

Social and Physical Influences on Wading Bird Foraging Patch Selection

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ABSTRACT

The aim of this study was to clarify social foraging, habitat use and choice of cohabitating Ciconiiformes on Virginia's Eastern Shore. In a 2006 study I used two approaches, a manipulative experiment and an observational study. At Chincoteague (37° 56'N, 75° 25'W), I manipulated prey density and social cues using plastic decoys to address the relative importance of social features versus prey density. I also recorded feeding durations of birds at the different treatments. The observational portion also occurred at Chincoteague at six sites along a causeway from the mainland marshes east to Assateague Island. A second area was Hog Island (37° 27'N, 75° 40'W), a barrier island about 50 km south of Chincoteague. At both areas, I observed wading bird foraging in different habitats and recorded feeding efficiency, flock size and species use, and attempted to answer the following questions: how were species distributed across habitat types, how did feeding efficiency vary among species and habitat types, and how did tide and season affect habitat use, flocking and feeding efficiency? Multi-way ANOVAs were performed to analyze feeding efficiency data and χ^2 analyses of goodness-of-fit and association were performed on the flock and species use data. Species' use of habitats differed significantly at both locations, with generalists being more widespread than specialists. Ponds and impoundments were selected for foraging most often by most species. Generalist species tended to have lower feeding efficiencies while species specialized for particular habitats had higher average efficiencies at those locations. Overall, generalists tended to be more widespread but have low efficiency, but specialists had high efficiencies in fewer habitat types. Tidal and seasonal effects were less than habitat and species differences, presumably because of the high caloric demands on birds

during the breeding season. There were insufficient data to meaningfully analyze the experiment results, however the limited data suggested that all the species responded more to social cues than to prey densities. A similar experiment of increased scope and duration should be attempted, perhaps using mesocosms with more controlled prey densities. An important conservation-related finding was high late-summer use of impoundments for almost all wading birds. These habitats are probably especially attractive to recently fledged young from nearby colonies.

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INTRODUCTION

Background

The ecological role of wading birds within the Virginia Coast Reserve has not often been explored. However, as it has been shown in other areas, they may play a large role in the ecosystem in their potential for “top-down” influence on fish (Kushlan 1976, Kushlan 1978a, Bildstein 1993). In coastal Virginia, 11 species of wading birds (order: Ciconiiformes) coexist during the boreal summer period, with total populations of greater than 3000 birds (Erwin unpubl. data).

The particular Ciconiiformes that I chose for this study, herons, egrets and ibises (family: Ardeidae and Threskiornithidae), have previously been shown to be important members of many Atlantic estuarine systems due to their large size and high energy demands (Erwin and Korschgen 1979, Kushlan 1981). They are high trophic level predators and are often used as bioindicators (Curry-Lindahl 1978, Erwin and Custer 2000) due to their heavy dependence on estuarine productivity (Brzorad *et al.* 2004).

With the presence of so many different, ecologically similar, high trophic level predators, there is a great deal of pressure to efficiently exploit feeding habitat. Resource partitioning is a mechanism that has co-evolved to reduce competition over finite resources. It allows for separation, in either time or space, behaviorally or morphologically, which allows differential use of foraging habitat (Jenni 1969).

Resource partitioning among birds has been well supported in the literature. In Florida, Jenni (1969) found that four different species of herons utilized different foraging behaviors to reduce their competition for the same food resources. In addition Kushlan (1976) found that, while Black-crowned Night Herons (*Nycticorax nycticorax*,

hereafter abbreviated BCNH) make use of a different time of day to forage, Great Blue Herons (*Ardea herodias*, GBHE) and Great Egrets (*Ardea alba*, GREG) partition on a spatial scale. In fact, Willard (1977) found that as foraging habitat (spatial) overlap increases, behavioral overlap decreased.

Resource partitioning can occur in Ciconiiformes because of their behavioral plasticity and different morphologies that allow them to utilize a greater range of environmental conditions, as well as readjusting their strategy as those conditions change (Gawlick 2002). This is a useful adaptation as many wading bird species are distributed across almost every continent in a variety of habitats. Indeed, GREG and Snowy Egrets (*Egretta thula*, SNEG) were shown to have a great deal of behavioral plasticity when foraging in very different habitats (Maccarone and Brzorad 2002).

When Maccarone and Brzorad (2005) compared foraging microhabitat preference, SNEG and GREG preferred slow-moving water over mudflats. They suggested that this may be due to less turbulence and therefore more clarity in slower moving water. Overall, they found that Glossy Ibises (*Plegadis falcinellus*, GLIB) and SNEG had more a clustered spatial distribution, perhaps due to water depth as smaller species are restricted to shallower water. GREG were more widely distributed, maybe due to morphology and foraging behavior (Maccarone and Brzorad 2005). In addition, as generalists, GREG and GBHE can exploit less productive environments than specialized species (Recher and Recher 1980).

Along with variable behaviors, wading birds are opportunistic when it comes to obtaining food, and will readily take advantage of locally abundant and vulnerable prey (Fasola 1994). Ciconiiformes also frequently exhibit flocking behavior when foraging.

This is yet another tactic used to efficiently exploit a super-rich but ephemeral food patch (Kushlan 1978a).

Along the Eastern Shore of Virginia and the Atlantic Coast, flocking is probably related to feeding benefits, as these birds tend to gather in areas of high prey availability (Kushlan 1981, Kersten *et al.* 1991). Frequently these flocks are made up of multiple species, and it is believed that there are advantages to mixed-species foraging, which outweigh the competitive disadvantage (Caldwell 1981).

A flock begins forming by local enhancement, which is the attraction of foraging birds by the presence of other foraging birds (Kushlan 1976). This strategy may be a way to decrease searching time for an adequate foraging site. In addition, if others are foraging there already, it is more likely that the patch is a productive one (Kushlan 1979). Information regarding food availability gained from the environment is greater when foraging in a group rather than solitarily, therefore more time can be spent feeding rather than searching (Clark and Mangel 1984).

However, group foraging benefits vary, depending on species involved and foraging habitat (Master *et al.* 1993). Energy gained per unit time may or may not be substantial depending on the species foraging repertoire and their abilities to utilize different resources. Those participating in a flock are most likely obtaining advantages in securing food resources, at least up to some threshold where interference will dominate (Morse 1970). Flocking is seen to be most valuable when resources are patchy or scarce. In a coastal area where highly mobile aquatic prey have many refuges from predation, flocking would seem most advantageous.

White plumage has been shown to be one morphological adaptation to enhance group feeding (Kushlan 1977). There appears to be a relationship between this very visible white plumage and the function of White Ibises (*Eudocimus albus*, WHIB) and SNEG as “core species” of flocks. These two species have been deemed “searchers”, as they search for high quality food patches instead of utilizing those that are declining in “payoff” (Gawlick 2000). Searchers are typically social with white plumage (Gawlick 2002), a generalization that does include WHIB and SNEG. If these species are effective at locating suitable habitat, selection would then favor those who associate white color with good feeding patches (Kushlan 1979).

In addition to being attracted to the most lucrative sites, aggregations may be formed due to other benefits. In the preceding case of the WHIB and Little Blue Herons (*Egretta caerulea*, LBHE for instance, Kushlan hypothesized that perhaps the WHIB’s white plumage made fish more visible for the LBHE. Master *et al.* (1993) also indicated that “prey beating” or the driving of prey out from hiding and toward other species may be another benefit of aggregative foraging. Regardless of species composition, an increase in energy intake is typically found when inter- or intra-specific flocks of birds form foraging groups (Krebs 1974, Kushlan 1978b, Caldwell 1981, Erwin 1985).

To continue feeding in a flock, selection dictates that the feeding benefits must outweigh the disadvantages. Aggressive interactions taking away from feeding time would be a possible negative effect of flock foraging. However, Petit and Bildstein (1987) found that in flocks of WHIB, aggression was negligible. In another study, Gawlick (2002) found that interspecific interactions in mixed-species foraging aggregations were most likely commensal rather than competitive. However, Kent (1986)

suggests that SNEG foraging efficiency is negatively impacted due to competition with Tricolored Herons (*Egretta tricolor*, TRHE) and LBHE for resources.

In addition to aggression, a decrease in prey intake might be a detriment to foraging in a flock. While it is possible that species such as GREG, which frequently stand and wait for prey to cross their paths, might be disturbed by the more active feeding activity of SNEG, their behavioral plasticity can allow them to exploit the disturbed fish (Brzorad *et al.* 2004). Petit and Bildstein (1987) found that while there were no prey intake disadvantages to flock foraging for WHIB, there was no increase in prey acquisition either. Indeed there may be a fine line in flock foraging between conferring advantages and disadvantages. This negative impact on foraging efficiency may result in a decreased amount of time spent at a particular foraging habitat due to a shorter time before “giving-up” (Erwin 1985).

The time period when wise foraging decisions are most crucial in the mid-Atlantic region is late May through July, when it is necessary to feed dependent young (Erwin 1985). Master *et al.* (1993) found that during this time period, foraging efficiency did increase in New Jersey. WHIB were also seen to choose better foraging habitat during periods of nestling reliance in Florida (Kushlan 1979). It is during this time that choice of foraging habitat is probably most critical.

Species Descriptions

The study species are all gregarious colonial breeders of the order Ciconiiformes (family: Ardeidae and Threskiornithidae). Each of the following species were chosen due to previous observations of breeding presence in marshland colonies nearby (within a few km) to the study sites on both the Chincoteague marshes and Hog Island. As Cattle Egrets

(*Bubulcus ibis*, CAEG) are primarily terrestrial foragers, they were only infrequently found feeding in my experimental area, so were only used in certain portions of the study. BCNH were not included during the study due to the fact that they are primarily nocturnal foragers and all of my observations were diurnal.

Great Egret:

The GREG is a large, white-plumaged wader with black legs and a yellow bill, with both sexes looking similar. Its body is on average 85-102 cm in length (Hancock and Kushlan 1984). This is the second largest wader species in my study area after the GBHE. The GREG is a deliberate predator, and mostly uses the “Sit and Wait” method of foraging (Maccarone and Brzorad 2002). This involves standing still in one place and waiting until a potential prey item comes close enough to catch. However, the GREG has a number of other foraging methods in its repertoire (Kushlan 1978b).

GREG have a very diverse diet, and are extremely opportunistic, but eat mostly fish (Brzorad *et al.* 2004). In nestling regurgitations, fish accounted for 73.4% of the diet in Florida (Smith 1997) and almost the entirety of the diet in the Yucatan (Ramo and Busto 1993). GREG also take a wider range of prey sizes than other smaller waders (Smith 1997).

GREG expend very little energy with their preferred method of foraging and they have a high foraging efficiency (Maccarone and Brzorad 2005). They have been shown to prefer slow-moving water to a mudflat feeding habitat (Maccarone and Brzorad 2005). Because of their long legs, GREG are able to forage at greater water depths than other shorter-legged waders such as SNEG or TRHE (Custer and Osborn 1978). This can be

important because they have been shown to have little to no habitat segregation from SNEG (Willard 1977) and overlap can result in difficulty securing adequate resources.

When foraging alone, GREG may be extremely territorial, but they also typically forage with other species (Hancock and Kushlan 1984). They have been shown to derive benefits from associating with SNEG, (Brzorad *et al.* 2004) however SNEGs' much more active method of foraging may flush prey out of hiding and into the paths of waiting GREG.

Snowy Egret:

The SNEG is a much smaller wader than the GREG, with a body length of about 56-66 cm (Hancock and Kushlan 1984). Like the GREG, the SNEG's plumage is entirely white and the sexes are non-dimorphic. It has a mostly black bill, yellow feet and black legs, which have been hypothesized to be useful in "foot-stirring" to find prey (Kushlan 1978b).

The SNEG has extremely varied feeding behavior (Willard 1977) and moves quickly and strikes frequently (Maccarone and Brzorad 2002). It will actively pursue prey through shallow water (Jenni 1969) and is largely restricted by high water levels when foraging, as they prefer shallow areas (Maccarone and Parsons 1994). They have been shown to prefer slow-moving water like the GREG (Maccarone and Brzorad 2005). SNEG prefer fish, and moves three times faster when foraging than the GREG (Brzorad *et al.* 2004). Young SNEG in Florida were shown to have about 90% fish in their diet (Jenni 1969, Smith 1997).

SNEG are considered a "core species" for aggregation formation. This is thought to be due to their frequent close association with high quality feeding sites (Gawlick

2000). In addition, their white plumage makes them more visible for wading birds searching for an adequate foraging patch (Kushlan 1977).

Cattle Egret:

The CAEG is a medium size bird that has recently expanded its range to North America. It is a medium sized bird about 50 cm in length with a short yellow bill white plumage with buff areas on the head chest and back developed during the breeding season (Hancock and Kushlan 1984). The CAEG is primarily a terrestrial forager. It typically feeds commensally with farm animals or machinery and has been shown to forage most successfully that way (Kushlan 1978). However, it is also an opportunistic predator and will forage for aquatic prey (Hancock and Kushlan 1984).

There has been some concern that their recent arrival may have introduced harmful competition to the other resident Ciconiiformes. When it comes to nest site selection competition has been shown to occur in colonies (Burger 1978). However, foraging competition between CAEG and other species is fairly low due to their differing preferences in foraging locations (Jenni 1969).

Great Blue Heron:

The GBHE is the largest of the wading bird species in the Mid-Atlantic. It is a mostly gray bird at about 120 cm in length (Sibley 2003). Adults have noticeable black plumes on the head and dark flight feathers. The sexes have similar plumage, however females tend to be of smaller size (Hancock and Kushlan 1984).

Its foraging methods are similar to that of the GREG with 90% of their time foraging spent Standing and Walking Slowly (Hancock and Kushlan 1984). However, unlike the GREG, the GBHE is not often seen feeding with others. However, Pratt (1980)

showed them to be attracted to foraging conspecifics. The GBHE has been shown to alter its feeding behavior based on prey density, showing that it too can be opportunistic (Kushlan 1976).

Tricolored Heron:

The TRHE is similar in size to SNEG at 60-70 cm in length (Hancock and Kushlan 1984). It has a noticeably white belly, and is mostly blue with patches of yellow and reddish colors. Both sexes appear similar. It nests in mixed-species colonies with the other species noted here.

This heron is also frequently a solitary and territorial feeder, and pursues prey at the margins of deeper habitats (Smith 1997), but Master *et al.* (1993) observed them foraging at the edge of SNEG and GREG-centralized flocks. TRHE have a number of diverse and specialized foraging tactics (Smith 1997).

While TRHE are opportunistic and will feed on whatever is most abundant (Recher and Recher 1980), medium-sized fish have been found to comprise almost the entirety of their diet (Smith 1997). For instance, Smith (1997) found that fish accounted for almost all of TRHE nestling diet in Florida. These birds have a large prey type and size similarity with SNEG. Based on Jenni's (1969) data, Smith (1997) found a very high diet overlap between the two species.

Little Blue Heron:

The LBHE is an entirely slate blue species with grey-colored legs and feet, but is entirely white during its first year (Hancock and Kushlan 1984). It is another medium-sized heron at about 70 cm in length which nests in mixed-species colonies.

Typically the LBHE forages in shallow water Walking Slowly and Peering Over (Hancock and Kushlan 1984). They also utilize more active behaviors involving their wings and feet, however these behaviors are exhibited infrequently. In both New York and Florida, Recher and Recher (1980) found that over 75% of the LBHE's diet was comprised of fish of a wide variety of species. The size of prey taken was found to be very similar to that of the similar-sized SNEG and TRHE.

White Ibis:

WHIB are small short birds with a long, curved bill and a body length of about 64 cm (Sibley 2003). It is white with black wingtips and a reddish-orange bill and legs. WHIB typically begin nesting in late April (Custer and Osborn 1978). Unlike the rest of the waders mentioned already, this bird is a tactile forager, and only uses vision to initially select a site to forage (Kushlan 1979). Its foraging repertoire is limited and fish less than 10 cm long dominate its diet (Kushlan 1979, Bildstein 1993).

The WHIB is typically at the center of a feeding flock and usually initiates aggregation of other species. It can also be attracted to feeding areas by others of its species and other white birds (Kushlan 1979). Often, other birds are seen feeding commensally with them (Kushlan 1978a)

Glossy Ibis:

The GLIB is similar in size to the WHIB with the same long, curved bill. It has glossy blue-green wings and is otherwise darkly colored. Again like the WHIB, the GLIB nests in late April (Custer and Osborn 1978) and is a tactile forager. However, like visual predators they are able to take advantage of prey abundance and are opportunistic

(Kushlan 1979). The percentage of fish in their diet is directly correlated to the availability of prey.

