showed lower foraging success in artificial habitats, particularly impoundments (Table 2). Foraging success dropped from about 81% in natural to about 62%in artificial. Although not significant, foraging success of Great Blue Herons was also markedly lower in artificial habitats. It is not clear why Great Egrets should be the only species to exhibit this pattern. They are intermediate in strike rate, movement rate, and water depth used among the species discussed here. My results are similar to the findings of Richardson and Taylor's (2003) study of rice fields in southeastern Australia. However, it is interesting to note that Great Egrets do strike for prey more often in impoundments even though it is with less success. Even though there is lower foraging success in the artificial habitats, the increased strike rate leads to about the same number of prey items captured per unit time. It is possible that impoundments contain fish species or a prey size distribution that is not well suited to the foraging style of Great Egrets. One recent study (Master et al. 2005) showed that prey density is a consideration when choosing foraging habitats.

This last point raises an important caution regarding my finding of similar success in artificial and natural wetlands. I have no data on the species of prey or their nutritional quality. Although I was able to show that three species catch qualitatively similar-sized prey at similar rates, it is an open question whether these prey are quantitatively of similar quality. Prey quality may be related to the type of habitat. White Ibis (*Eudocimus albus*) are crustacean specialists that feed primarily on crayfishes (*Cambaridae*) in freshwater during nesting while they feed primarily on estuarine crabs (*Ocypodidae*) in coastal marshes at other times. Interestingly, these two prey items comprise 90 percent of this bird's diet (Bildstein 1993).

A second important finding of my study is the fact that the herons and egrets that I studied were able to shift from natural to artificial wetlands with little change in behavior. Regardless of habitat, each species showed similar strike rates, movement rates, and water depth use. This again suggests that artificial wetlands are viable habitats that lie within the "behavioral range" of herons and egrets. Although there were some habitat differences (e.g., varying vegetation height and cover), these were not sufficient to alter heron behavior significantly.

There are few studies of the use of artificial habitats by herons and egrets. Those that do exist suggest that the birds may use artificial habitats if the natural habitat available is degraded or if there is no natural habitat (Ma et al. 2004). In my study, both natural and artificial habitat types were available within close proximity. These birds are likely partitioning their foraging effort among natural and artificial habitats based upon factors such as prey distribution, abundance, and quality within these various habitats. As noted earlier, some wading birds may select freshwater habitats for one particular prey item and salt or brackish water for another (Bildstein 1993).

Although the species I studied were able to use different habitats using similar behavior, the species themselves differed widely in foraging ecology. Generally speaking, the species in this study ranged from large species that move slowly and strike rarely for large prey in deeper water (e.g., Great Blue Heron) to small species that move often and strike frequently for small prey in shallower water (e.g., Snowy Egret). This is consistent with the findings of a recent study (Papakostas et.al. 2005).

Management Implications

My results indicate that artificial habitats such as ponds and impoundments are viable habitat for wading birds. Herons and egrets appear to enjoy similar success rates in these habitats in comparison with natural habitats (with some exceptions; e.g., Great Egret). However, several important points need to be considered. Some species don't use some habitats or rarely use them (Snowy Egrets in ponds). However, it is interesting to note that density may not be a good indicator of habitat quality. For instance, despite congregations of breeding-aged birds in poor-quality habitats, reproduction may not take place (Van Horne 1983). We also need a better understanding of prey base and their impacts on foraging success in these habitats. It should also be noted that although not significant, there is a strong trend for the Great Blue Heron to forage at higher efficiencies within the natural habitats. More work is needed on vegetation limits (i.e., what happens as grass and woody plants close in and less open water. This is the case in ponds and impoundments that are neglected). For non-game species like herons, we need more information on what affects their success in artificial wetlands.

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Table 1. Sample sizes for all species across habitats.

	Artificial		**Natural**		
	Ponds	Impoundments	Estuaries	Rivers	Total
Great Blue Heron	27	59	18	34	138
Great Egret	13	64	51	10	138
Little Blue Heron	1	26	11	23	61
Snowy Egret	0	30	23	0	53
Tricolored Heron	0	14	4	0	18
Green Heron	10	1	0	0	11
Black-Crowned Night Heron	0	1	0	0	1
Yellow-Crowned Night Heron	1	0	0	0	1
Total	52	195	107	67	421

Table 2. Bird foraging efficiency over habitat types. Results are mean ± SE.

