DIFFERENCES IN REPRODUCTIVE ECOLOGY AND BEHAVIOR OF THE

POLYMORPHIC REDDISH EGRET (*EGRETTA RUFESCENS*)

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by

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Assessing and maintaining genetic diversity is a concern for the conservation and management of a species, since variations within a species dictate its evolutionary potential. The Reddish Egret *Egretta rufescens* is a relatively rare heron species that exhibits white-dark plumage polymorphism. Different regions within the Reddish Egret's geographic range have different ratios of dark and white morphs. This may imply different microevolutionary processes affecting the frequency of the two morphs in different habitats and populations. I investigated how this phenotypic difference influences the behavior and reproductive ecology of the white and dark morph Reddish Egrets in the upper Laguna Madre of Texas. On dredge spoil islands in the Laguna Madre, Reddish Egret nesting pairs were observed during forty minute focals as they courted, built nests, and raised young. I collected time-spent behavioral data, reproductive ecology information, and characterized vegetation of nests and the

surrounding area. Regurgitant from chicks was collected opportunistically to determine differences in diversity and abundance of prey fed to young. Nest vigilance and nest initiation did not differ between morphs or nest sites, but nest attendance varied between morphs depending on nest site. Feeding time of chicks differed between morphs and is potentially related to foraging efficiency and time of day. Nest cover did not vary between morphs within sites, but varied significantly between sites and between random points and nests within sites. This indicates strong selection of nest sites within colonies. The information obtained provides valuable insights into the ecological diversity of polymorphic species, and information on nest site selection and prey diversity that could be considered for the conservation of this rare waterbird.

FOREWORD

Polymorphic species are intriguing because of the possibility of sympatric

divergence of a species through resource partitioning or reproductive isolation. Though

the evolution and maintenance of color morphs in wildlife species is poorly understood

(Munday 2003), recent studies have attempted to expose the mechanisms that maintain or

segregate morphs (Smith and Skulason 1996, Galeotti et al. 2003, Munday et al. 2003,

Roulin 2004, Gray and McKinnon 2006). The amount of gene flow among sympatric

morphs changes both temporally and spatially, and if restricted can lead to the divergence

of species (Smith and Skulason 1996). Gene flow restriction could occur because of pre-

zygotic barriers such as assortative mating, or post-zygotic barriers such as reduced

fitness of hybrids. Assortative mating may result from individuals preferring mates of

similar color, differences in breeding display rituals, or differences in habitat selection

between the two morphs during the breeding season. These kinds of isolating

mechanisms may co-evolve with polymorphism and ecological adaptations (Smith and

Skulason 1996) such as foraging strategy. Traits important in reproductively isolating

populations can be correlated to the traits important in utilizing resources (Smith and

Skulason 1996). For instance, if plumage is used in mate choice it would isolate dark-

plumaged morphs from white-plumaged morphs, and could restrict gene flow between

the two morphs. In addition, plumage is important when utilizing resources since

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plumage provides camouflage during foraging (Caldwell 1986) and should affect an individual bird's foraging success and fitness.

Reddish Egrets *Egretta rufescens* are a unique Ardeid in the New World in that they are the only species of heron that is consistently polymorphic as an adult throughout a majority of its range. The four other heron species known to display plumage polymorphism as adults within local populations independent of age or sex are the Great Blue Heron *Ardea herodias*, the Little Egret *Egretta garzetta*, the Madagascar Reef Heron *E. dimorpha*, and the Eastern Reef Heron *E. sacra* (Mock 1980, Hancock and Kushlan 1984, Itoh 1991). All polymorphic heron species exhibit dark-white plumage polymorphism. Studies examining these species have found differences between morphs in habitat use, foraging strategy and crypsis (see Rohwer 1990, Itoh 1991, Green 2005).

Reddish Egrets may distinguish between the discrete white and dark plumage morphs. If pairing is non-random, this may lead to restriction of gene flow between Reddish Egret morphs since plumage and visual display are an important part of heron breeding rituals. Aviary and field experiments have demonstrated that in a wide array of vertebrate species, conspecifics assess each other's color morph (Roulin 2004). Since coloration is used for intraspecific communication (Butcher and Rohwer 1988), the maintenance of dark and white color morphs may result from preferences in mate-choice (Galeotti et al. 2003). McGuire (2001) found that Great Blue Herons *Ardea herodias* did not pair randomly with respect to plumage color where both white and dark color morphs were sympatric. This evidence supports the idea that polymorphic heron species may

assess each other's plumage color during mate selection. Reddish Egrets were shown to flock with like-plumaged morphs outside of the breeding season (Green and Leberg 2005) indicating that this species may also assess plumage color.