Research Questions

In coastal areas, prey density is very patchy and any information as to location, status and quality of patches is important (Clark and Mangel 1984). With my manipulative experiment, I attempted to determine the importance of social aspects versus prey densities for wading bird choice of foraging microhabitats. I hypothesized that the response to experimental decoy treatments would differ among species with social influence being more important than prey density. More specifically, I aimed to answer a number of questions:

1. Which species preferred white versus dark birds (in this experiment, decoys)?
 - ❖ Because SNEG are searcher species and have been shown to be indicative of suitable foraging habitat (Kushlan 1979), most birds will prefer the white decoys to dark.
2. Did any species utilize prey density cues rather than the social ones?
 - ❖ Since SNEG as searchers would be looking for high quality food patches (Gawlick 2002), they would be more likely to use prey density as cues rather than social cues.
3. Did length-of-stay differ among treatments for any species?
 - ❖ Erwin (1985) used giving up time, or length of stay in a patch, as an indication of habitat quality, therefore I expect increased length-of-stay to be greater at treatments with high prey densities.

With my observational studies, I focused on species' distributions among habitat types and feeding efficiencies. I hypothesized that feeding efficiency and distribution of species would vary across foraging microhabitats and that feeding efficiency would vary among species within a habitat. I asked the following questions:

1. How were species distributed across habitat types?
 - ❖ Generalists (e.g. SNEG, GREG) have been found to be more widely distributed across habitats than specialists (e.g. LBHE, TRHE; Erwin 1985). WHIB and GLIB are intermediate between these two classifications. Therefore, SNEG and GREG should be observed to be distributed more evenly across more habitat types than the other species.
2. How did feeding efficiency vary across species and among habitat types?
 - ❖ Because species would be more likely to exploit habitats for which they are most specialized (Kushlan 1979), generalists will likely have lower average feeding efficiency across sites while specialists will have higher efficiencies at particular habitats for which they are specialized. In addition, some habitats with simple structure (e.g. impoundments; Willard 1977) may be more conducive to higher feeding efficiencies than others.
3. Did tide and season affect habitat use, flocking or feeding efficiency?
 - ❖ Foraging decisions have been shown to be most crucial in the mid-Atlantic from late May through July when nestlings are growing (Erwin 1985); thus, season should have a significant effect on efficiency, flocking and habitat use. Because certain habitats are more tidally influenced than others, tide will likely influence habitat use by some species more than others (Custer and Osborn 1978).

METHODS

Research Design

This study was conducted in three locations located along the Virginia portion of the Delmarva Peninsula from April to August 2006 (Fig. 1). The lagoonal marshes of Assateague and Chincoteague Islands (37° 56'N, 75° 25'W), the northernmost barrier islands in Virginia, are where the manipulation study took place (Fig. 2). The observational portion also occurred here at six points along the causeway from the westward marshes to Assateague Island. A second observational study site was on Hog Island (37° 27'N, 75° 40'W), a barrier island about 80 km south of the Chincoteague marshes (Fig. 3). Here I observed wading birds foraging in different habitats. At these locations, breeding colonies of over a hundred pairs of the target species were located within a few kilometers of the study sites. At Chincoteague, the nearest colony had close to 1000 pairs of birds in 2006: 146 GREG, 159 SNEG, 29 CAEG, 132 LBHE, 167 TRHE, 160 GLIB, 63 BCNH. The nearest breeding colony to Hog Island, at Chimney Pole Marsh, had about 220 pairs of birds: 120 GREG, 40 SNEG, 17 BCNH, 25 TRHE, 16 GLIB, 5 WHIB.

Chincoteague Experiment

In the Chincoteague marshes, I manipulated prey density and social cues to determine their effects on the choices of foraging habitats for Ciconiiformes. The experiment was run once every week, for temporal independence, from mid-April to mid-June 2006. Observation occurred for the two hours before and after low tide, with two prey density treatments, two social treatments and a control.



Fig 1: Map of the Virginia barrier islands. Adapted from <http://www.deq.state.va.us/coastal/seasidewatertrail/visitationpolicies.html>



Fig. 2: Chincoteague Island and the western marshes. Two experimental sites located within marked circles. Six observational sites marked with numbered boxes. Adapted from www.chincoteaguechamber.com.



Fig. 3: Photograph of the Machipongo Station and the surrounding 3 ponds and 2 creeks used in the study. Picture taken by Linda Blum. From <http://savanna.lternet.edu/gallery/vcr>.

Seventeen non-tidal ponds were selected based on size and depth within 25 hectares. They were between 10-25 cm deep, so that drying would not occur throughout the course of the experiment, while still being available for exploitation for shorter-legged species. They varied in size, roughly 4-6 m in diameter and from 10 to 30 m² and were free of dense algal cover. From this larger population of ponds, six were randomly chosen each week for manipulation.

I determined initial average prey fish density (fish/m²) in the ponds using minnow traps. A trap was placed within each of the experimental ponds for 30 minutes, baited with dog food to estimate an index of fish density (fish/m²). Both fish inside and outside the traps were counted. Since this index was typically very low, (on the order of one fish per 2 m²) I supplemented the high density ponds were supplemented to reach the density of three to four fish per m². The low-density ponds had no fish added to them, as their densities remained low throughout the experiment. Each week, when treatments were randomly assigned, prey density was first measured, and then fish were supplemented as necessary. I collected fish for supplementation from much larger ponds in the surrounding area using additional minnow traps baited with dog food.

The three social choices involved the use of model wading birds (plastic decoys obtained from Flambeau Inc.). The control consisted of three 1-m rebar sections with no decoys. The white social treatment consisted of three white decoys mounted on metal rods resembling GREG, spaced 1-m apart along the edge of the treatment pond. The dark social treatment included three dark decoys mounted on metal rods resembling GBHE. Both white and dark decoys were the same size, controlling for differences in visibility due to size.

Locations of the six different treatments (Table 1) were randomly assigned to a different pond every week. Treatment ponds were located sufficiently distant from one another to be socially independent, but close enough to be seen simultaneously by birds flying past, as they search for feeding sites. Depth, size, clarity and salinity of the ponds were similar in each pond to control for confounding variables to my study. Gawlick (2002) found that prey vulnerability negatively correlated with water depth.

Table 1: The six treatments randomly assigned to 6 ponds weekly.

Treatments	Low Prey Density	High Prey Density
control – rebar rod	low/none	high/none
white decoys	low/white	high/white
dark decoys	low/dark	high/dark

The experiment was monitored from scaffolding placed within a hunting blind, 25 to 100 m away from the study ponds, using binoculars and spotting scopes. Two observers independently collected data using data sheets and tape recorders for later transcription onto data sheets. The first observer recorded flock size at all ponds once a minute on the data sheet. In addition, this observer kept a record of the species, arrival time, and treatment at which each bird arrived. The second observer randomly chose birds arriving at a treatment and determined the length-of-stay of those birds, while simultaneously keeping track of inter-pond movements of the birds. The duration of the experiment during each time treatment was variable based on bird attendance, from two to four hours in duration.

Observational Study

On Hog Island I conducted feeding observations twice a week during the two hours preceding low tide. Study sites were monitored by spotting scope from the tower of

the Machipongo Station (Fig. 3), a building about 10-m high. Spotting scope observations were recorded on tape for later transcription onto data sheets.

The site was additionally monitored daily by a remotely operated camera (Axis 2400) able to pan, tilt and zoom. The camera was programmed to take five minutes of live video at each patch in rotation, from June 28 to July 28 (mechanical problems precluded using earlier or later images). From the video, the middle video frame at each patch was converted to a still image and analyzed. From these camera images, habitat use was determined for each species

I monitored three non-tidal ponds and two tidal creeks. Potential prey items at each of the areas were sampled by throw trap once a month. Nekton were the focus, therefore infaunal prey were not sampled. Two observers monitored the order of species arrival, length-of-stay, feeding efficiency, and flock size for wading birds, during the two hours before low tide. Length-of-stay was again determined by randomly selecting arriving birds at each feeding habitat. The first observer determined this, as well as order of species arrival for each patch in rotation for a two-hour period. The second observer determined feeding efficiency and flock size. One bird in each patch was selected at random and the ratio of successful strikes per minute to the number of attempts per minute was determined for each patch in rotation for the duration of the two hours. The number of birds foraging along with this particular bird was also recorded.

At Chincoteague, I conducted a similar observational study from May to August 2006. Six locations along a causeway and in the Chincoteague National Wildlife Refuge were visited twice weekly (Fig. 2). Their order was selected randomly each time and they were each observed for 30 minutes in the two hours before and after both high and low

tide. Initial species presence, length-of-stay, feeding efficiency and flock size were determined for birds at particular non-tidal ponds (saline ponds only inundated at very high tides), tidal creeks (any size continuous tidal waterway), oyster beds, brackish impoundments, and protected coves (protected areas off larger bodies of saline water) that were chosen beforehand at each of the six sites. Sites 1, 2 and 4 had non-tidal ponds and tidal creeks. Site 3 had oyster beds and a protected cove. Site 5 had a brackish impoundment and site 6 had a brackish impoundment and a protected cove. These latter two sites were located within the Chincoteague National Wildlife Refuge.

Data Analysis

For species use, a χ^2 analysis of goodness-of-fit was performed comparing species presence and use of each habitat to a uniform distribution at both Chincoteague and Hog Island, using SAS (Version 9.1). χ^2 tests for independence were performed on habitats species, tide (only at Hog), and season. The data was then partitioned by season (before July 25, early season; after July 25, late season) at Chincoteague and by month (Hog), with individual χ^2 goodness-of-fit and independence analyses being performed on each. Due to the popularity of non-tidal ponds and impoundments as foraging locations, χ^2 analyses of goodness-of-fit and independence were performed using only these habitats.

Using data from the species use of habitats, a Shannon Index was calculated for each habitat at both Chincoteague and Hog Island. For flock size analysis, χ^2 tests of independence and goodness-of-fit were performed for each location. The data for flock size was compiled using birds for which feeding efficiency was also recorded. I conducted Spearman Rank Correlation tests relating group sizes to feeding efficiency for selected species.

For feeding efficiency, a multi-way ANOVA was performed on all data for each location using proc GLM (SAS version 9.1). At Chincoteague, an additional ANOVA was performed considering just non-tidal ponds and impoundments due to their increased use in comparison to the other habitats. For the ANOVA analyses, a power analysis was performed on species, habitat and season to determine how likely it was that my analysis detect effects of a certain magnitude.

RESULTS

Chincoteague Experiment

Because only 24 individuals in a total of 28 hours over 7 days (sampled over 8 weeks) were attracted to the study site, I was unable to conduct extensive statistical analyses. The experiment was run from mid-April to mid-June before it was abandoned. A few observations however suggested there might be a treatment preference.

The white/high treatments were chosen significantly more frequently than the rest (Table 2), even though the species by treatment association indicated independence (Table 3), SNEG and LBHE were attracted to the treatment ponds significantly more frequently than the other species. The greater difference between the social response (17 at white, 3 at dark) and prey density response (8 at low, 16 at high) suggests that social cues dominate in patch finding (Table 2).

Table 2: χ^2 goodness-of-fit tests for species and separate and overall treatment choice as compared to a uniform distribution.

		Frequency	Percent	χ^2
Species	GLIB	3	12.5	
	GREG	2	8.3	
	LBHE	7	29.2	
	SNEG	10	41.7	
	TRHE	2	8.3	10.6 (df = 4, P = 0.03)
Social	control	4	16.7	
	dark	3	12.5	
	white	17	70.8	15.2 (df = 2, P = 0.01)
Prey	high	16	66.7	
	low	8	33.3	2.7 (df = 1, P = 0.10)
Treatment	control/high	4	16.7	
	dark/high	1	4.2	
	dark/low	2	8.3	
	white/high	11	45.8	
	white/low	6	25.0	13.1 (df = 4, P = 0.01)

prey = high and low density, social = control, white and dark decoys

Table 3: χ^2 tests of association for experimental treatment categories and species.

Association	df	χ^2	P
species*total treatment	16	11.8	ns
species*social	4	1.9	ns
species*prey	4	2.3	ns
social*prey	2	3.5	ns

prey = high and low density, social = control, white and dark decoys

Question 1: Which species preferred white versus dark decoys?

The white/high treatment was selected significantly more than the others (Table 2). However, when a χ^2 test of association was performed between species and social (decoy) cues, they were independent (Table 3, 4).

Table 4: Contingency table of social (white and dark decoys) and physical (high and low density) association with all species combined.

		high	low
white	observed	11	6
	expected	(5)	(5)
dark	observed	1	2
	expected	(5)	(5)

All species that were attracted to the treatment ponds were present at the white/high (three to four fish per m²) treatment at least once (Fig. 4). All but the GLIB were attracted to the white/low (one fish per two m²) treatment.

Question 2: Which species utilized higher prey density cues rather than the social ones?

While white/high treatments were chosen more frequently than all others, there was little apparent density preference (Table 2). In addition, there was no species that seemed to choose one density over another (Table 3), although SNEG and LBHE appeared to have a slight preference for the white/high treatment choice (Fig. 4).

Question 3: Did length-of-stay differ among treatments?

Length-of-stay at the treatments tended to be very short as compared to lengths-of-stay at unmanipulated ponds in the area observed in the other part of my study (Fig. 5,

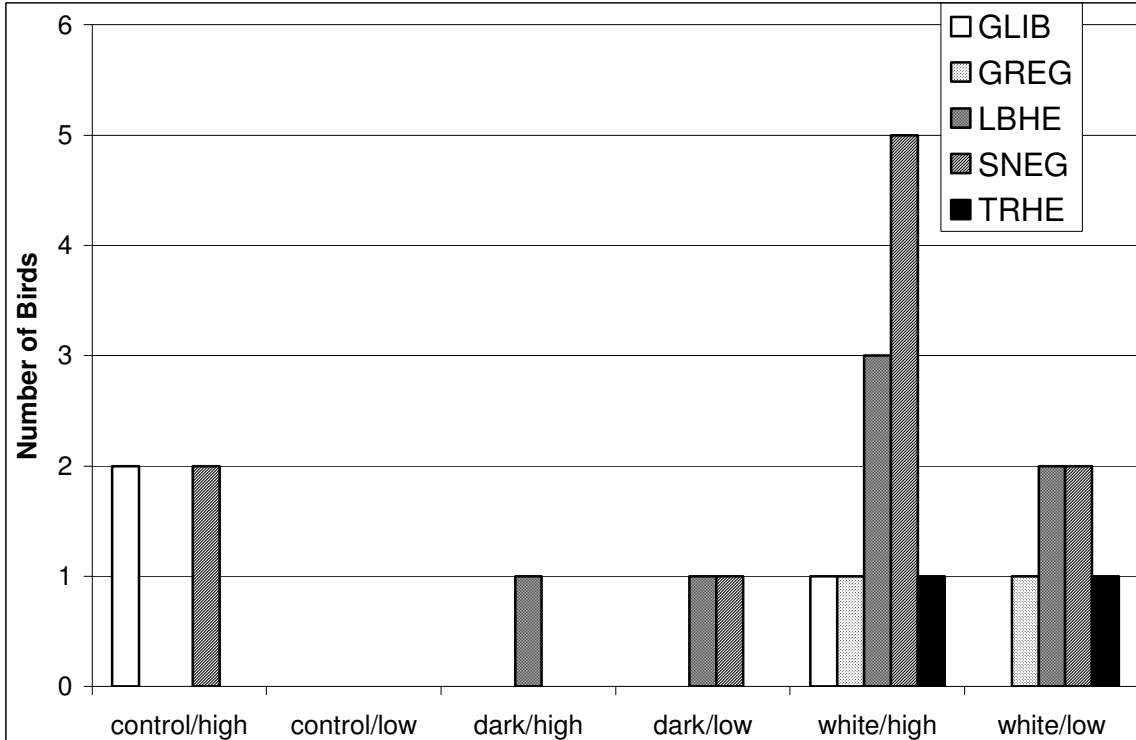


Fig. 4: Number of birds of each species, Glossy Ibis (GLIB), Great Egret (GREG), Little Blue Heron (LBHE), Snowy Egret (SNEG), and Tricolored Heron (TRHE), attracted to treatments in the Chincoteague experiment under various combinations of decoy type (white, dark, control) and fish density (low, high).