Species	Overall	Artificial	(ponds)	(impoundments)	Natural	(estuaries)	(rivers)
Great Blue Heron	0.73± 0.05	0.67± 0.67	0.78± 0.09	0.57± 0.10	0.82± 0.07	0.93± 0.07	0.72± 0.11
Great Egret	0.70± 0.03	0.62± 0.04	0.68± 0.10	0.61± 0.04	0.81± 0.03	0.78± 0.04	0.94± 0.06
Little Blue Heron	0.70± 0.04	0.65± 0.06	0.33 *	0.66± 0.06	0.74± 0.05	0.66± 0.10	0.78± 0.06
Snowy Egret	0.70± 0.04	0.65± 0.05	*	0.65± 0.05	0.75± 0.04	0.75± 0.04	* *

Table 3. Vegetation and water depth ($\bar{x}$ ± SE) for sites used by foraging birds in the four habitat types in this study.

Habitat	n	Vegetation Height(cm)	Vegetation Cover(%)	Water Depth(%)
Artificial	247	33.82±2.71	33.26±2.19	13.11±0.54
Ponds	52	16.58±3.28 b	21.35±3.94 b	12.38±1.16 a
Impoundments	195	38.42±3.25 a	36.44±2.52 a	13.30±0.62 a
Natural	174	33.66±3.10	28.62±2.54	12.20±0.55
Rivers	67	16.19±4.29 b	10.94±2.77 b	11.27±1.01 a
Estuaries	107	44.60±3.93 a	39.63±3.33 a	12.78±0.64 a
ANOVA (df=3, 417)				
F		10.7	14.4	1.08
P		0.00	0.00	0.36

Habitats with different letters differ significantly (Tukey-Kramer)

Table 4. Foraging characteristics ($\bar{x}$ ± SE) of Great Blue Herons across the four habitat types.

	Habitats			
Variable	Ponds	Impoundments	Rivers	Estuaries
Efficiency	0.78±0.08	0.57±0.10	0.72±0.11	0.93±0.07
Strikes (per 5 min)	0.85±0.12	0.54±0.12	0.53±0.09	0.83±0.09
Vegetation Height(cm)	15.3±4.82	43.03±6.90	24.12±7.99	39.17±8.62
Vegetation Cover(%)	14.81±4.99	34.44±4.60	10.89±3.52	30.28±6.91
Distance Traveled(m)	0.46±0.20	1.36±0.44	1.26±0.52	1.50±0.63
Water Depth(cm)	11.96±1.54	14.32±1.28	12.82±1.73	17.22±1.42
Prey Size(cm)	6.21±0.67	7.36±1.10	8.96±1.16	8.27±0.84
Others	0.00	1.20±0.82	0.00	0.06±0.06
Conspecifics	0.00	0.02±0.02	0.00	0.00
Heterospecifics	0.00	1.19±0.82	0.00	0.06±0.06

Table 5. Foraging characteristics ($\bar{x}$ ± SE) of Great Egrets across the four habitat types.

	Habitats			
Variable	Ponds	Impoundments	Rivers	Estuaries
Efficiency	0.68±0.10	0.61±0.04	0.94±0.06	0.78±0.04
Strikes (per 5 min)	1.92±0.24	2.70±0.20	1.20±0.20	2.24±0.23
Vegetation Height(cm)	16.54±7.95	32.73±5.63	8.00±4.16	46.51±6.17
Vegetation Cover(%)	19.62±7.52	30.45±4.23	5.80±4.94	40.63±5.28
Distance Traveled(m)	4.62±1.04	4.70±0.63	9.30±5.34	4.82±0.76
Water Depth(cm)	18.69±2.34	16.75±0.97	12.50±2.27	14.41±0.91
Prey Size(cm)	6.36±0.62	5.53±0.27	4.44±0.37	5.33±0.35
Others	2.15±1.11	0.78±0.15	0.30±0.21	0.96±0.33
Conspecifics	0.85±0.46	0.52±0.10	0.30±0.21	0.57±0.18
Heterospecifics	1.31±1.06	0.27+0.06	0.00	0.39±0.28

Table 6. Foraging characteristics ($\overline{x}$ ± SE) of Little Blue Herons across the four habitat types.