Differences in micro-habitat selection, foraging and crypsis may vary for Reddish Egret morphs. White and dark morph Reddish Egrets exist along a geographic gradient. Bird counts in the 1950's revealed ratios of 89% white morphs in the southern Bahamas (Bolen and Cottam 1975), about 25% white morphs in southern Texas (Amy Hanna, Texas Parks and Wildlife Department, unpublished data), and no white morphs have been reported in the Pacific coast colonies (Howell and Pyle 1997). This may imply an advantage for each morph in different habitats and that different plumaged birds would have different selective pressures. Selective pressures influencing plumage coloration in egrets may include thermal stress (Ellis 1980), camouflage from predators (Caldwell 1986) and crypsis to prey (Mock 1980, Green 2005, Green and Leberg 2005). Egrets with white plumage have lower solar heat loads and are less prone to heat stress during incubation and early brooding than darker birds (Ellis 1980). White plumage is more conspicuous to predators (Caldwell 1986) potentially causing white birds to seek denser nesting cover or to aggregate. Findings that white morphs spend more time actively foraging in intermediate water depths while dark morphs spend more time actively foraging in shallow waters (Green 2005) exemplify differing foraging strategies related to prey crypsis. Similar results were documented for Pacific Reef Heron *Egretta sacra*; white morphs preferred deeper, turbid water and dark morphs selected still, shallow water (Rowher 1990).

Assuming that differences in color morph are associated with differences in life-history strategies, multiple studies have shown that in a majority of species, polymorphism is associated with reproductive parameters, behavior, life-history and physiology (Galeotti et al. 2003, Roulin 2004). Previous work on polymorphism and correlated life-history traits suggests that morphs are more different than in appearance only. If morphs differ in their requirements, it seems logical that morphs would need to be managed as separate evolutionary significant units to protect the genetic diversity within the species as a whole (Moritz 1994, Ryder 1986). Conservation for this species is important because Reddish Egrets are a globally restricted species with a total population estimated at 5,000-7,000 adults (Green 2006). With only a general understanding of Reddish Egret behavior and ecology (Lowther and Paul 2002), it is difficult to protect and designate appropriate breeding and foraging habitat for Reddish Egrets. Hopefully, analysis of Reddish Egret behavior and reproduction can elucidate solutions to these problems.

The goal of this study was to better understand the ecology of Reddish Egrets and the influence of color polymorphism. Specific objectives were: (1) Document up-to-date information on nesting chronology, breeding behavior, and nesting behavior, and to determine if these factors differed between morphs and nesting colonies, (2) Compile regurgitant from nestlings across Reddish Egret range and determine if there are differences between morphs, nesting colonies, and regions in prey composition, (3) Sample nesting vegetation and map nesting locations to determine habitat selection, nest

dispersion and nest site characteristics and investigate whether these characteristics differed between morph and nest colonies. It is predicted that if thermal stress is an important factor in selection, then morphs will adapt by have differing preference in amount of nest cover or foraging times. If camouflage from predators is an important factor in selection, then morphs may differ in nest site selection in relation to cover or in nest dispersion. If crypsis to prey is an important factor in selection, then difference in prey species found in regurgitant or foraging time may occur.

I. REPRODUCTIVE BEHAVIOR

Polymorphism is the presence of two or more distinct, genetically determined forms within a single interbreeding population, the rarest of which is too frequent to be solely the result of recurrent mutation (Huxely 1955). Color polymorphism is exhibited by 334 species of birds, representing 3.5% of all bird species. The occurrence of color polymorphism is common in Strigiformes, Ciconiiformes, Cuculiformes and Galliformes. Of polymorphic birds, 7.5% exhibit black and white dimorphism and 20% show a cline in the relative frequency of morphs (Galeotti et al. 2003).

Many biologists have hypothesized that color morph affects Reddish Egret behavior (e.g, Mock 1980, Caldwell 1986, Itoh 1991, Green 2005). Reddish Egret reproductive behavior may be affected by mate choice. The assessment of plumage color can lead to either the preference or discrimination against like-morphs. There is some empirical support for assortative mating among Ardeidae (McGuire 2001) and assessment of color morph within polymorphic species (Roulin 2004). If Reddish Egrets mate assortively, differences in breeding displays and other behaviors may result.