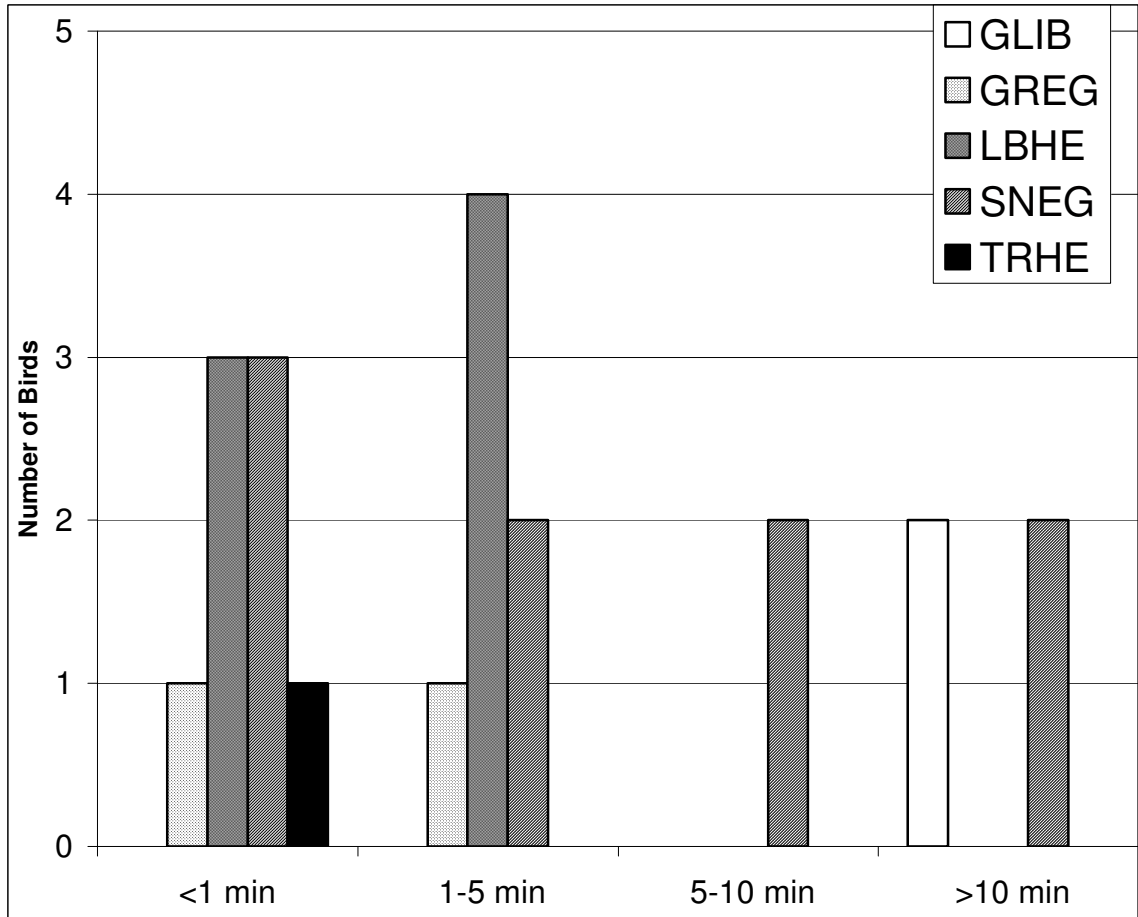


Fig. 5: Length-of-stay by species in the Chincoteague experiment.

Table 5, Appendix 3). The mean length-of-stay in my observational study was significantly greater than those in my experiment ($t=2.1$, $df=20$, $P=0.01$). All GLIB stayed in the treatment ponds for greater than 10 minutes. While most birds that were attracted to the white/high treatment stayed for fewer than 5 minutes (Fig. 6), the mean length-of-stay for birds at the white/high treatment was significantly greater than that of birds at the control/high treatment ($t=2.4$, $df=3$, $P=0.05$).

Table 5: Mean lengths-of-stay (min : sec) and standard errors for the observational and experimental portions of the study across the following Chincoteague habitats: coves, brackish impoundments, non-tidal ponds, oyster beds, and tidal creeks.

Study	Site	Average	Std. Err. (sec)
Observational	cove	18:44	27
	impoundment	26:52	0
	NTP	18:24	4
	oyster	13:08	50
	creek	18:19	10
Experimental	NTP	06:29	29

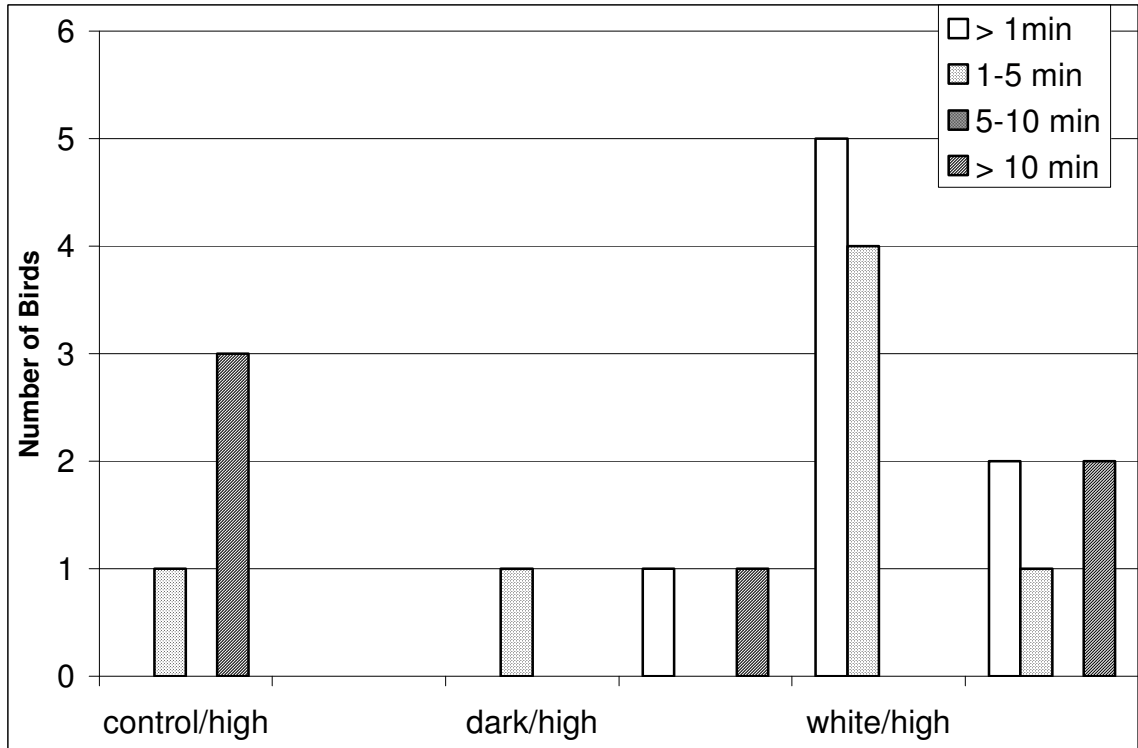


Fig. 6: Length-of-stay across treatments in the Chincoteague experiment.

Observational Study

Question 1: How were species distributed across habitat types?

At Chincoteague, species were not distributed equally among habitats either in space or time (Table 6). During observations, GREG were more abundant than any other species with 554 birds recorded. I observed 458 SNEG, making them the second most abundant species. When a χ^2 test of association was performed (SAS 9.1), there was a significant habitat-by-species association indicating species were not using habitats independently (Table 6, Table 7). This is evident in the fact that SNEG and GREG were more widely distributed across habitats than the specialist species (Fig. 7 top and bottom). Both species used all of the study habitats. Both GLIB and GBHE only used 2 habitat types, while CAEG were only ever found in impoundments. LBHE and TRHE only used three and four of the study habitats, respectively. However, at all habitats except NTPs and impoundments, fewer than 5 individuals of these species were found.

Additional χ^2 analyses of goodness-of-fit and association were performed using only NTPs and over all days, since all species in the study used impoundments and all but GBHE and CAEG used NTPs, (Fig. 7). I found that species were again present in different amounts and use of the two habitats was different (Table 6). There was a species-by-habitat association with species being present in different amounts across the 2 habitats (Table 6). GREG had a significant habitat-by-species association; they were seen in impoundments much more frequently than NTPs.

At Chincoteague, I analyzed flock size distribution across habitats, species and season (early and late) (Table 8). Flocks were broken up into 4 size classes: single birds, two to five birds, five to ten birds and groups of more than ten birds. The χ^2 analysis

Table 6: Chincoteague summary χ^2 table for species distribution among habitats.

χ^2 test	Habitat		df	χ^2	P
Goodness-of-Fit	all	season	1	327.5	0.01
		tide	1	113.0	0.01
		habitat	4	3973.4	0.01
Association		species	6	1683.7	0.01
		season*species	6	40.6	0.01
		season*habitat	4	172.5	0.01
		habitat*species	24	284.8	0.01
		tide*species	6	90.6	0.01
		tide*species (imp)	6	53.7	0.01
		tide*species (NTP)	6	n/a	n/a
		tide*species (oyster)	6	n/a	n/a
		tide*species (cove)	6	n/a	n/a
		tide*species (creek)	6	n/a	n/a
		tide*habitat (CAEG)	4	n/a	n/a
		tide*habitat (GBHE)	4	n/a	n/a
		tide*habitat (GLIB)	4	n/a	n/a
		tide*habitat (GREG)	4	50.5	0.01
		tide*habitat (LBHE)	4	n/a	n/a
		tide*habitat (SNEG)	4	56.4	0.01
		tide*habitat (TRHE)	4	n/a	n/a
		tide*season (imp)	1	1.32	ns
		tide*season (NTP)	1	13.9	0.01
		tide*season (oyster)	1	n/a	n/a
		tide*season (cove)	1	1.10	ns
		tide*season (creek)	1	0.64	ns
		tide*season (CAEG)	1	n/a	n/a
		tide*season (GBHE)	1	0.28	ns
		tide*season (GLIB)	1	37.9	0.01
		tide*season (GREG)	1	5.4	0.05
		tide*season (LBHE)	1	2.26	ns
tide*season (SNEG)	1	2.80	ns		
tide*season (TRHE)	1	1.23	ns		

ns = not significant, n/a = not available

Table 6 (continued): Chincoteague summary χ^2 table for species distribution among habitats.

χ^2 test	Habitat		df	χ^2	P
Goodness-of-Fit	NTP and imp	season	1	410.6	0.01
		tide	1	84.3	0.01
		habitat	1	793.2	0.01
		species	4	759.3	0.01
Association		season*species	4	27.8	0.01
		season*habitat	1	11.3	0.01
		habitat*species	4	202.0	0.01
		tide*species	4	90.8	0.01
		tide*species (imp)	4	53.1	0.01
		tide*species (NTP)	4	9.2	ns
		tide*habitat (GLIB)	1	2.97	ns
		tide*habitat (GREG)	1	46.9	0.01
		tide*habitat (LBHE)	1	1.64	ns
		tide*habitat (TRHE)	1	0.00	ns
		tide*habitat (SNEG)	1	33.9	0.01
		tide*season (NTP)	1	13.9	0.01
		tide*season (GLIB)	1	37.9	0.01
		tide*season (GREG)	1	6.7	0.01
		tide*season (SNEG)	1	21.5	0.01

ns = not significant, n/a = not available

Table 7: Significant χ^2 association of habitat (impoundments, non-tidal ponds, oyster beds, coves and tidal creeks) and species.

Species		Imp	NTP	Oyster	Cove	Creek
CAEG	observed	9	0	0	0	0
	expected	7.4	1.2	0.05	0.2	0.3
GBHE	observed	19	0	0	2	0
	expected	17.2	2.7	0.1	0.4	0.6
GLIB	observed	331	12	0	0	0
	expected	280.3	44.2	1.9	6.7	9.9
GREG	observed	554	78	1	11	17
	expected	540.2	85.3	3.6	12.9	19.0
LBHE	observed	35	52	0	3	0
	expected	73.6	11.6	0.5	1.8	2.6
SNEG	observed	355	52	8	14	29
	expected	374.3	59.1	2.5	9.0	13.2
TRHE	observed	34	17	0	2	1
	expected	44.1	7.0	0.3	1.1	1.6

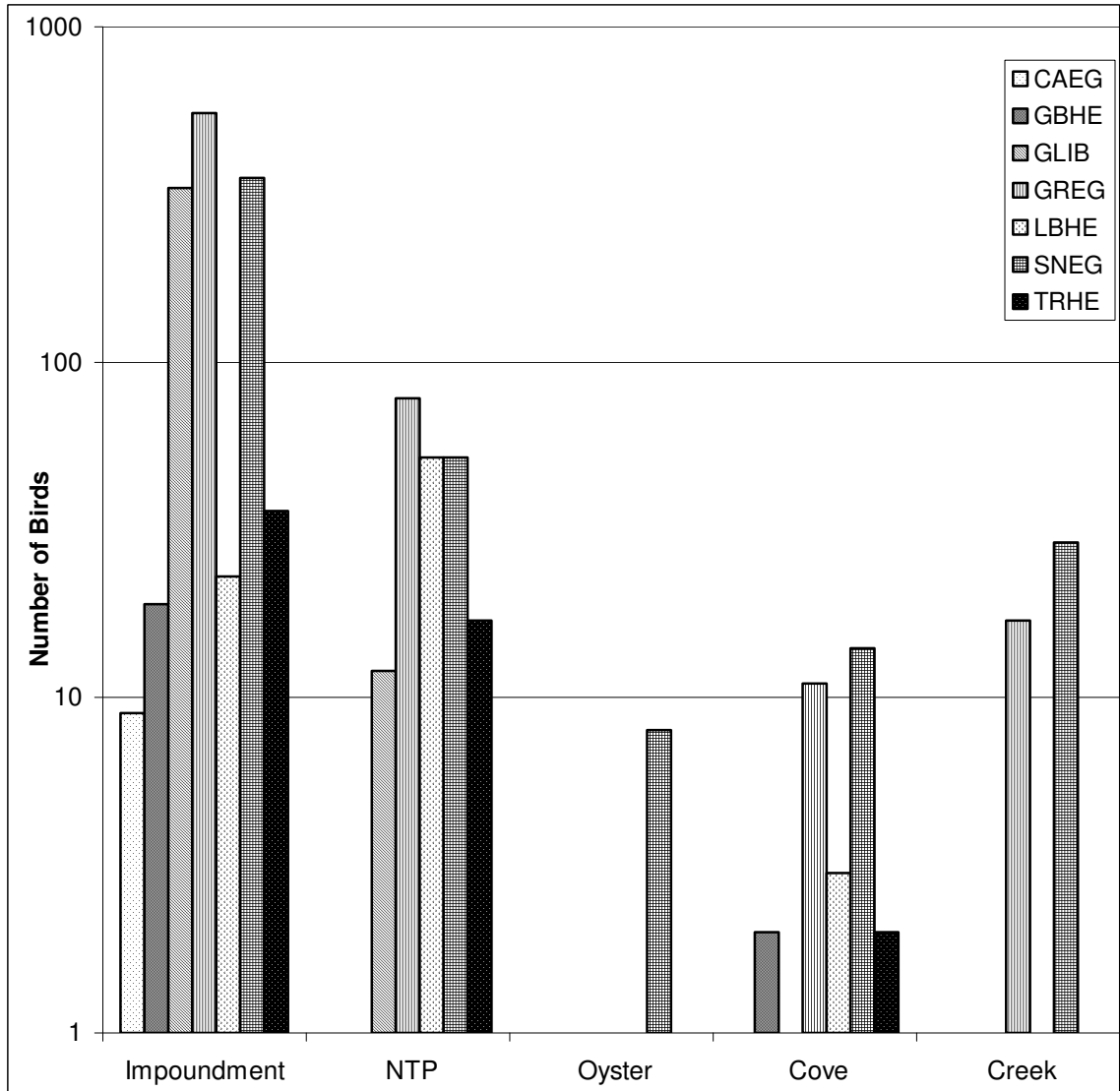


Fig 7: Species presence of Cattle Egrets (CAEG), Great Blue Herons (GBHE), Glossy Ibises (GLIB), Great Egrets (GREG), Little Blue Herons (LBHE), Snowy Egrets (SNEG), and Tricolored Herons (TRHE) across Chincoteague habitats: brackish impoundments, non-tidal ponds, oyster beds, protected coves and tidal creeks.

Table 8: Summary χ^2 table for differences in flock size of single birds, groups of 2-5, 6-10 and greater than 10 birds at Chincoteague.