	Habitats			
Variable	Ponds	Impoundments	Rivers	Estuaries
Efficiency	0.33	0.66±0.06	0.78±0.06	0.66±0.10
Strikes (per 5 min)	3.00	3.85±0.73	3.52±0.44	2.82±0.40
Vegetation Height(cm)	0.00	56.15±8.30	8.04±2.79	40.91±9.02
Vegetation Cover(%)	0.00	50.81±6.77	13.26±5.88	41.36±8.00
Distance Traveled(m)	20.0	8.35±8.43	17.83±3.11	10.18±1.09
Water Depth(cm)	10.00	9.12±1.29	8.43±0.89	7.82±1.15
Prey Size(cm)	5.00	3.78±0.29	4.18±0.29	4.17±0.42
Others	0.00	0.54±0.17	0.22±0.11	0.09±0.09
Conspecifics	0.00	0.19±0.08	0.17±0.08	0.00
Heterospecifics	0.00	0.35±0.17	0.04±0.04	0.09±0.09

Table 7. Foraging characteristics ($\bar{x}$ ±SE) of Snowy Egrets across the four habitat types.

	Habitats	
Variable	Impoundments	Estuaries
Efficiency	0.65±0.05	0.75±0.04
Strikes (per 5 min)	4.67± 0.43	4.65±0.38
Vegetation Height(cm)	28.40±6.51	45.43±8.57
Vegetation Cover(%)	38.43±6.82	45.22±7.38
Distance Traveled(m)	8.80±1.31	9.13±1.48
Water Depth(cm)	6.57±0.72	7.52±0.69
Prey Size(cm)	2.44±0.37	2.73±0.35
Others	2.60±0.56	0.78±0.20
Conspecifics	2.47±0.54	0.70±0.17
Heterospecifics	0.13±0.13	0.09±0.06

Table 8. Pearson's correlation coefficients among habitat and behavioral variables for Great Blue Herons across all habitats.

(n=138)

	Efficiency	Vegetation Height	Vegetation Cover	Distance Traveled	Water Depth	Prey Size	Others
Strikes	-0.22	-0.15	0.08	*0.27	0.16	-0.14	0.01
Efficiency		0.09	0.00	0.00	0.16	*0.31	0.06
Vegetation Height			*0.39	-0.05	-0.08	*0.31	0.06
Vegetation Cover				0.00	0.03	-0.10	0.06
Distance Traveled					0.16	0.23	-0.01
Water Depth						*0.35	0.07
Prey Size							*0.27

Table 9. Pearson's correlation coefficients among habitat and behavioral variables for Great Egrets across all habitats.

(n=138)

	Efficiency	Vegetation Height	Vegetation Cover	Distance Traveled	Water Depth	Prey Size	Others
Strikes	*-0.27	-0.12	0.04	*0.17	0.14	0.02	0.06
Efficiency		0.16	0.02	0.02	0.09	0.04	0.17
Vegetation Height			*0.25	-0.16	*-0.21	-0.03	-0.04
Vegetation Cover				-0.08	-0.02	0.08	0.13
Distance Traveled					0.11	-0.15	0.01
Water Depth						*0.32	0.03
Prey Size							-0.06

Table 10**.** Pearson's correlation coefficients among habitat and behavioral variables for Little Blue Herons across all habitats.

(n=61)

	Efficiency	Vegetation Height	Vegetation Cover	Distance Traveled	Water Depth	Prey Size	Others
Strikes	0.00	-0.02	0.03	0.21	0.08	0.03	-0.11
Efficiency		-0.03	-0.12	*0.36	-0.08	-0.08	-0.15
Vegetation Height			*0.47	*-0.30	-0.05	-0.27	0.09
Vegetation Cover				*-0.34	0.10	0.08	0.02
Distance Traveled					-0.16	0.09	-0.15
Water Depth						-0.07	*0.33
Prey Size							0.00

Table 11**.** Pearson's correlation coefficients among habitat and behavioral variables for Great Snowy Egrets across all habitats.