Assortative mating in polymorphic species could be strengthened by differences in breeding behavior between morphs. Differences in timing of nesting between different morphs could lead to temporal reproductive isolation (Smith and Skulason 1996). By not

nesting at the same time, egrets would have less opportunity to breed with members of

the opposing morph. Furthermore, differences in timing between same-morph nests and

opposing-morph nests would indicate assessment of plumage color. Mates chosen later in

the season reflect a balance of the cost of continuing to search for mates and the strength

of preference (Schluter and Price 1993) for same-morph mates.

Two behaviors correlated to nest success are nest vigilance and nest attendance.

Reddish Egrets spend approximately eighty days a year involved in courtship, mating,

egg-laying, incubating and caring for hatchlings at the nest site; a large investment of

food and resources. Incubation reduces foraging opportunities and increases adult

vulnerability to predation. Eggs or chicks left unguarded can perish due to overexposure

to the sun or from attacks by gulls, grackles, fire ants, or mammalian predators (McMurry

1971). After hatching, one to six chicks must be fed continuously for at least four weeks

(McMurry 1971) or longer. Thus, differences in vigilance and nest attendance could

affect reproductive success of both parents. Vigilance and attendance can both be

affected by external factors such as predation pressure and foraging efficiency (Kushlan

1981) that may be associated with color morph (Caldwell 1986, Green 2005).

Vigilance is often measured in wildlife behavior studies by quantifying time spent

in a "head-up posture" (e.g. Slotow and Rothstein 1995, Fernández-Juricic et al. 2002). A

head-up posture indicates an individual is alert and assessing the surrounding area for

potential danger (Rodgers 1983). Caldwell (1986) hypothesized detection by predators

was a major selective force in egret polymorphism. If this is true, it is logical to predict

that birds that receive higher predation pressure will be more vigilant than their less conspicuous neighbors.

Attendance is a measure of parental care and effort. There is a strong correlation between nest attendance and nest success. One factor that severely limits a parent's ability to remain at the nest is food availability (Chalfoun and Martin 2007). When food is limited, parents must spend more time foraging and less time at the nest. When food is in surplus, less time is needed to forage to satiate chicks, and more time can be spent nest guarding. Nest guarding can increase survival of chicks, especially young (first two weeks) chicks (St. Clair Raye and Burger 1979, Chalfoun and Martin 2007).

My objective of studying the reproductive ecology of Reddish Egrets is to gain knowledge on Reddish Egret reproduction in general and investigate differences between the morphs in this respect. Specifically, I examined the behavior of dark and white morph Reddish Egrets during the breeding season to determine differences between morphs in breeding strategies and parental care, collected and compared information on the nesting parameters of dark and white morph Reddish Egrets, and determined if there is any basis for classifying the two morphs as potentially different Evolutionarily Significant Units (ESU) (Moritz 1994). Morphs would be potentially different ESUs if mating was non-random and/or they differed in behavior or ecology.

Methods

Behavioral data were collected during the breeding season at three major nesting colonies: Kennedy Causeway Island (Zigzag), Rabbit Island and Green Island (Fig. 1). Instantaneous observations were recorded on the type and duration of breeding displays. Display types were characterized as those described by Meyerriecks (1960).

Nest initiation was determined through a series of weekly nest checks. During these searches, nests that were empty, with eggs, or with chicks were recorded. Nests that differed in the number of eggs between consecutive nest checks were documented as in egg laying stage for the previous observation. Hatch date was estimated for nests that had eggs and then hatched between consecutive nest checks. If unhatched eggs were in the nest and chicks were less than a week old, then the nest was considered in the hatching stage. Eggs were assumed to be laid every other day (McMurry 1971), therefore chicks were also assumed to hatch approximately every other day. Nests were then categorized as laying, incubating, hatching, brooding, or fledgling for each day of the nesting season. Early Brooding was considered the first two weeks after hatching. During this period parents were observed constantly at nests and chicks were relatively stationary. This is consistent with other estimates of egret chick independence (Pratt 1970, St. Clair Raye and Burger 1979, Rodgers 1983). After two weeks, egret chicks explore further and further from the nest, but do not actually abandon the nest area until they are at least six weeks of age.