χ^2 Test		df	χ^2	P
Goodness-of-Fit	flock	3	172.4	<0.0001
	species	3	22.4	<0.0001
Association	flock*species	9	5.95	Ns
	flock*season	3	26.8	<0.0001
	flock*habitat	12	12.3	Ns
	flock*tide	3	7.5	Ns
	habitat*species (A)	12	40.5	<0.0001
	habitat*species (B)	12	n/a	n/a
	habitat*species (C)	12	n/a	n/a
	habitat*species (D)	12	n/a	n/a
	species*season (A)	3	12.8	0.0052
	species*season (B)	3	3.1	ns
	species*season (C)	3	n/a	n/a
	species*season (D)	3	n/a	n/a
	habitat*season (A)	4	7.4	ns
	habitat*season (B)	4	n/a	n/a
	habitat*season (C)	4	n/a	n/a
	habitat*season (D)	4	n/a	n/a
	species*tide (A)	3	7.9	0.0479
	species*tide (B)	3	3.4	ns
	species*tide (C)	3	n/a	n/a
	species*tide (D)	3	1.9	ns
habitat*tide (A)	4	11.8	0.0187	
habitat*tide (B)	4	n/a	n/a	
habitat*tide (C)	4	n/a	n/a	
habitat*tide (D)	4	n/a	n/a	

ns = not significant, A = one bird flock size, B = 2-5 birds, C = 6-10 birds, D = more than 10 birds

of goodness-of-fit showed that flock sizes were represented differently with single birds and small associations of two to five birds being the most prevalent (Table 8). Flock size was found to be slightly negatively correlated with feeding efficiency for SNEG (Spearman $r = -0.41$, $P = 0.02$) and GREG ($r = -0.37$, $P = 0.02$) in the impoundments. Lack of data precluded additional correlation analysis of flock and feeding efficiency.

At Hog Island, the χ^2 analysis of association on habitat and species showed that creeks and ponds were used differently. (Table 9). Many more birds were observed in ponds than in the creeks, and ponds were used much more frequently (Fig. 8). All species were recorded in the ponds, while all but ibises were found in the creeks. Species were represented significantly differently; more specifically, WHIB were the most abundant overall, followed by SNEG and then GREG (Table 9). There was a significant habitat by species association (Table 9). In the creek, SNEG were the most prevalent followed by GREG, while in the pond WHIB were the most abundant followed by SNEG and then GREG.

At Hog Island, flocking was again analyzed across habitats species and season (spring vs. summer). The χ^2 analysis for association showed that different flock sizes were represented differently with individual birds and flocks of two to five birds being the most abundant (Table 10).

The Shannon Index was calculated for all habitats at both Chincoteague and Hog Island (Table 11). While most species at Chincoteague were recorded in the brackish impoundments, the NTPs had the highest index. Oysters and creeks had the lowest number of species and accordingly, the lowest Shannon indices. At Hog Island, the pond had six species represented and a correspondingly high Shannon index. The ponds at Hog

Table 9: Hog Island summary χ^2 table for species use.

χ^2 Test	Species		df	χ^2	P
Goodness-of-Fit	all	tide	1	54.6	0.01
		species	5	158.8	0.01
		habitat	1	119.8	0.01
	no ibises	tide	1	33.7	0.01
		species	3	57.4	0.01
		habitat	1	43.0	0.01
Association	all	habitat*species	5	20.8	0.01
		tide*species	5	13.1	0.05
		tide*species (creek)	5	n/a	n/a
		tide*species (pond)	5	16.2	0.01
		tide*habitat	1	5.0	0.05
		tide*habitat (GLIB)	1	n/a	n/a
		tide*habitat (GREG)	1	0.6	ns
		tide*habitat (LBHE)	1	1.2	ns
		tide*habitat (SNEG)	1	3.2	ns
		tide*habitat (TRHE)	1	3.0	ns
		tide*habitat (WHIB)	1	n/a	n/a
		habitat*species (high)	5	2.0	ns
	no Ibises	habitat*species (low)	5	n/a	n/a
		habitat*species	3	1.6	ns
		tide*species	3	10.1	0.05
		habitat*tide	1	5.1	0.05
		tide*species (creek)	3	0.9	ns
		tide*species (pond)	3	12.9	0.01
		tide*habitat (GREG)	1	0.6	ns
		tide*habitat (LBHE)	1	1.2	ns
		tide*habitat (SNEG)	1	3.2	ns
		tide*habitat (TRHE)	1	3.0	ns
		habitat*species (high)	3	0.7	ns
		habitat*species (low)	3	4.8	ns

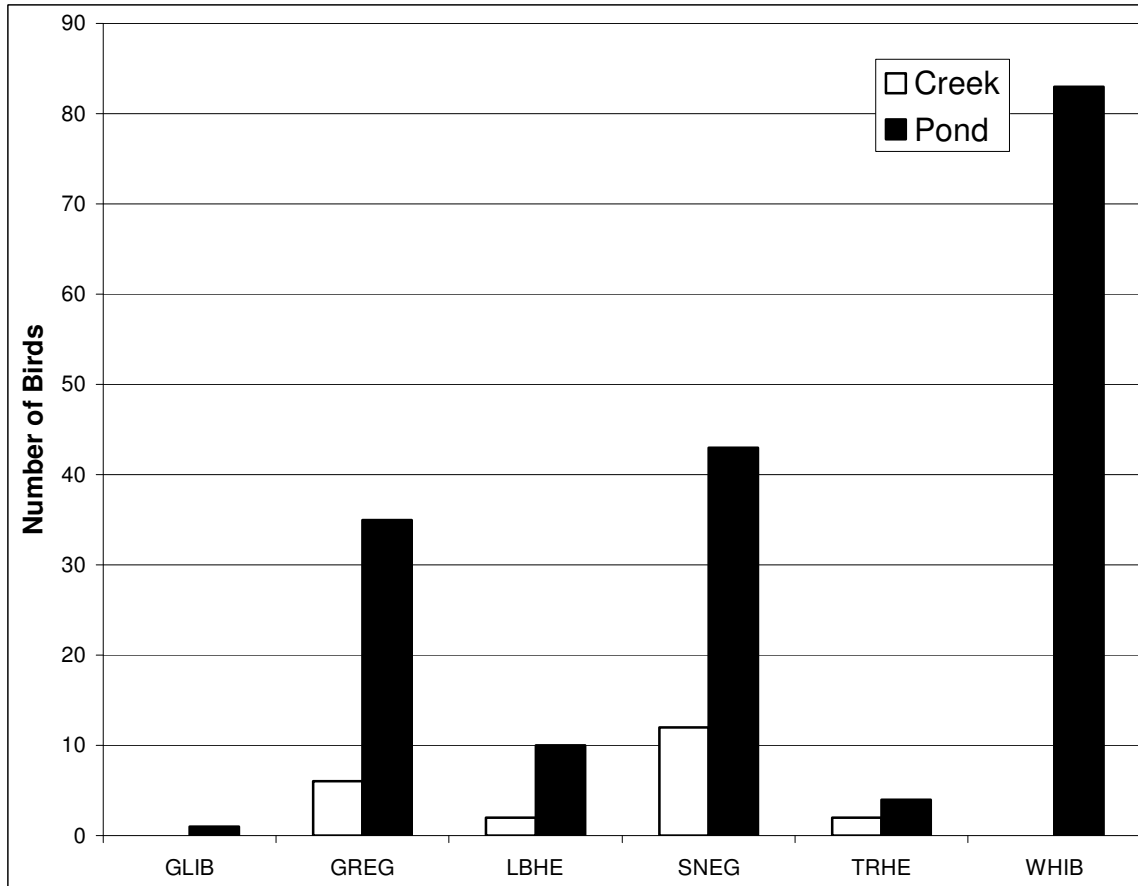


Fig. 8: Hog Island habitat use across non-tidal ponds (pond) and tidal creek (creek) habitats.

Table 10: Summary χ^2 table for differences in flock size of single birds, groups of 2-5, 6-10 and greater than 10 birds at Hog Island.

χ^2 test		df	χ^2 value	P value
Goodness-of-Fit	flock	3	89.2	0.01
	species	3	22.8	0.01
	habitat	1	0.3	ns
Association	flock*season	3	7.7	ns
	flock*habitat	3	12.2	0.01
	flock*species	9	14.1	ns
	habitat*species (A)	3	11.4	0.01
	habitat*species (B)	3	4.1	ns
	habitat*species (C)	3	n/a	n/a
	habitat*species (D)	3	n/a	n/a
	species*season (A)	3	1.5	ns
	species*season (B)	3	4.8	ns
	species*season (C)	3	n/a	n/a
	species*season (D)	3	2.1	ns
	habitat*season (A)	1	0.1	ns
	habitat*season (B)	1	2.7	ns
	habitat*season (C)	1	n/a	n/a
	habitat*season (D)	1	n/a	n/a

ns = not significant, A = one bird flock size, B = 2-5 birds, C = 6-10 birds, D = more than 10 birds

Table 11: Shannon Index of species richness and equitability across habitats at Hog Island and Chincoteague. See Fig. 7 for Chincoteague and Fig. 8 for Hog habitat classifications.

Location	Habitat	Species Count	Index
Chincoteague	NTP	5	1.424
	impoundment	7	1.346
	cove	5	1.297
	creek	3	0.748
	oyster	2	0.349
Hog	pond	6	1.298
	creek	4	1.121

Island had roughly the same Shannon value as the coves at Chincoteague, which had the third highest of all Chincoteague habitats.

Question 2: How did feeding efficiency vary across species and among habitat types?

An ANOVA analysis (SAS 9.1) on mean feeding efficiencies at Chincoteague revealed that they were much higher for LBHE than the other species, while at Hog Island TRHE had the highest efficiencies (Table 12). At Chincoteague, SNEG had the lowest mean efficiency, but it was very similar to the mean efficiencies of GREG and TRHE. GREG and SNEG at Hog Island were much lower than the other two species. Overall, efficiencies were much higher for all species at Chincoteague than Hog Island with the exception of TRHE (Table 12).

Table 12: Average feeding efficiencies for species at Chincoteague and Hog Island

Location	Species	Mean	Standard Error
Chincoteague	GREG	0.38	0.04
	LBHE	0.56	0.05
	SNEG	0.31	0.04
	TRHE	0.34	0.06
Hog Island	GREG	0.19	0.06
	LBHE	0.29	0.08
	SNEG	0.18	0.04
	TRHE	0.35	0.09

The ANOVA analysis at Chincoteague showed an overall significance across the entire experiment duration (Table 13). However this analysis had low power (Power = 0.38).

Not all species at Chincoteague had recorded feeding efficiencies for all habitats, however GREG was the only species to have mean efficiencies of zero even though they were making strike attempts (Appendix B). At high tide, GREG had feeding efficiencies of zero at NTPs and creeks. At low tide, this species also had efficiencies of zero at the

Table 13: ANOVA table for average feeding efficiency across species and habitats.

Location	Season		df	F	P	
Chincoteague	all	model	26	1.69	0.05	
	all	habitat	4	1.20	ns	
	all	species	3	1.74	ns	
	all	tide	1	1.10	ns	
	all	habitat*species	9	1.30	ns	
	all	habitat*tide	3	1.18	ns	
	all	species*tide	3	0.32	ns	
	all	habitat*species*tide	3	1.46	ns	
	early	model	22	1.73	0.05	
	early	habitat	4	1.43	ns	
	early	species	3	1.28	ns	
	early	tide	1	0.69	ns	
	early	habitat*species	6	1.24	ns	
	early	habitat*tide	3	0.21	ns	
	early	species*tide	3	0.64	ns	
	early	habitat*species*tide	2	3.25	0.05	
	late	model	20	1.29	ns	
	late	habitat	4	0.30	ns	
	late	species	3	2.41	ns	
	late	tide	1	0.01	ns	
	late	habitat*species	6	1.70	ns	
	late	habitat*tide	1	0.58	ns	
	late	species*tide	3	0.39	ns	
	late	habitat*species*tide	2	0.12	ns	
	Hog Island	all	model	7	2.07	ns
		all	habitat	1	1.93	ns
		all	species	3	1.07	ns
		all	habitat*species	3	1.27	ns
April/May		model	6	1.91	ns	
April/May		habitat	1	6.18	0.05	
April/May		species	3	2.27	ns	
April/May		habitat*species	2	2.64	ns	
June		model	5	10.35	0.01	
June		habitat	1	16.71	0.01	
June		species	3	5.80	0.01	
June		habitat*species	1	21.68	0.01	
July		model	6	1.44	ns	
July		habitat	1	1.83	ns	
July		species	3	0.64	ns	
July		habitat*species	2	0.30	ns	
August	model	5	1.39	ns		
August	habitat	1	3.68	ns		
August	species	3	0.69	ns		
August	habitat*species	1	0.87	ns		

oyster beds. At the NTPs and creeks, the zeros occurred in the early season and at the oysters in the late season.

When an ANOVA analysis was performed on the Hog Island data, the overall model was close to significant across all months (Table 13). In the Hog Island creeks, TRHE feeding efficiency was significantly higher than GREG or SNEG (Fig. 9). LBHE efficiency was indistinguishable from all other species. At the ponds, all species had indistinguishable feeding efficiencies, however, GREG and SNEG had greater feeding efficiency there than in the creeks.

At Chincoteague feeding efficiencies were negatively correlated with flock size (Table 14). The larger the flocks containing SNEG and GREG, the lower their recorded feeding efficiency became in impoundments ($r = -0.41, P = 0.02$; $r = -0.37, P = 0.02$). These were the only cases where significant relationships were found between flock size and efficiency. At Hog Island, there was insufficient data to attempt a correlation (Table 15).

Question 3: How does tide and season affect habitat use, flocking or feeding efficiency?

Overall, seasonal effects appear to have a greater influence on all variables than tide at both Hog Island and Chincoteague. When a χ^2 analysis for association was performed on habitat use data from all days at Chincoteague there was a significant difference found between the early and late season (Table 6). There were many more birds recorded in the late season (Fig. 10). Tide level and habitats yielded different results than expected; at low tide more birds were present than at high tide, and NTPs and impoundments had the largest number of species (Table 6).

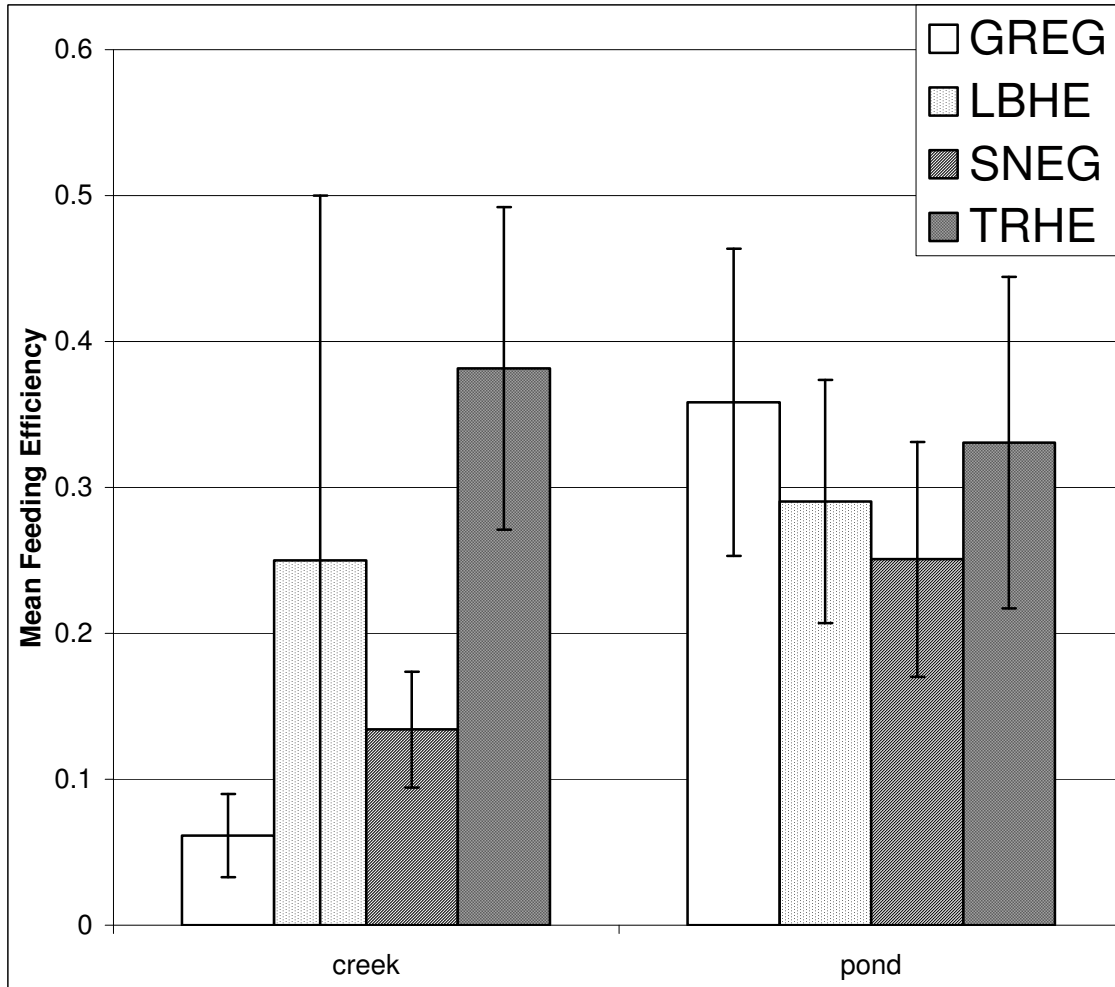


Fig. 9: Mean feeding efficiency \pm SE on Hog Island across habitats for Great Egrets (GREG), Little Blue Herons (LBHE), Snowy Egrets (SNEG), and Tricolored Herons (TRHE).