(n=53)

	Efficiency	Vegetation Height	Vegetation Cover	Distance Traveled	Water Depth	Prey Size	Others
Strikes	0.06	*-0.28	0.11	*0.45	*0.32	-0.06	*0.32
Efficiency		0.09	-0.10	0.20	0.22	0.11	0.19
Vegetation Height			*0.31	-0.18	-0.21	0.03	-0.14
Vegetation Cover				-0.08	0.02	0.21	*0.27
Distance Traveled					0.11	0.19	0.01
Water Depth						0.09	0.17
Prey Size							-0.09

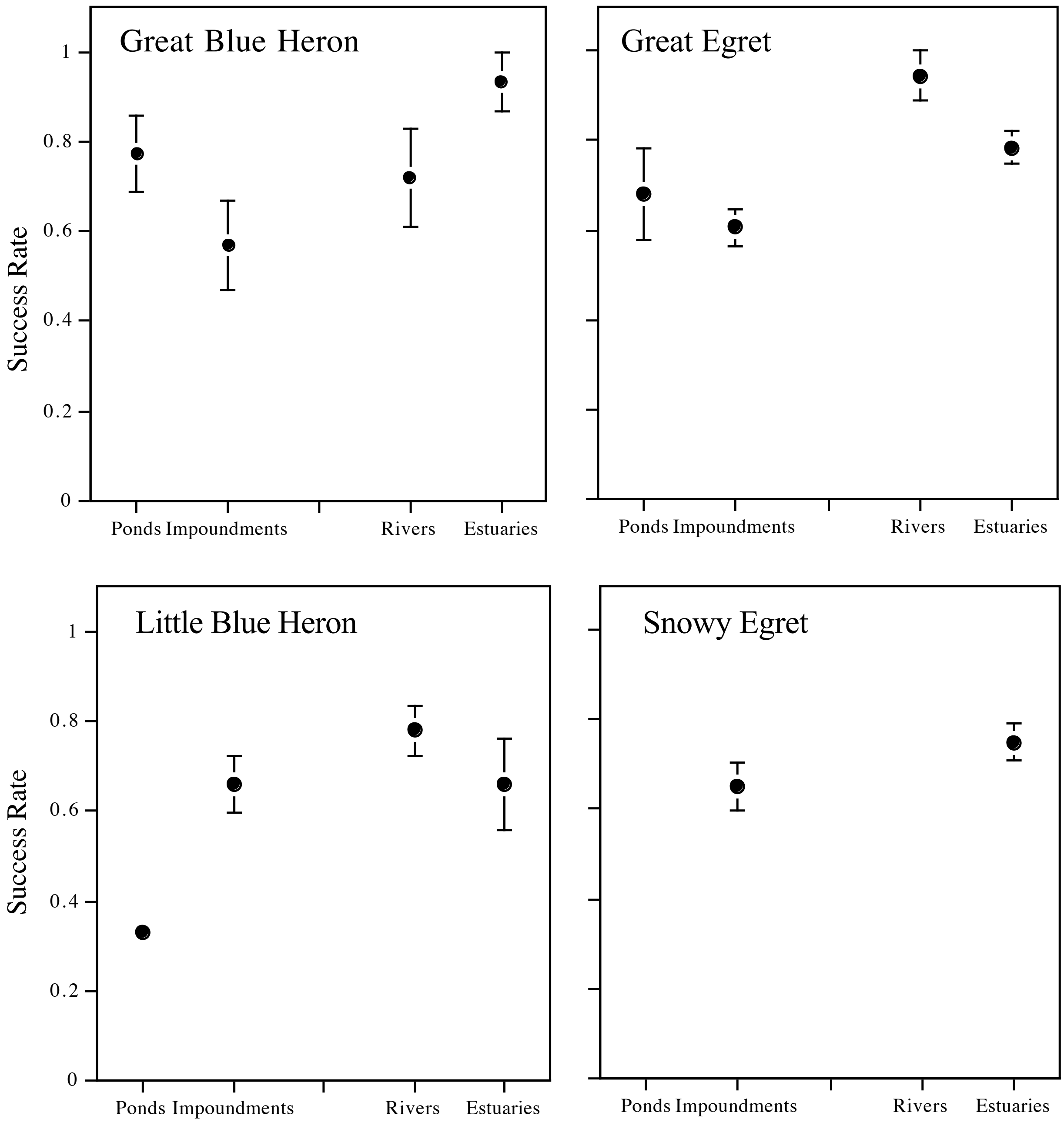

Figure 1. Foraging success rate (captures/strike) for four species of herons and egrets in each of four habitats.