Colony attendance data was collected on Rabbit Island (Fig. 1). The entire colony and island could be observed from a single point. Data was collected by documenting birds arriving at the island throughout the day. Observations were made during consecutive hours at differing time intervals from June 8 – 21. Most egrets were feeding chicks that were two to six weeks old. Tallies of birds attending nests for each morph during each daylight hour were obtained. The average proportion of the number of each morph arriving at the colony to the number nesting at the colony for each hour of the day was compared.
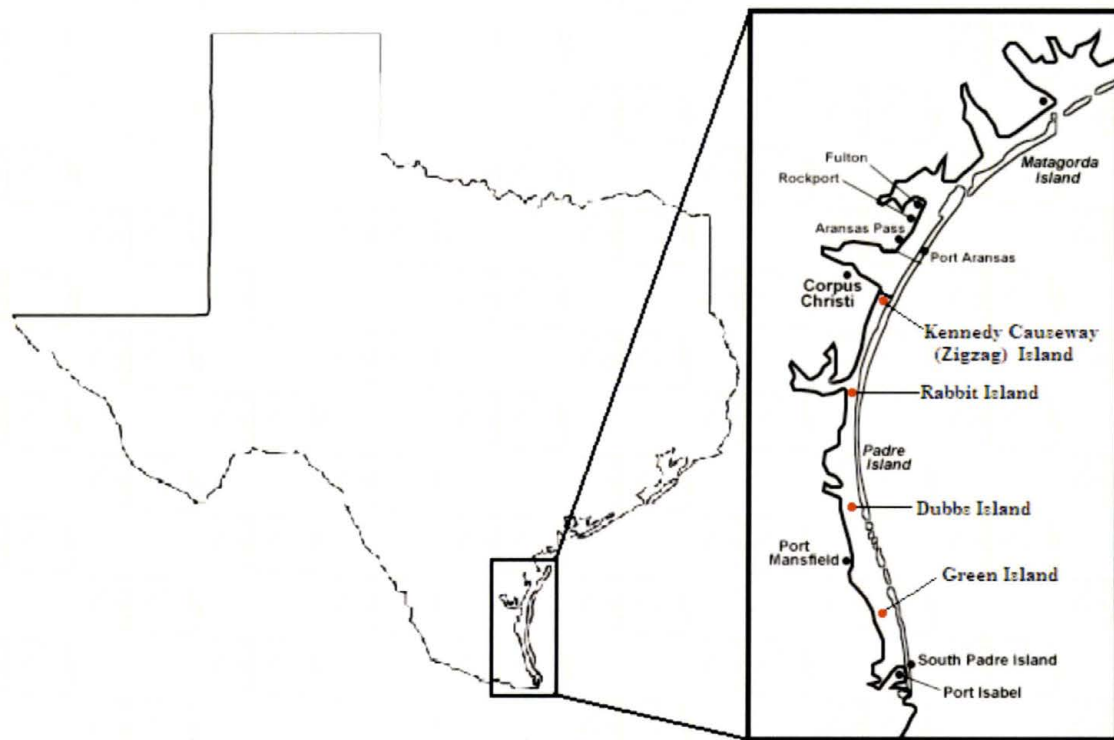
Figure 1 – Major Reddish Egret colonies in the Laguna Madre, TX.

Focal observations were conducted on birds within subsets of Rabbit Island and Kennedy Causeway Island colonies (Fig. 1). Forty minute observations were made from either an uninhabited part of the island or a platform constructed 50m offshore.

Environmental parameters such as wind speed, cloud cover and temperature were recorded. Focal observations were used to measure parental vigilance and attendance. Vigilance was determined by proportion of time the adult egret spent with head up above vegetation during each interval. Attendance was determined by the presence of an adult egret in the immediate vicinity of the nest. Nest checks were also done on these nests infrequently to determine stage of nesting. Changes in nest attendance and vigilance through the different stages, as well as differences between morphs and sites were also examined.

Data analyses were done using R version 2.5.1© (R Development Core Team 2008). Differences between site and morph in nest initiation times were compared using Type III ANOVA (Zar 1996). The effect of time of day on morph visitations was analyzed using Type III ANOVA (Zar 1996). Also, the effects of site, morph and life history stage on vigilance and nest attendance was examined using Type III ANOVA (Zar 1996).