Table 14: Chincoteague average feeding efficiency and standard deviation for all habitats and flock categories. See Fig. 7 for habitat classifications.

Season	Species	Flock Cove		Imp		NTP		Oyster		Creek		
		Size	Ave	SD	Ave	SD	Ave	SD	Ave	SD	Ave	SD
Early	GREG	1	0.229	0.208	0.491	0.294	0.417	0.500	--	--	0.125	0.250
		2-4	--	--	0.563	0.088	--	--	--	--	--	--
		5-10	--	--	--	--	--	--	--	--	--	--
		>10	--	--	--	--	--	--	--	--	--	--
	LBHE	1	--	--	0.438	0.377	0.574	0.262	0.250	--	--	--
		2-4	--	--	--	--	0.490	0.205	--	--	--	--
		5-10	--	--	--	--	--	--	--	--	--	--
		>10	--	--	--	--	--	--	--	--	--	--
	SNEG	1	0.278	0.347	0.338	0.280	0.225	0.062	0.263	0.254	0.226	0.257
		2-4	--	--	0.274	0.286	0.325	0.409	--	--	0.500	--
		5-10	--	--	--	--	--	--	--	--	--	--
		>10	--	--	--	--	--	--	--	--	--	--
	TRHE	1	0.393	--	0.028	0.048	--	--	--	--	--	--
		2-4	--	--	0.375	--	--	--	--	--	--	--
		5-10	--	--	--	--	--	--	--	--	--	--
		>10	--	--	--	--	--	--	--	--	--	--
Late	GREG	1	--	--	0.597	0.238	0.000	0.000	0.000	--	--	--
		2-4	--	--	0.393	0.290	0.644	0.229	--	--	0.283	0.202
		5-10	--	--	0.417	0.520	--	--	--	--	--	--
		>10	--	--	0.181	0.214	--	--	--	--	--	--
	LBHE	1	--	--	0.500	0.354	0.688	0.252	--	--	--	--
		2-4	0.633	--	0.547	0.339	0.750	0.118	--	--	--	--
		5-10	--	--	--	--	--	--	--	--	--	--
		>10	--	--	--	--	0.917	0.118	--	--	--	--
	SNEG	1	0.150	0.212	0.502	0.344	0.375	0.323	0.639	0.337	0.167	0.289
		2-4	0.250	--	0.055	0.069	--	--	--	--	0.222	0.314
		5-10	--	--	0.375	--	0.350	--	--	--	--	--
		>10	--	--	0.083	0.118	0.000	0.000	--	--	--	--
	TRHE	1	--	--	0.504	0.119	0.424	0.233	--	--	--	--
		2-4	--	--	0.438	0.163	0.500	0.000	--	--	--	--
		5-10	--	--	--	--	--	--	--	--	--	--
		>10	--	--	0.426	0.269	0.000	--	--	--	--	--

early = before July 26, late = after July 26

Table 15: Hog Island average feeding efficiency and standard deviation for all habitats and flock categories. See Fig. 8 for habitat classifications.

Season	Species	Flock Size	Creek Ave	Creek SD	Pond Ave	Pond SD
Spring	GREG	1	0.054167	0.087202	0.216667	0.306413
		2-4	0	--	--	--
		5-10	--	--	--	--
		>10	--	--	--	--
	LBHE	1	--	--	0.108333	0.137689
		2-4	--	--	0.328148	0.22691
		5-10	--	--	0.4	0.2
		>10	--	--	--	--
	SNEG	1	0.128444	0.120426	0.133333	0.133333
		2-4	0.141667	0.082496	--	--
		5-10	--	--	--	--
		>10	--	--	--	--
	TRHE	1	0.533333	--	0.125	0.176777
		2-4	--	--	--	--
		5-10	--	--	--	--
		>10	--	--	--	--
Summer	GREG	1	0.066667	0.149071	0.425	0.234323
		2-4	0	0	0.666667	--
		5-10	--	--	--	--
		>10	--	--	0.45	--
	LBHE	1	0.5	--	0.3125	0.265165
		2-4	0	--	--	--
		5-10	--	--	--	--
		>10	--	--	0.1	--
	SNEG	1	0.3129	0.29654	0.233333	0.18807
		2-4	0.033333	0.05164	0.395833	--
		5-10	--	--	--	--
		>10	--	--	0.411603	0.424173
	TRHE	1	--	--	0.234722	0.212309
		2-4	0.333333	0.235702	0.833333	--
		5-10	--	--	--	--
		>10	--	--	0.1	--

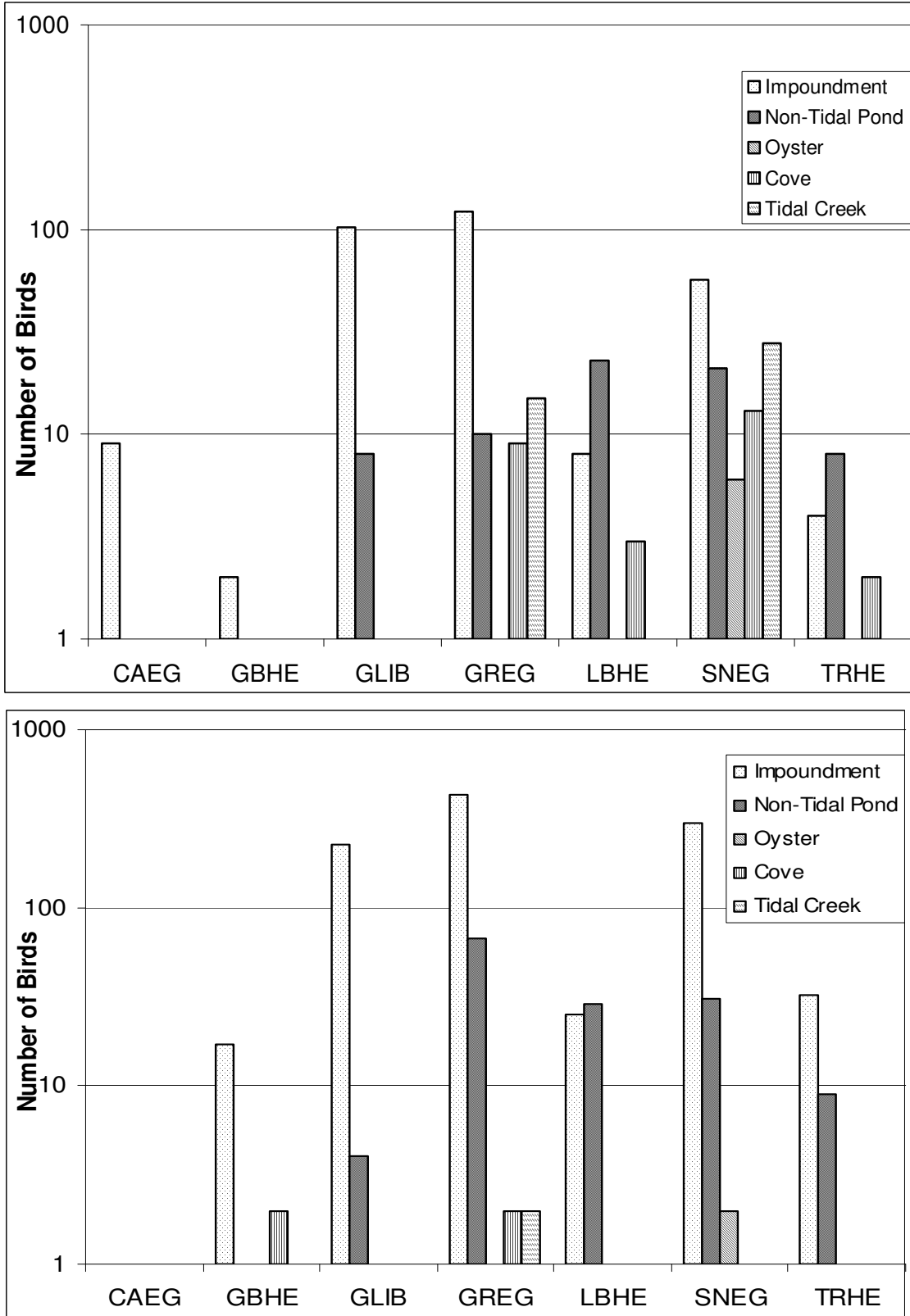


Fig. 10: Early (before July 25, top) and late (July 25 and after, bottom) season species presence across Chincoteague habitats.

When χ^2 tests of association were performed, species patterns differed between early and late season; all species except CAEG were more abundant in the late season (Table 6). Habitats also were used differently between seasons. Many more birds were present in impoundments during the late season, apparently as a result of a shift away from all other habitats (Fig. 10). CAEG were only found in the brackish impoundments, and they were only found there in the early part of the season. The incidence of GBHE was greater in the late season when more birds used the brackish impoundments.

For Chincoteague, χ^2 analyses of association and goodness-of-fit were performed on each season separately (there was a significant difference between early and late season) to examine species use differences among habitats. The early season results revealed that habitats were again not used with equal frequency and that each species was not equally distributed across habitats (Table 16). However, for the early season, tide effects were not found, nor was there a tide-by-species association. The χ^2 analysis of association for the late season found that low tide foraging occurred more than did high tide feeding (Table 16). Again the habitats were not used with equal frequency and the species were not represented in equal proportions. In the late season, unlike the early season, the tide-by-species association for impoundments and the tide-by-habitat association for GREG was present (Table 16).

GREG used all habitats in the late season, but predominantly impoundments; they used all but the oyster beds in the early season (Fig. 10). They increased in presence on oyster beds and in brackish impoundments from early to late, while the coves and creeks decreased in use.

Table 16: Chincoteague summary χ^2 table for distribution among habitats in the early and late season.

Season	χ^2 test		df	χ^2 value	P value
Early	goodness-of-fit	tide	1	3.3	ns
		habitat	4	366.5	0.01
	association	species	5	504.0	0.01
		habitat*species	20	157.4	0.01
		tide*species	5	51.7	0.01
		tide*species (imp)	5	27.1	0.01
		tide*species (NTP)	5	n/a	n/a
		tide*species (oyster)	5	n/a	n/a
		tide*species (cove)	5	n/a	n/a
		tide*species (creek)	5	n/a	n/a
		tide*habitat (GBHE)	4	n/a	n/a
		tide*habitat (GLIB)	4	n/a	n/a
		tide*habitat (GREG)	4	67.9	0.01
		tide*habitat (LBHE)	4	n/a	n/a
		tide*habitat (SNEG)	4	58.2	0.01
		tide*habitat (TRHE)	4	n/a	n/a
Late	goodness-of-fit	tide	1	74.0	0.01
		habitat	4	3389.0	0.01
	association	species	5	963.8	0.01
		habitat*species	20	1174.7	0.01
		tide*species	5	51.7	0.01
		tide*species (imp)	5	27.1	0.01
		tide*species (NTP)	5	n/a	n/a
		tide*species (oyster)	5	n/a	n/a
		tide*species (cove)	5	n/a	n/a
		tide*species (creek)	5	n/a	n/a
		tide*habitat (GBHE)	4	n/a	n/a
		tide*habitat (GLIB)	4	n/a	n/a
		tide*habitat (GREG)	4	67.9	0.01
		tide*habitat (LBHE)	4	n/a	n/a
		tide*habitat (SNEG)	4	29.6	0.01
		tide*habitat (TRHE)	4	n/a	n/a

early = before July 26, late = after July 26

LBHE were found only in impoundments, NTPs and coves. Their use of impoundments and NTPs was greater in the late season than early (Fig. 10). Alternatively, their use of the coves were only recorded in the early season. TRHE used impoundments and NTPs both early and late in the season, and their use increased over time. They used coves only in the early season and tidal creeks only late; they did not use the oyster beds at all.

In the NTPs, GLIB decreased in use late in the season, but GREG, SNEG, LBHE, and TRHE did the opposite (Fig. 11). The only species to use the oyster beds were GREG and SNEG. SNEG use of the oyster beds decreased through the season, but GREG only used them in the late season. Only CAEG and GLIB did not use the coves. GBHE were only found there in the late season, while all others decreased their use of coves in the late season. Only TRHE, GREG and SNEG used the creeks. TRHE were only found there in the late season, while GREG and SNEG decreased their use greatly from early to late.

Tide-by-season associations were only found to be significant for NTPs but only for GLIB and GREG (Table 6). Both of these species were present in different numbers at different tides between the seasons.

Numbers of feeding birds differed between tides across species (Table 6, Fig. 11). Indeed, low tide was used more than high tide by feeding birds in most habitats. In fact, the coves and oyster bars were only used at low tide, while NTPs were mostly used at high tide by GREG, SNEG, TRHE and LBHE.

A significant tide-by-habitat association for GREG was found (Table 6). This species used habitats differently at high and low tide as more were found in NTPs at high

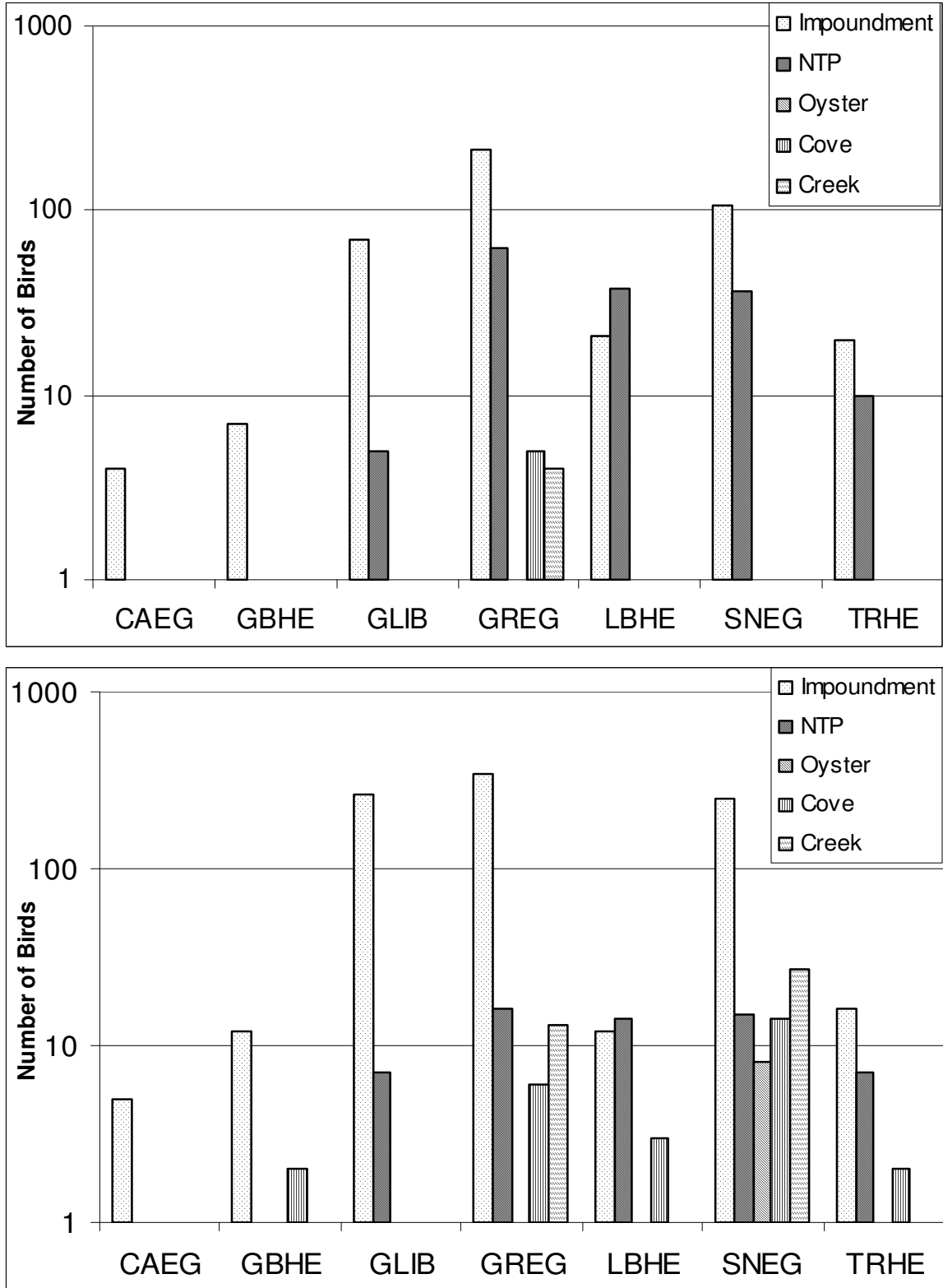


Fig. 11: High (top) and low (bottom) tide species presence across Chincoteague habitats.

than low tide (Fig. 11). There was a tide-by-species association for impoundments because more species were seen using impoundments during low tide (Table 6). GLIB foraged primarily at low tide and more SNEG were present in more habitats at low tide. Recorded numbers of GREG were not different at high and low tide, however they did use the habitats differently across tides. LBHE used the coves only at low tide and mostly used the NTPs at high tide. However, some species were less tidally influenced than others. For example, TRHE and LBHE were found in similar numbers, used habitats similarly, but had no tidal preference other than at coves.