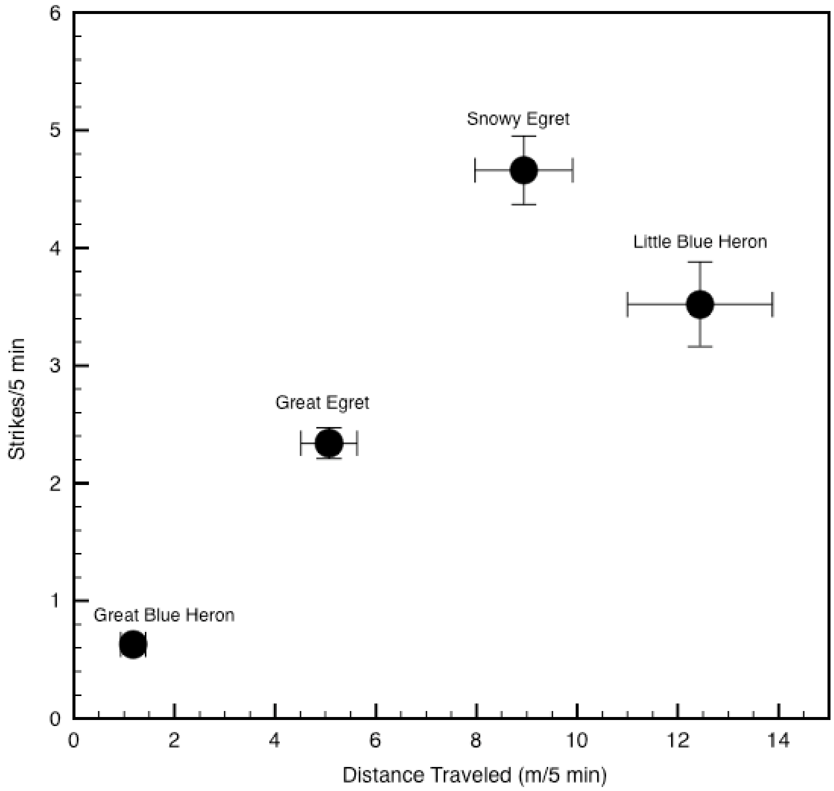

Figure 2. Relationship between strike rate and distance traveled among four species of heron and egret

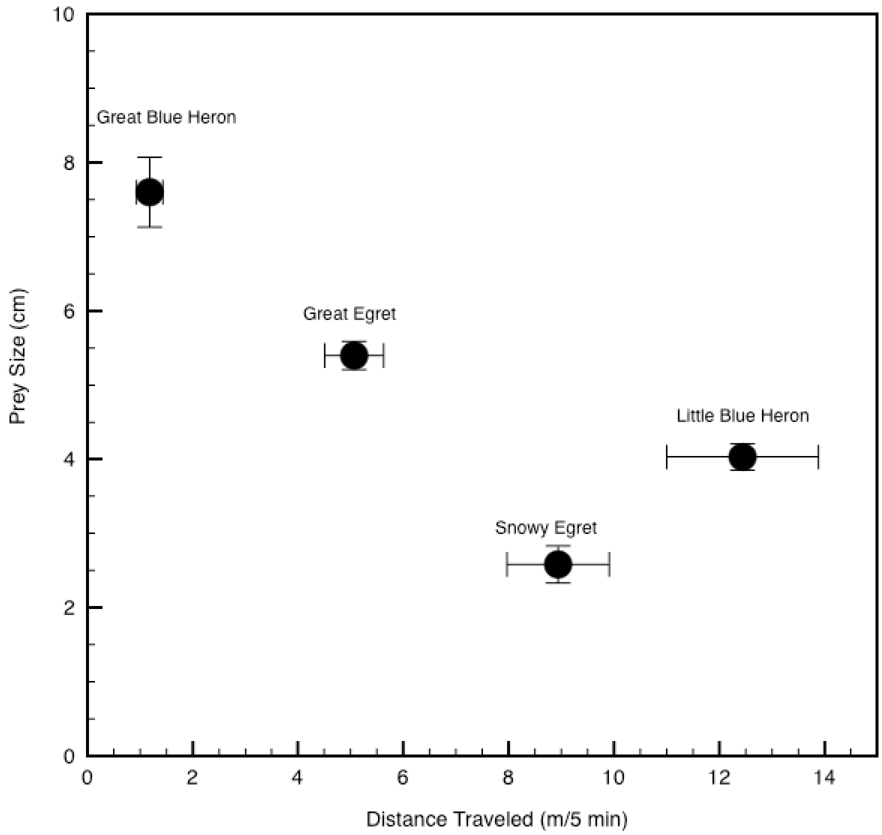

Figure 3. Relationship between foraging rate and prey size among four species of heron and egret