Results

Between two nesting sites within the Laguna Madre both proportion of nesting birds and timing of nesting varied. On Rabbit Island 53 egret nests were dark morph and 26 were white morph, and 4 were mixed morph. On Zigzag Island 38 egret nests were dark morph, 40 were white morph, and 2 were mixed morph. Chi-squared test of independence indicated that morph frequency was dependent on colony site (χ^2=10.821, df=1, P=0.001). At both sites combined, 96% of the nests had same morph chicks. Observations indicate that this percentage is similar to the percentage of observed same morph parentage.

Reddish Egrets nesting on different islands throughout the Laguna Madre differ dramatically in nest initiation dates and the difference is in a non-latitudinal fashion (Fig. 2). On Rabbit Island May 6th was the mean nest initiation date for dark morph egrets, May 3rd was the mean nest initiation date for white morph egrets, while May 8th was the mean nest initiation date of mixed-morph nests. On Zigzag Island, March 29th was the mean nest initiation date for dark morph egrets, March 28th was the mean nest initiation of white morphs, while April 4th was the mean nest initiation date of mixed-morph nests. There was a significant difference in nest initiation date between the two sites (ANOVA: $F_{(1,158)}$=5.732, P=0.018) in 2007. Nest types (Dark, White and Mixed-nest) did not differ in nest initiation date (ANOVA:$F_{(2,158)}$=0.199, P=0.820), and there was no significant interaction between site and nest type ($F_{(2,158)}$=0.047, P=0.955).
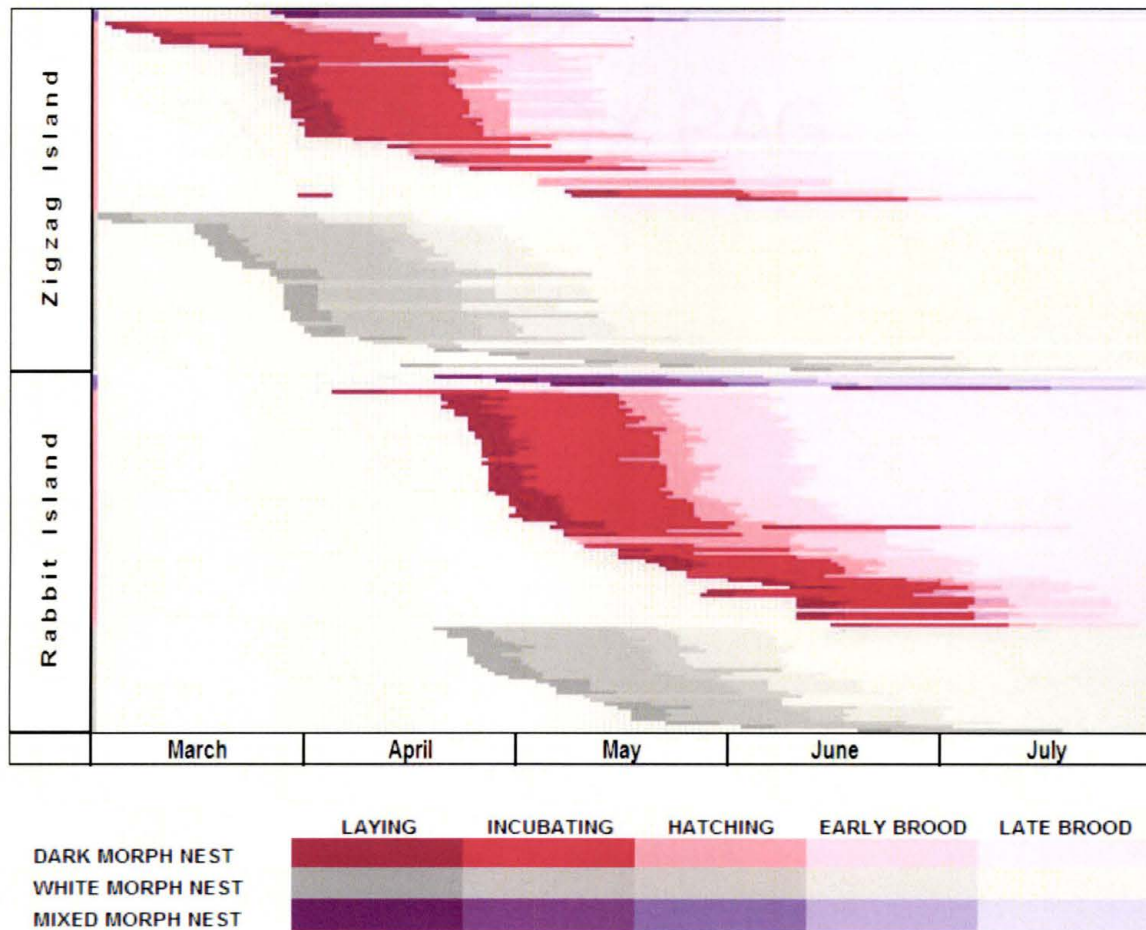
Figure 2 – Monochromatic nesting chronology of Reddish Egrets. Data obtained from the Laguna Madre, TX, 2007. Each line corresponds to a nest that was successful in hatching.