When I examined Chincoteague NTPs and impoundments separately, tides were used differently and there were tide-by-species associations (Table 6). SNEG had a significant tide-by-habitat association. For impoundments, there was a significant species-by-tide association found (Table 6).

At Hog Island, species were represented in the ponds differently than expected across tides (Table 9). At both tide levels, WHIB were most abundant. At low tide, GLIB was the only species not present in the ponds (Fig. 12). In the ponds at high tide, SNEG and LBHE were the next two abundant. At low tide, GREG were the most prevalent after WHIB, followed by SNEG.

Tidal use also differed significantly (Table 9). More species were found at all habitats at low tide. There was a tide-by-species association because all species were represented more frequently at low tide than high. There was also a significant tide-by-habitat association (Table 9). At high tide, all species were found in ponds (Fig. 12 top). The creek was used almost exclusively at low tide; SNEG were the only ones found in the creeks at high tide (Fig. 12 top, bottom).

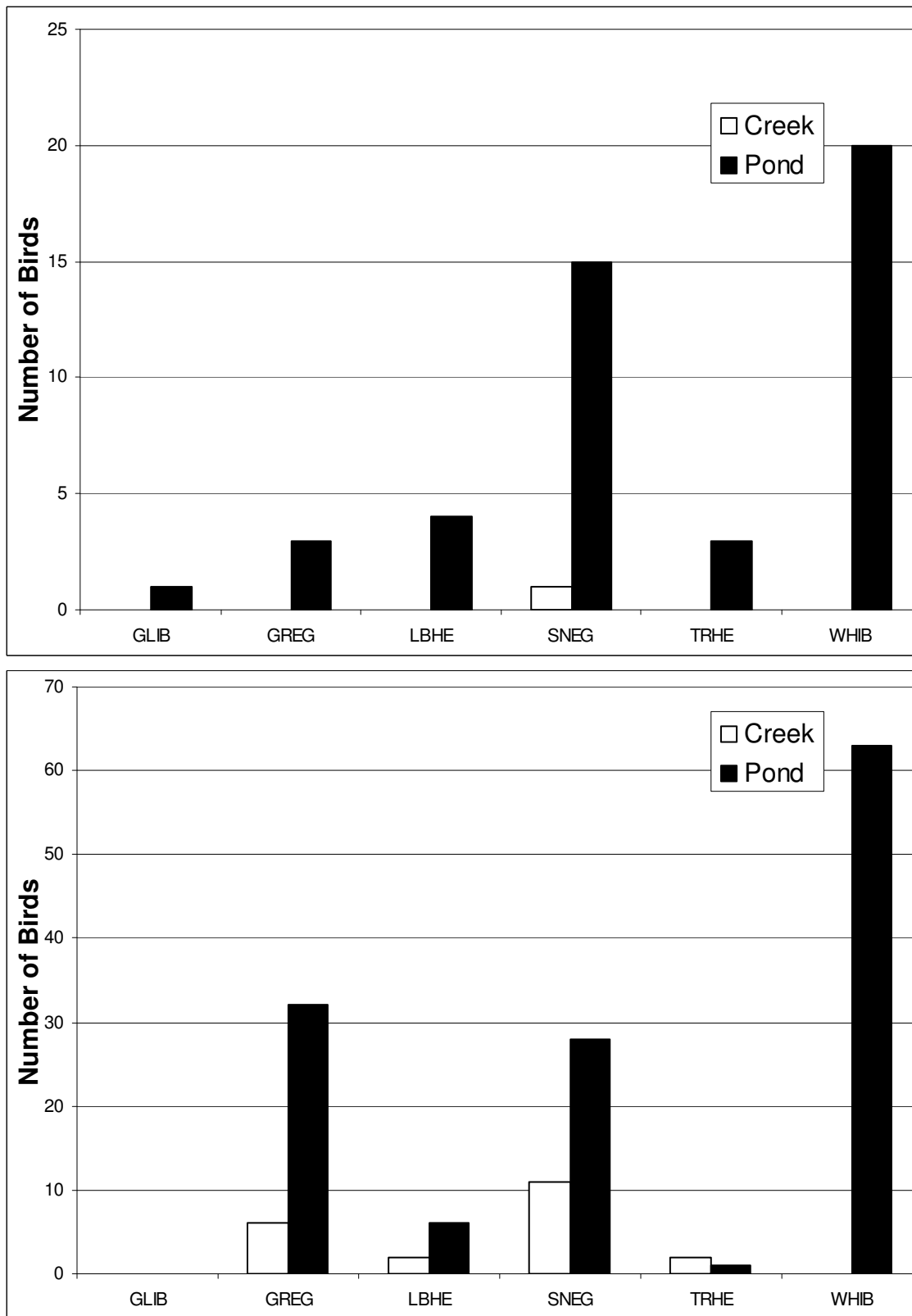


Fig. 12: Hog Island habitat use across habitats at high (top) and low (bottom) tide.

Chincoteague flock size was skewed toward individual birds and flocks of 2-5 birds were the most prevalent (Table 8). There was a significant difference in flock size between the seasons with increasing flock size during the late season. Hog Island flock size was also skewed toward individuals and flocks of 2-5 birds. There was a flock by habitat association as ponds more frequently had larger flocks than did creeks (Table 8).

For feeding efficiency at Chincoteague, the early season had an overall model significance (Table 13) and a habitat-by-species-by-tide significance, indicating that the feeding efficiency of species were different across habitats between tides. In the late season nothing in the model was significant (Table 13).

Mean feeding efficiency for high tide was indistinguishable for all species in the impoundments, but LBHE had the highest in NTPs (Fig. 13 top). At low tide, LBHE tended to have a high FE and was indeed the highest in impoundments and coves (Fig. 13 bottom). SNEG had the highest feeding efficiency of all species on oyster beds, but their average efficiency was not different across habitats at both high and low tides. GREG were more efficient at high tide at the impoundments than at low tide, but they tended to have low efficiencies overall.

Hog Island efficiency data were separated by month rather than early or late season as at Chincoteague because I was able to make more observations at Hog Island. The only month with significant ANOVA outcomes was June; the overall model for this month was significant (Table 13). There were both habitat and species differences. There was also a habitat-by-species significance (Table 13). Efficiencies for GREG were much higher in ponds than in creeks (Fig. 14). SNEG had the highest mean efficiency in creeks.

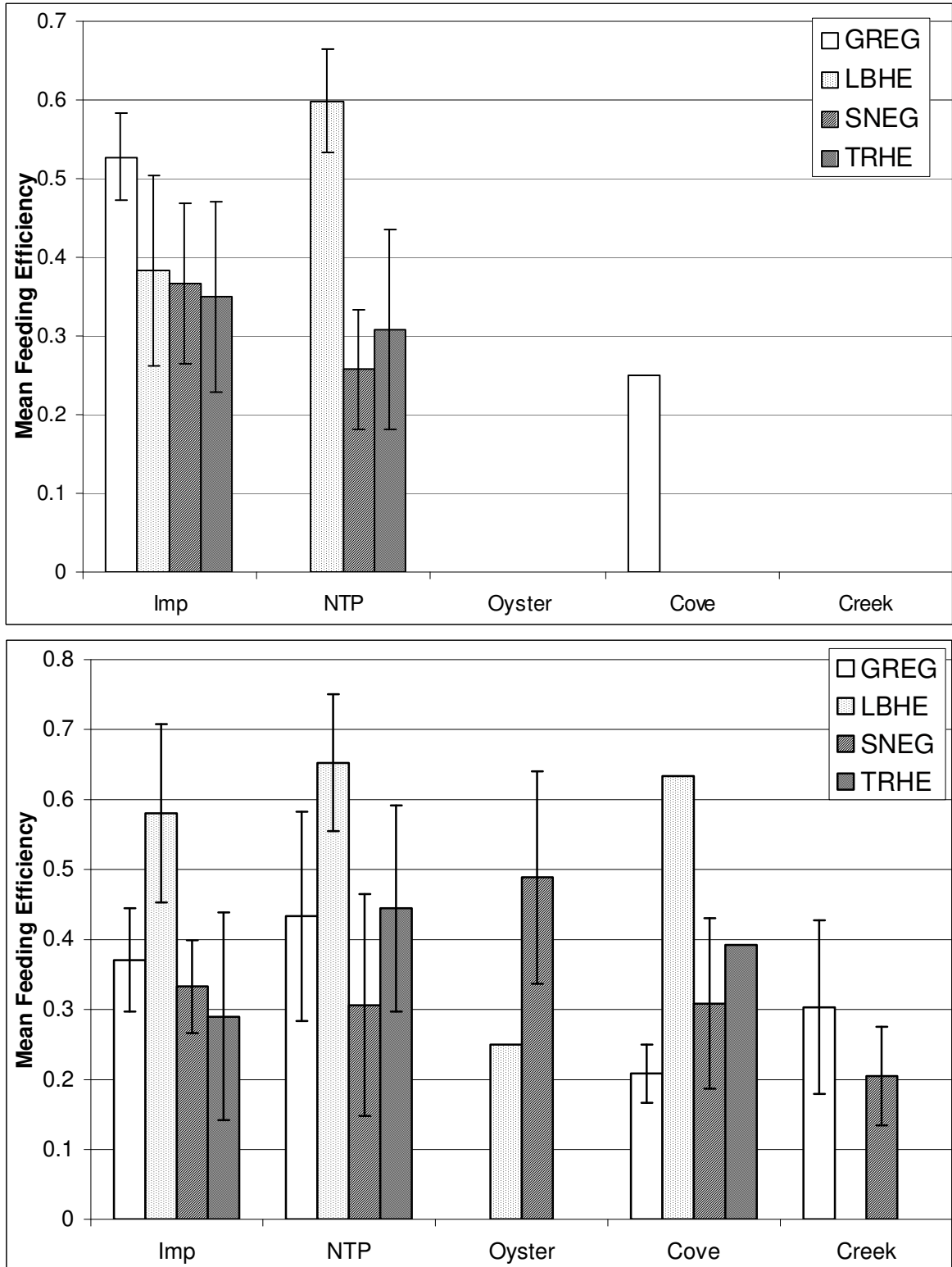


Fig. 13: Mean feeding efficiency \pm SE across Chincoteague habitats at high (top) and low (bottom) tides for Great Egrets (GREG), Little Blue Herons (LBHE), Snowy Egrets (SNEG), and Tricolored Herons (TRHE). See Fig. 7 for habitat types.

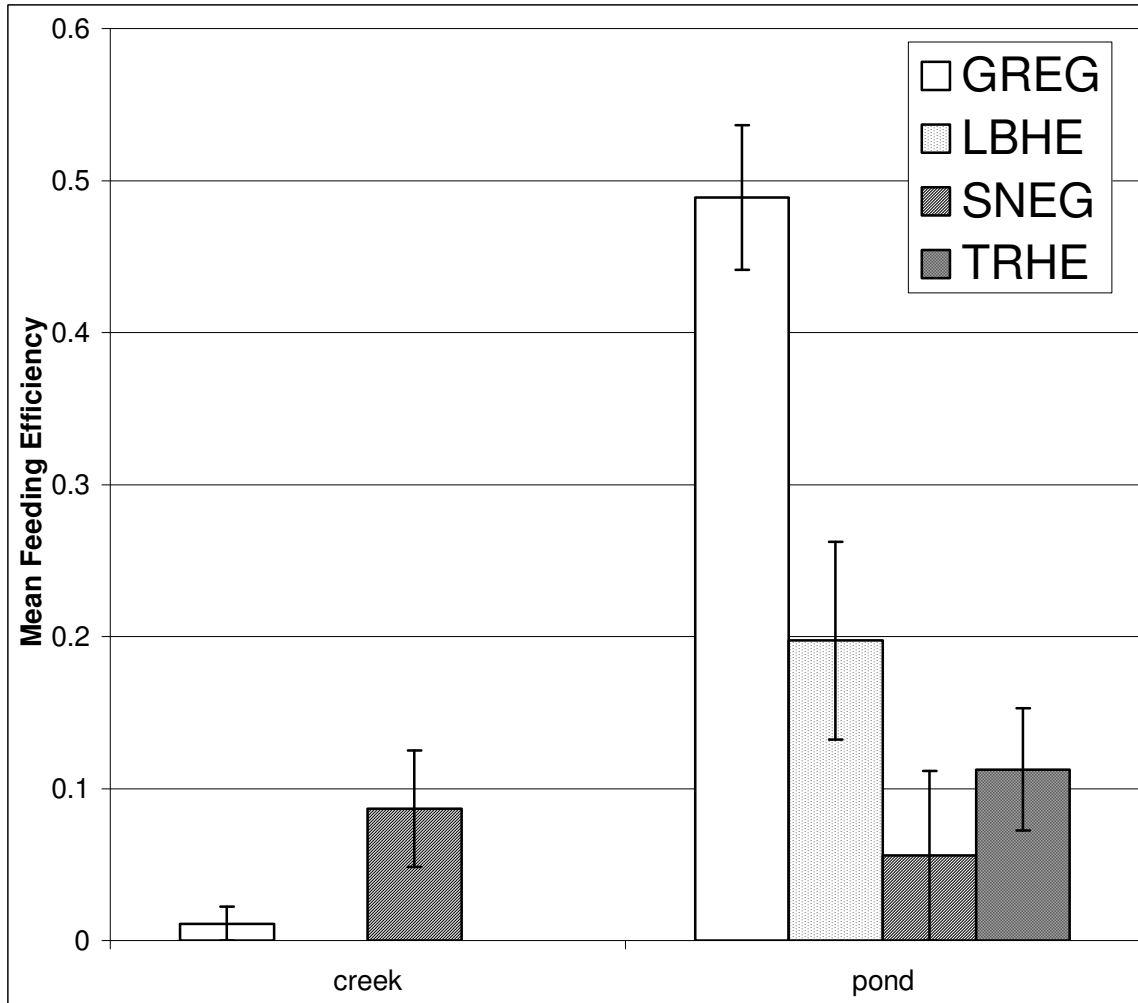


Fig. 14: Mean feeding efficiency \pm SE for the month of June on Hog Island across habitats for Great Egrets (GREG), Little Blue Herons (LBHE), Snowy Egrets (SNEG), and Tricolored Herons (TRHE).

At Chincoteague, season played an important role in species use for certain habitats (Fig. 10). Many more birds of most species were found in the impoundments and NTPs in the late season; fewer were found in the other habitats in the late season although the number of days of observation were the same in both seasons. On the other hand, season did not seem to have a large impact on feeding efficiency (Table 13). At Hog Island, June data revealed significant differences in feeding efficiency. At both locations, flocking increased over time and tide played a large part in habitat use (Table 8, 10). At Hog Island, numbers of birds decreased with increasing tidal stage (Table 9).

DISCUSSION

Chincoteague Experiment

The experiment in Chincoteague did not produce enough data for meaningful analysis, however a few trends are worth noting.

Question 1: Which species preferred white versus dark decoys?

LBHE and SNEG visited the white/high treatment more frequently than any of the others and TRHE and GREG only visited the white decoy treatments. This would seem to indicate that these species did in fact prefer the white decoy treatments.

Question 2: Which utilized higher prey density cues rather than the social ones?

SNEG and LBHE, while preferring the white decoy treatments, also prefer the high prey density treatments, perhaps indicating a choice based partially on prey density. Masters *et al.* (2005) had similar findings where initially arriving SNEG visited pools with increased prey density. They found that other species such as GREG and LBHE did not respond to density, most likely due to equal numbers of SNEG decoys at each experimental pond. This supports the hypothesis that these other birds are choosing foraging habitat based on SNEG presence, and would account for the numerous LBHE that chose the white/high treatment as SNEGs were already present at these locations when the LBHE made their habitat choice. Due to limited data for most of the species, additional comments about species' cues in foraging would only be speculation.