During the late brooding stage, adult egrets return to the nest only periodically to feed their chicks. Visits typically last about 10 minutes. There were significant interaction effects in time of day that the two morphs returned to Rabbit Island to feed their young ($F_{(12,102)}$=4.0046, P< 0.001). Dark morphs returned more frequently from 08:00 – 10:00, while white morphs appeared to arrive throughout the mid-day (Fig. 3).
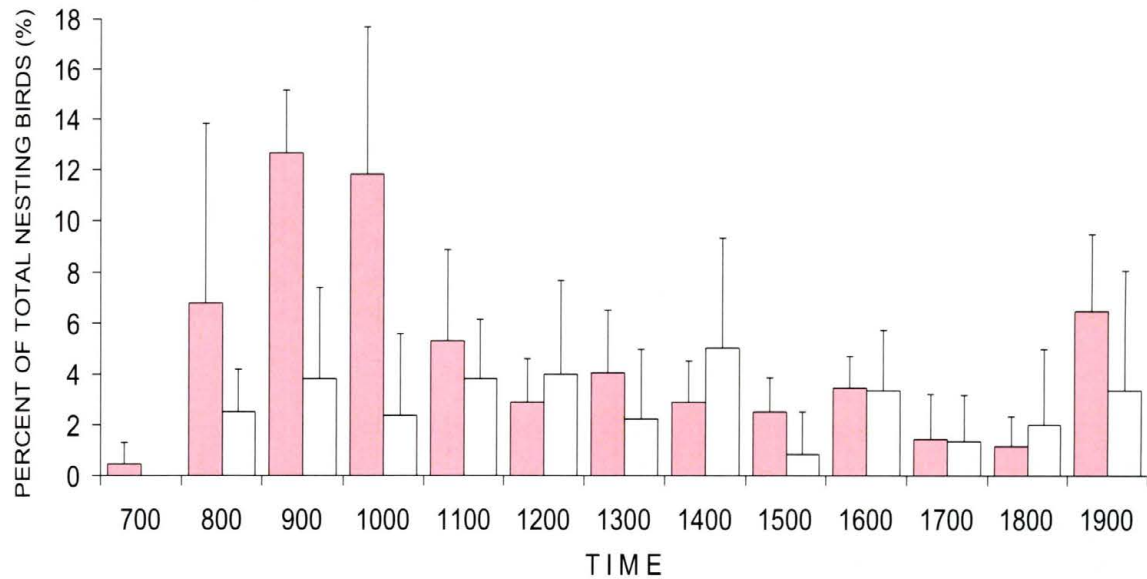
Figure 3 – Arrival frequencies of returning Reddish Egret adults during the late brooding stage at Rabbit Island, Laguna Madre, TX. Measurements are mean proportion of nesting birds of each morph that returned each hour. Pink bars represent dark morph egrets; Grey bars represent white morph egrets.

Behavior during courtship was examined from approximately 3 hours of instantaneous observations (immediate individual observations when birds where found displaying) at three nesting colonies. Aggression toward other egrets consisted of bill snapping, chasing and fighting. Bill pointing, head nodding, aerial displays, jump on top, and stick passing (Meyerriecks 1960) are generally thought to indicate recognition of an individual or are part of pair-bonding rituals. Copulation was rarely witnessed, only twice. Copulation lasted 13-14 seconds. Bill nodding is a large portion of Reddish Egret displays (Fig. 4).
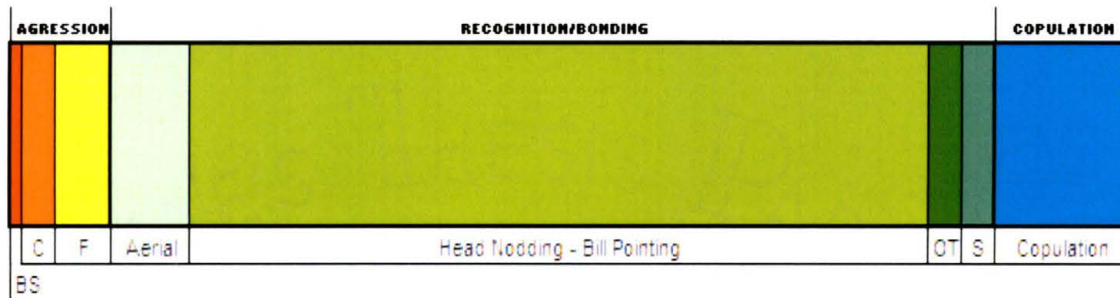
Figure 4 – Time observed doing various displays during the courtship period of the breeding season. BS = Bill snapping (1%), C = Chase (3%), F = Fighting (5%), Aerial displays (7%), Head Nodding and Bill Pointing (66%), OT = Jump on Top (3%), S = Stick Passing (3%), Copulation (12%).

During incubation Reddish Egrets devote approximately 20-30% of their time to vigilance (i.e. head above vegetation where they have the ability to scan for danger) (Fig. 5). During the hatching stage, vigilance is increased. After chicks have hatched, attendance begins to wane and decreases from 100% (Fig. 5). There is a sharp decrease in attendance over the first two weeks as chicks begin to gain motor control and thermoregulatory capabilities (St. Clair Raye and Burger 1979). At this point, attendance is at about 10-20% (Fig. 5). Visits last from ten minutes to an hour, but often decrease as chicks mature. Nest visits can be as few as one a day to as many as five during the later weeks of nesting. Attendance remains low at about 5% until chicks move to the waters near the colony and then presumably off the island at six to eight weeks (Fig. 5).
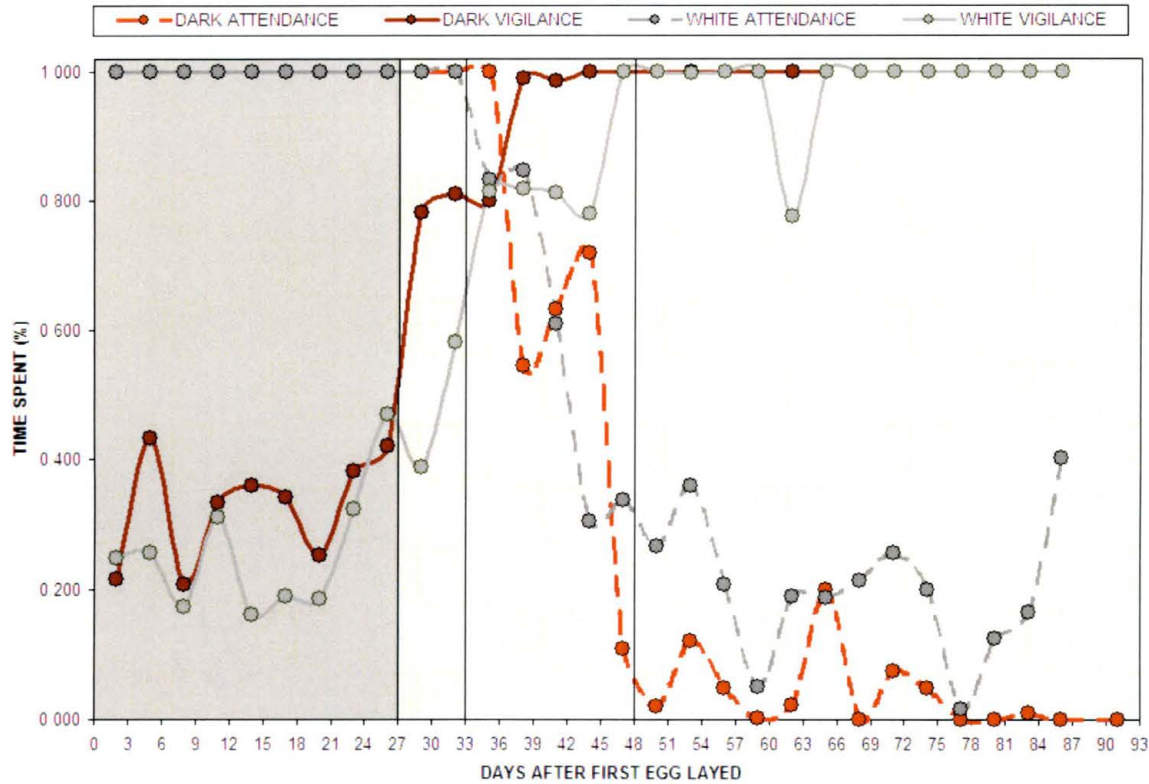
Figure 5 – Mean parental vigilance and attendance of Reddish Egrets through nesting season. Gray sections correspond to life history stages: Incubation, Hatching, Early Brood and Late Brood consecutively. Hatching is included in Incubation for analyses.