Question 3: Did length-of-stay differ among treatments?

Lengths-of-stay at all treatments were fairly short (typically less than five minutes) compared to the time spent by these species in the ponds used in the observational study in which the birds frequently stayed for over 30 minutes. The observational study ponds were chosen based on known species presence; these ponds

were much larger than the ponds used in this experiment. Small experimental ponds were selected because they could be more easily manipulated. The limited pond sizes may be the reason that the length-of-stay was so short. In Caldwell's (1981) study, she found that when decoys were present in foraging habitat, their presence would sometimes be such a strong attractant for birds that they would leave the decoys after foraging unsuccessfully, then return after a short period. Unfortunately, her study did not include the duration that these birds remained to forage unsuccessfully before they departed. Species in my experiment that were attracted to the white/high treatment tended to stay for a very short time, indicating that they were probably merely sampling their environment.

This study might have yielded some significant results had it been conducted over a longer time period with a larger number of ponds of greater size range, or even in a number of artificial pools of known fish density. In addition, if it were feasible for the experiment to be run early in the morning when the fish may have been drawn to the surface due to the decreased oxygen content caused by overnight respiration by plant species (Kersten *et al.* 1991), perhaps an increased response to prey density would have been seen.

Observational Study

Question 1: How were species distributed across habitat types?

Overall, the generalist species were found more widely distributed across the habitat types than the specialists at Chincoteague. GREG and SNEG were found in all habitats. CAEG were only found in impoundments, GLIB in ponds and impoundments, and TRHE and LBHE used impoundments, ponds and tidal creeks. While GBHE would be considered a generalist species, they are primarily an inland species and they tend to

use mostly freshwater habitats during the spring and early summer (Willard 1977), which would account for their presence in impoundments in the early season, expanding into coves later in the study. Although CAEG typically are found in fields foraging with livestock (Kushlan 1978b), they were found in impoundments. However, the only impoundment they were found in was located less than 50 m away from an enclosed area where wild ponies frequently came to feed. The GLIB favored impoundments and were frequently present there in large flocks, and the LBHE and TRHE favored ponds.

On Hog Island, there were fewer types of habitats available to wading birds. There were multiple non-tidal ponds and tidal creeks of a similar size to those at Chincoteague. There was a clear pond preference by all species. However, only GREG, LBHE, SNEG and TRHE were found in creeks. SNEG and GREG used the creeks most frequently, and after ibises, they were found second and third most frequently in ponds, respectively. The generalist species, GREG and SNEG were indeed found across both habitat types, but TRHE and LBHE were also found here. This corresponds to what was found in Chincoteague, but since there are only two habitat types, it is not possible to distinguish between the generalist and specialist habitat use. Intermediate species, GLIB and WHIB however, only used the ponds. Similarly, in Frederick and Bildstein's (1992) study on a variety of ibises, they never found any foraging in flowing water.

While ponds were preferred by all species, large aggregations most often were seen in ponds, suggesting a potential competition (a significant habitat*flock comparison). This is partially supported by Frederick and Bildstein's study (1992) where they found WHIB and GLIB tend to prefer foraging in flocks in standing water.

Question 2: How did feeding efficiency of different species vary among and within habitat types?

As expected, specialists such as LBHE and TRHE had higher overall efficiencies at either Hog Island (both species) or Chincoteague (LBHE) than did the generalists, GREG and SNEG. In the brackish impoundments at the Chincoteague site, feeding efficiency tended to be very high, even though this habitat tended to encourage large congregations of birds. This supports the suggestion that late-season drawdowns in this foraging habitat lead to increasingly available prey items. With the exception of impoundments, SNEG had similar feeding efficiencies across habitats, as did GREG. In the impoundments, most SNEG and GREG had high efficiencies, which is perhaps an artifact of the later season drawdown. The majority of LBHE had high feeding efficiencies in the ponds, while TRHE were equally high in both ponds and impoundments. As specialists in particular habitats, these species should be most efficient at these sites. SNEG utilized oyster beds more efficiently and were also found there more frequently than GREG, the only other species found there. While both these species are generalists, SNEG tend to select the highest quality patches and leave rather than utilize a patch declining in quality, while GREG typically remain until fish are at very low densities (Erwin 1985, Gawlick 2002). This was corroborated by the fact that GREG were the only species I found to have average feeding efficiencies of zero at multiple locations.

At Hog Island ponds, feeding efficiencies were varied across all categories for all species. In the creeks however, most SNEG and GREG had very low feeding efficiencies. These species were present in creeks most frequently. Being generalists, it is expected

that they would exploit all available habitats, even those that they do not utilize efficiently (Recher and Recher 1980). Lombardini *et al.* (2001) found that relative use of habitats was related to relative foraging success: my results support this; the low feeding efficiency of both GREG and SNEG parallels the low numbers of these generalists in the creeks compared to ponds.

Question 3: How does tide and season affect habitat use, flocking or feeding efficiency?

The habitat types at Chincoteague were not used in equal frequency. Some of these habitats were not readily available during all tides (oysters, tidal creeks), which were evident in their differential use at high and low tide. The generalist species tended to exploit these variable habitats, while the specialists did not. While the impoundments did not vary with tides, their use still reflected a tidal influence, reflecting the dynamics of prey availability in the surrounding tidal habitats. GLIB were the only species to forage almost exclusively at low tide in the impoundments. At this time of year, wading birds should be maximizing their prey intake to feed their growing offspring (Erwin 1985, Bryan *et al.* 2005), so it is possible that the GLIB were utilizing other habitats not studied during high tide, such as nearby *Spartina* marshes (pers. obs.).

Numbers of both TRHE and GBHE increased throughout the season at Chincoteague. Willard (1977) reported similar findings in his study on the New Jersey coast. He found virtually no overlap of Great Blue Herons with other species in habitat use in the spring months but increasing overlap in the late summer and fall. During the spring and summer, GBHE tend to use inland, freshwater areas for foraging (Willard 1977). As in this study, Willard found that impoundments increased in use toward the end of summer and fall as species shifted to freshwater habitats. Erwin *et al.* (1996) also

implied a similar pattern for recently fledged wading birds near Chincoteague. This habitat also typically had large flocks of birds later in the season which could perhaps be attributed to drying and therefore increased prey availability and accessibility in this habitat (Kushlan 1978a, Master *et al.* 2005). These large aggregations should be an indication of a highly productive patch leading to maximal prey intake (Sih 1998).

There was an obvious tidal influence on Hog Island. SNEG were the only species to use creeks at rising tides, however only when the water was still low enough to allow wading below the line of *Spartina*. As at Chincoteague, difficult-to-exploit habitats (creeks at high tide) were not used by wading birds. WHIB and GLIB tended to spend most of their time in the *Spartina* marsh (pers. obs.), however, according to my camera data, WHIB were present in the pond more frequently than GLIB (based on video camera results). This is contrary to the findings of Frederick and Bildstein (1992), who found that GLIB and WHIB tend to prefer similar habitats. This is also contrary to what I observed in the field. GLIB seemed to venture from the *Spartina* marsh into the adjacent ponds as frequently as WHIB (pers. obs.). The disparity between camera data and observations may be an artifact; white birds are more conspicuous than dark, especially at a distance.

Data on species use of Hog Island habitats were only taken for one month, so a seasonal effect could not be observed. Because my species use data relied on a mounted camera that was prone to malfunctioning, the amount of data available for analysis was limited. In the future, monitoring the stored video imagery from the camera more often could mitigate the problems of malfunction and data loss.

Relative to feeding efficiency, both tidal and seasonal influences were minimal. Presumably tides do not affect feeding efficiency to such an extent due to the fact that

species have already chosen not to use particular habitats that are difficult to exploit at particular tides (e.g. tidal creeks at high tide). Erwin (1985) found a seasonal decline in feeding rates (intensity and efficiency) for SNEG and GREG between summer and winter, however, while my study did span significant time to show a difference in habitat use, my feeding efficiency data (which ended in early August), most likely did not go late enough into the season to see a difference.

Along with the small feeding efficiency differences across the ponds at Hog Island, seasonal and tidal influence was also minimal. In June, differences were noted in habitat and species distribution. In June, these species are feeding young nestlings, so they should be exploiting the most prolific habitats (Erwin 1985, Bryan *et al.* 2005), which may explain why June yielded more significant results at Hog Island.

Summary

During the breeding season, nestling success is dependent on parental foraging success and demands on adults are high (Erwin 1985). Overall little tidal influence overall was found in most habitats, perhaps because of nestling needs requiring increased parental activity (Bryan *et al.* 2005). The Chincoteague study gave the most valuable insight into habitat choice and resource use. Species used habitats with a frequency expected based on their specialization and these corresponded to feeding efficiency and length-of-stay. The Hog Island study, while resulting in similar findings would have benefited from a more diverse amount of habitat to draw conclusions. While this study shed light on how species use available habitats and how successful they are there, I believe that having prey data at Chincoteague would have been useful in the interpretation of the study or perhaps a more controlled study with artificial ponds with

known fish density. I believe the next step to take would be to compare data throughout the seasons, to see whether length-of-stay can be used as an indicator of prey density across many habitats, and to more fully explore how the amount of time a species remains in a patch relates to the other factors.

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Appendix 1: Major Nekton in the area: Striped Killifish (*Fundulus majalis*), Sheepshead Minnow (*Cyprinodon variegatus*), Mummichog (*Fundulus heteroclitus*), Grass Shrimp (*Palaemonetes pugio*), Atlantic Silverside (*Menidia menidia*), collected at Hog Island habitats throughout study duration in an 7744-cm² throw trap.

Habitat	Species	May	June	July	August
Pond 1	Striped Killifish	0	0	--	15
	Sheepshead Minnow	0	3	--	9
	Mummichog	0	1	--	3
	Grass Shrimp	0	0	--	2
	Atlantic Silverside	0	0	--	0
Pond 2	Striped Killifish	0	1	--	1
	Sheepshead Minnow	0	22	--	14
	Mummichog	0	4	--	0
	Grass Shrimp	0	0	--	1
	Atlantic Silverside	0	0	--	1
Pond 3	Striped Killifish	0	10	--	41
	Sheepshead Minnow	0	45	--	214
	Mummichog	0	17	--	0
	Grass Shrimp	6	0	--	0
	Atlantic Silverside	0	0	--	2
Creek 1	Striped Killifish	0	4	--	--
	Sheepshead Minnow	0	0	--	--
	Mummichog	3	9	--	--
	Grass Shrimp	57	85	--	--
	Atlantic Silverside	0	0	--	--
Creek 2	Striped Killifish	2	--	--	0
	Sheepshead Minnow	0	--	--	0
	Mummichog	0	--	--	3
	Grass Shrimp	23	--	--	5
	Atlantic Silverside	0	--	--	0

Appendix 2: Mean feeding efficiency by location, season, tide, species and habitats. Habitats monitored at Hog Island were creeks and ponds. Habitats monitored on Chincoteague were brackish impoundments (imp), non-tidal ponds (NTP), oyster beds (oyster), coves (cove), and tidal creeks (creek).

Location	Season	Tide	Habitat	Species	N	Mean	St. Dev.
Hog	total	low	creek	GREG	13	0.0612638	0.1030737
				LBHE	2	0.25	0.3535534
				SNEG	19	0.1341583	0.1730629
				TRHE	3	0.3814813	0.19127
Hog	total	low	pond	GREG	10	0.3583333	0.3322436
				LBHE	12	0.2903373	0.288986
				SNEG	13	0.2506756	0.2898906
				TRHE	8	0.3307074	0.321213
Hog	April May	low	creek	GREG	2	0.1625	0.053033
				LBHE	0	--	--
				SNEG	5	0.1139682	0.0745054
				TRHE	1	0.533333	--
Hog	April May	low	pond	GREG	3	0	0
				LBHE	3	0.1333333	0.2309401
				SNEG	6	0.1222222	0.1558726
				TRHE	2	0.125	0.1767767
Hog	June	low	creek	GREG	6	0.0111112	0.0272167
				LBHE	--	--	--
				SNEG	5	0.0869048	0.0857061
				TRHE	--	--	--
Hog	June	low	pond	GREG	3	0.4888887	0.0822146
				LBHE	6	0.1973412	0.1590782
				SNEG	2	0.0558335	0.0789605
				TRHE	3	0.1125	0.0695971
Hog	July	low	creek	GREG	5	0.0809524	0.1444356
				LBHE	1	0.5	--
				SNEG	9	0.171627	0.2402316
				TRHE	1	0.166667	--
Hog	July	low	pond	GREG	3	0.3722223	0.2562191
				LBHE	1	0.5	--
				SNEG	4	0.4677085	0.3794545
				TRHE	--	--	--
Hog	August	low	creek	GREG	--	--	--
				LBHE	1	0	--
				SNEG	--	--	--
				TRHE	1	0.444444	--

Appendix 2 (continued): Mean feeding efficiency by location, season, tide, species and habitats.

Location	Season	Tide	Habitat	Species	N	Mean	St. Dev.
Hog	August	low	pond	GREG	1	1	--
				LBHE	2	0.7	0.4242641
				SNEG	1	0.542949	--
				TRHE	3	0.686053	0.1936761
Chincoteague	total	high	imp	GREG	14	0.5277778	0.2079469
				LBHE	6	0.3835979	0.2944826
				SNEG	8	0.3666171	0.2879378
				TRHE	4	0.3499107	0.2421889
Chincoteague	total	high	NTP	GREG	1	0	--
				LBHE	11	0.5983586	0.2172151
				SNEG	8	0.2574653	0.2128426
				TRHE	5	0.3083333	0.2819821
Chincoteague	total	high	oyster	GREG	--	--	--
				LBHE	--	--	--
				SNEG	--	--	--
				TRHE	--	--	--
Chincoteague	total	high	oove	GREG	1	0.25	--
				LBHE	--	--	--
				SNEG	--	--	--
				TRHE	--	--	--
Chincoteague	total	high	creek	GREG	2	0	0
				LBHE	--	--	--
				SNEG	--	--	--
				TRHE	--	--	--
Chincoteague	total	low	imp	GREG	15	0.370418	0.2846402
				LBHE	6	0.5798611	0.3124768
				SNEG	9	0.3331749	0.199245
				TRHE	4	0.2897917	0.2963594
Chincoteague	total	low	NTP	GREG	6	0.4328704	0.3654036
				LBHE	8	0.6524306	0.2774817
				SNEG	4	0.3063492	0.3163015
				TRHE	3	0.4444445	0.2545875
Chincoteague	total	low	oyster	GREG	1	0	--
				LBHE	1	0.25	--
				SNEG	5	0.488492	0.3394783
				TRHE	--	--	--
Chincoteague	total	low	coves	GREG	2	0.2083334	0.0589255
				LBHE	1	0.6333333	--
				SNEG	4	0.3083334	0.242861
				TRHE	1	0.3928571	--

Appendix 2 (continued): Mean feeding efficiency by location, season, tide, species and habitats.

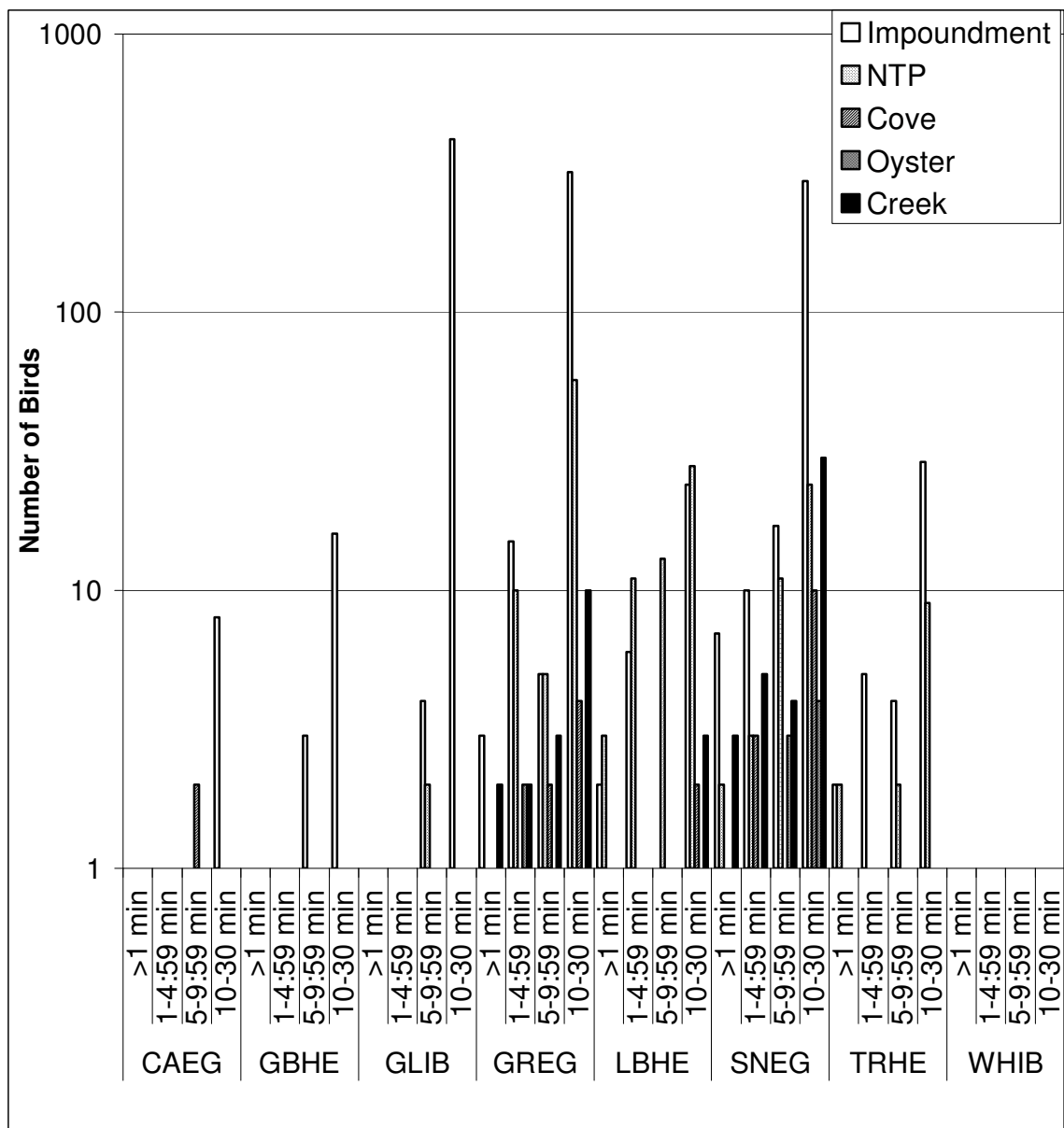
LOCATION	SEASON	TIDE	HABITAT	SPECIES	N	MEAN	STDEV
Chincoteague	total	low	creek	GREG	5	0.3033333	0.2769878
				LBHE	--	--	--
				SNEG	9	0.2049224	0.2115246
				TRHE	--	--	--
Chincoteague	early	high	imp	GREG	8	0.5371528	0.2066943
				LBHE	3	0.2777778	0.3469443
				SNEG	3	0.3035714	0.0643848
				TRHE	2	0.1875	0.265165
Chincoteague	Early	high	NTP	GREG	1	0	--
				LBHE	7	0.5267857	0.1762498
				SNEG	6	0.2599537	0.1959414
				TRHE	--	--	--
Chincoteague	Early	high	oyster	GREG	--	--	--
				LBHE	--	--	--
				SNEG	--	--	--
				TRHE	--	--	--
Chincoteague	early	high	coves	GREG	1	0.25	--
				LBHE	--	--	--
				SNEG	--	--	--
				TRHE	--	--	--
Chincoteague	early	high	creek	GREG	2	0	0
				LBHE	--	--	--
				SNEG	--	--	--
				TRHE	--	--	--
Chincoteague	early	low	imp	GREG	9	0.432672	0.2909838
				LBHE	2	0.6770834	0.3682848
				SNEG	5	0.4275	0.0882704
				TRHE	2	0.0416667	0.0589255
Chincoteague	early	low	NTP	GREG	3	0.5	0.4409585
				LBHE	5	0.5527778	0.2956735
				SNEG	1	0.2420635	--
				TRHE	--	--	--
Chincoteague	early	low	oyster	GREG	--	--	--
				LBHE	1	0.25	--
				SNEG	3	0.2863756	0.1841109
				TRHE	--	--	--
Chincoteague	early	low	coves	GREG	2	0.2083334	0.0589255
				LBHE	--	--	--
				SNEG	4	0.2458334	0.2903941
				TRHE	1	0.3928571	--

Appendix 2 (continued): Mean feeding efficiency by location, season, tide, species and habitats.

LOCATION	SEASON	TIDE	HABITAT	SPECIES	N	MEAN	STDEV
Chincoteague	early	low	creek	GREG	4	0.2125	0.2174665
				LBHE	--	--	--
				SNEG	7	0.196805	0.2028862
				TRHE	--	--	--
Chincoteague	late	high	imp	GREG	6	0.5152778	0.2286687
				LBHE	3	0.489418	0.250671
				SNEG	5	0.4044445	0.3718157
				TRHE	2	0.5123214	0.0120376
Chincoteague	late	high	NTP	GREG	--	--	--
				LBHE	4	0.7236111	0.249552
				SNEG	2	0.25	0.3535534
				TRHE	5	0.3083333	0.2819821
Chincoteague	late	high	oyster	GREG	--	--	--
				LBHE	--	--	--
				SNEG	--	--	--
				TRHE	--	--	--
Chincoteague	late	high	coves	GREG	--	--	--
				LBHE	--	--	--
				SNEG	--	--	--
				TRHE	--	--	--
Chincoteague	late	high	creek	GREG	--	--	--
				LBHE	--	--	--
				SNEG	--	--	--
				TRHE	--	--	--
Chincoteague	late	low	imp	GREG	6	0.277037	0.271922
				LBHE	4	0.53125	0.3287445
				SNEG	4	0.2152687	0.2492176
				TRHE	2	0.5379167	0.1172619
Chincoteague	late	low	NTP	GREG	3	0.3657407	0.3547336
				LBHE	3	0.8185185	0.1686304
				SNEG	3	0.3277778	0.3838161
				TRHE	3	0.4444445	0.2545875
Chincoteague	late	low	oyster	GREG	1	0	--
				LBHE	--	--	--
				SNEG	2	0.7916667	0.2946278
				TRHE	--	--	--
Chincoteague	late	low	coves	GREG	--	--	--
				LBHE	1	0.6333333	--
				SNEG	1	0.25	--
				TRHE	--	--	--

Appendix 2 (continued): Mean feeding efficiency by location, season, tide, species and habitats.

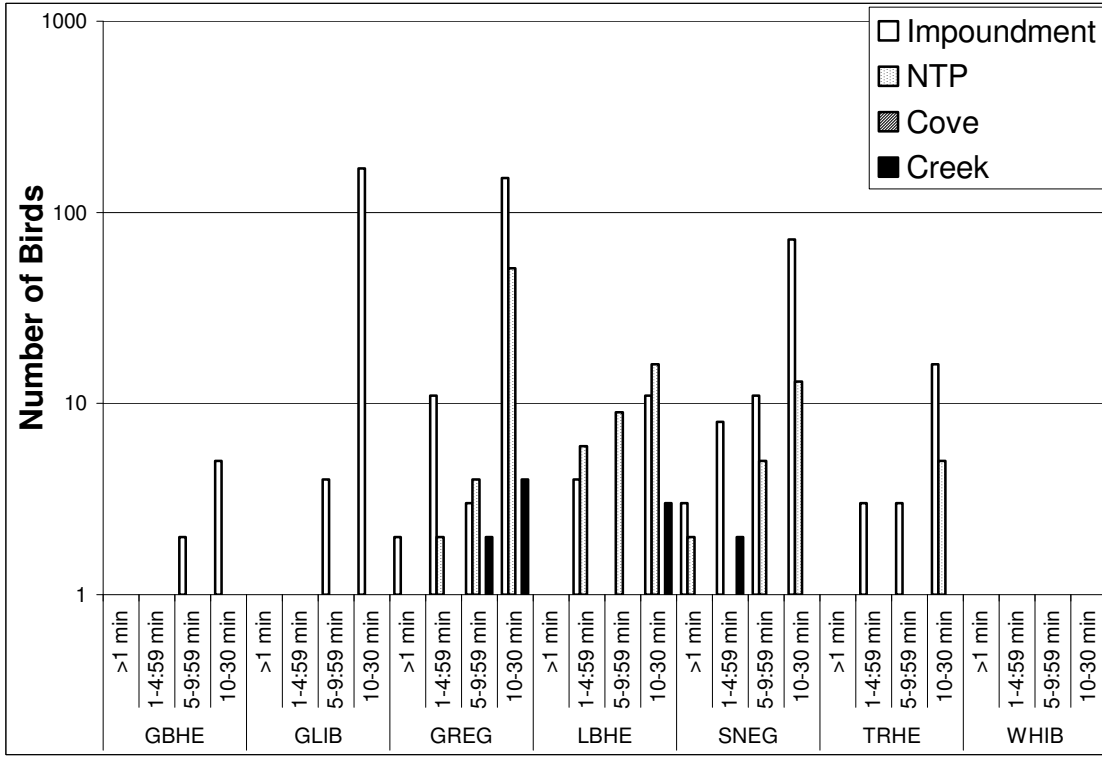
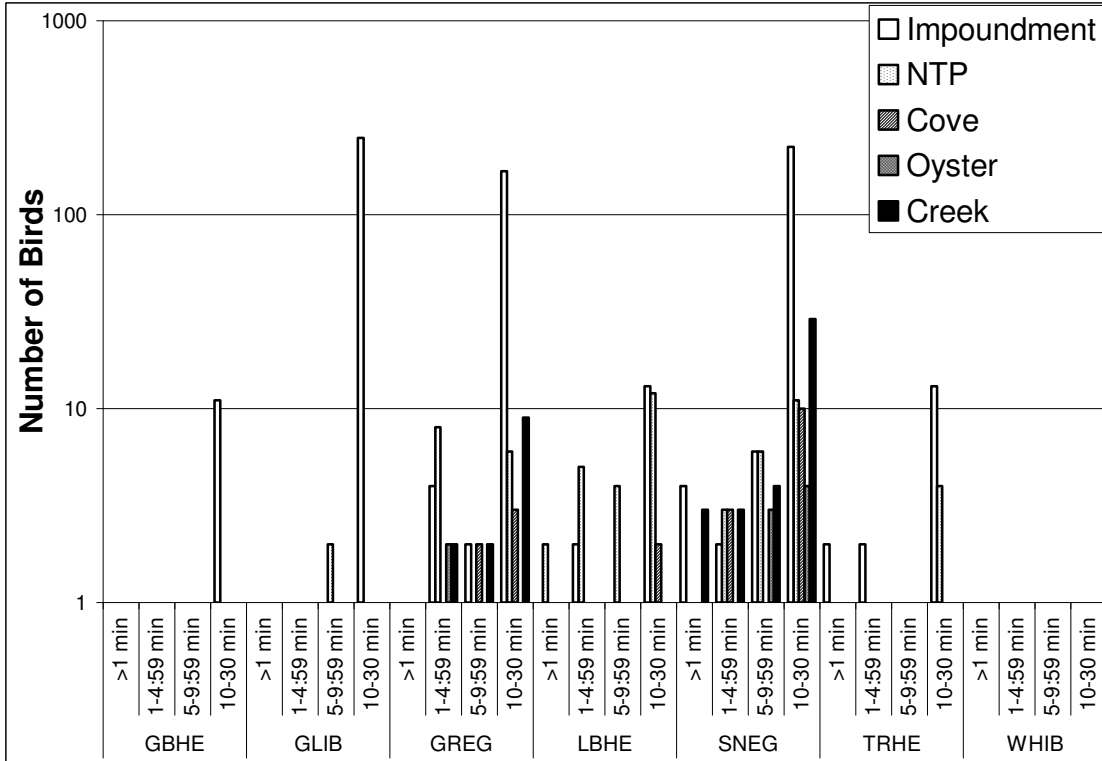
LOCATION	SEASON	TIDE	HABITAT	SPECIES	N	MEAN	STDEV
Chincoteague	late	low	creek	GREG	1	0.6666667	--
				LBHE	--	--	--
				SNEG	2	0.2333334	0.3299832
				TRHE	--	--	--



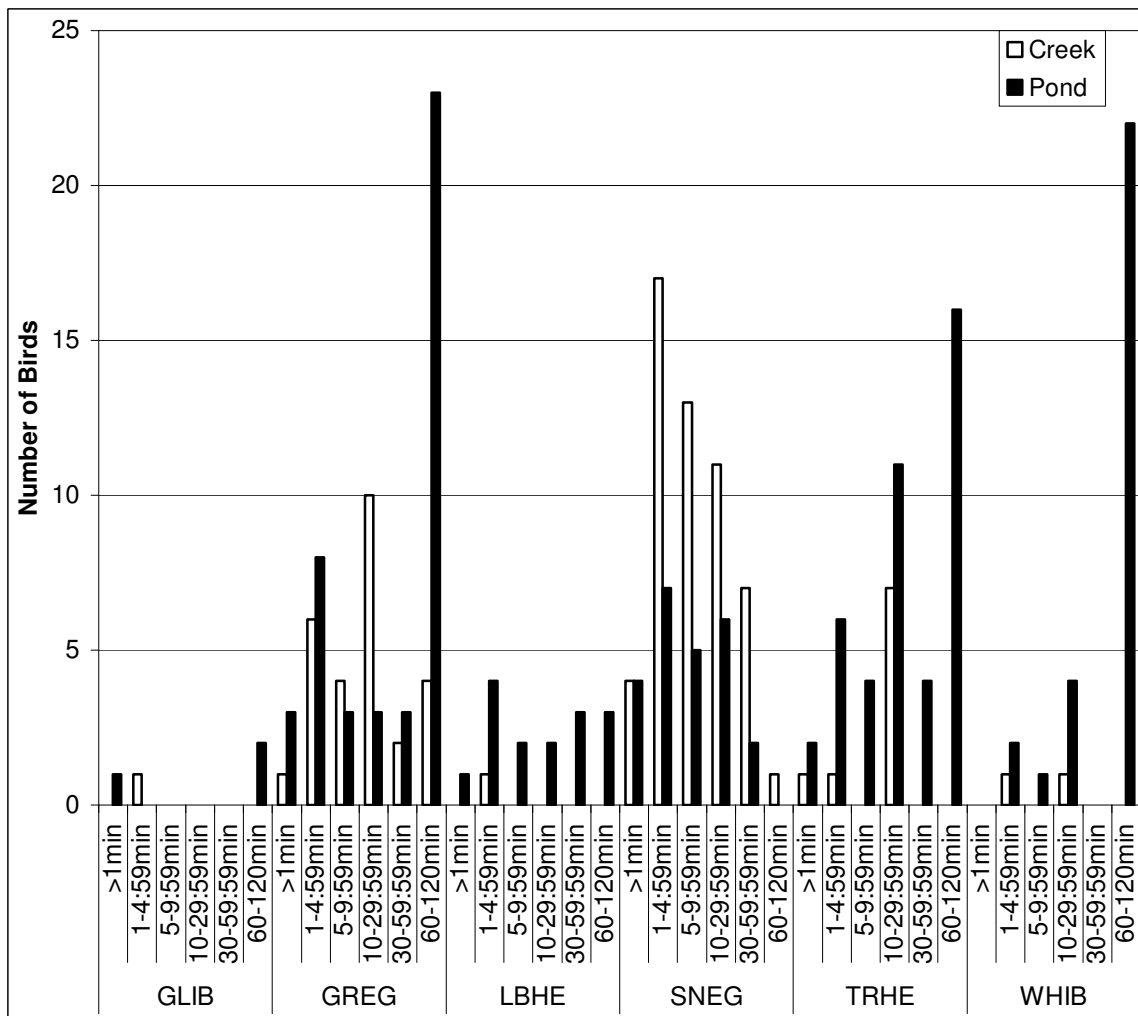
Appendix 3: Length-of-stay of species at Chincoteague across habitats. See Fig. 7 for habitat types.

Appendix 4: Average lengths-of-stay of species at Chincoteague.

Species	Average	Std. Dev.	Std. Err.
CAEG	0:20:24	0:11:19	0:01:02
GBHE	0:22:40	0:10:22	0:00:31
GLIB	0:28:27	0:05:14	0:00:01
GREG	0:25:53	0:08:49	0:00:01
LBHE	0:16:12	0:11:20	0:00:07
SNEG	0:24:14	0:09:50	0:00:01
TRHE	0:18:57	0:11:24	0:00:12



Appendix 5: Length-of-stay at Chincoteague across habitats at low (top) and high (bottom) tide. See Fig. 7 for habitat types.



Appendix 6: Length-of-stay of species at Hog Island across habitats.