Differences between life history stages in vigilance ($F_{(2,41)}$=17.480, P< 0.001) and attendance ($F_{(2,43)}$=37.591, P<0.001) were significantly different as would be predicted (Fig. 5). Vigilance did not vary significantly between sites ($F_{(1,41)}$=2.543, P=0.119) or between morphs ($F_{(1,41)}$=0.072, P=0.790). There were, however, significant interactions in attendance between morph and site, and between morph and stage. Dark morphs appeared to attend nests more frequently during the first two weeks after hatching and white morphs appeared to attend nests more frequently later in the nesting season ($F_{(2,43)}$=3.363, P=0.044). More pronounced is the difference in attendance of morphs between the two study sites. Dark morphs spend more time at the nests on Rabbit Island, while white morphs are more attentive at Zigzag Island ($F_{(1,43)}$=5.928, P=0.019).

Discussion

Reddish Egret morphs appear to be more different than just in plumage color. Observed differences in behavior indicate the two morphs are responding differently to the same environment. Also, colony site affects egret morphs and the species as a whole. Nesting chronology, foraging times and nesting behavior are all affected by morph, colony location, or an interaction between these two factors.

The non-latitudinal difference in nest initiation is somewhat enigmatic. One would expect colonies at higher latitudes to nest later, however this is not the case. One hypothesis to explain these differences is that late-nesting islands exhibit inferior nesting habitat and birds move there after quality colonies have become saturated. However, on years when early-nesting colonies had far fewer nesting egrets, late-colonies had relatively similar number of nesting birds (Texas Coastal Program: Texas colonial waterbird database 2004). Another hypothesis is that birds move to these late-nesting colonies in an attempt to renest after predation at an early-nesting colony. However, Reddish Egrets will congregate near late-nesting colonies early in the nesting season, but still nest later. It may also be possible that the asynchrony in nest initiation between colonies is related to water flow in the Laguna Madre and local abundance in Sheepshead Minnow *Cyprinodon variegatus* breeding. This prey item composes a bulk of the diet for young Reddish Egrets and the species can become very abundant during the Reddish Egret breeding season.

While Reddish Egrets seem to have paired assortatively, assortative mating did not affect nest initiation time. No differences were detected between morphs nesting within the same colony. Though the initiation of mixed-morph nests seemed later, the lack of significance results indicate this is not a substantial deviation. Mixed-morph nesting success is not likely affected by a later initiation time.

The differences between morphs in arrival time from foraging bouts at Rabbit Island may be indicative of differing foraging strategies. Most of the dark morph birds return from morning forays between the times of 8:00 and 10:00 AM. White morph egrets seem to return consistently throughout the day. If, as Mock (1980) suggested, white is more cryptic to prey against a bright, clear sky background, then white morphs may have an advantage when foraging during mid-day. Dark morphs might have higher success in the crepuscular hours when light is limited. Although both morphs forage throughout the day, attendance at the colony could be a reflection of foraging efficiency, assuming birds return as soon as they have attained a reasonable amount of food. For future research, observations made after sundown may find an increase of returning dark morph egrets later in the evening.

Courtship behavior consists mostly of mating and pair-bonding. Documented aggression such as bill snapping, chasing, and fighting (Meyerriecks 1960) was rare given the proximity of nesting egrets. Bill snapping is a first defense against an intruder that gets too close to a nest. If an intruder lands within the vicinity of a nest, the bird may be chased off with the trailing bird snapping at tail feathers. On rare occasions, but more

commonly during the nest building and egg laying stage, egrets will fight using stabbing motions with their beak or clawing at each other with their feet extended forward. Pair bond rituals are a much larger proportion of Reddish Egret behavior. With a bi-parental care system such as that exhibited in Reddish Egrets, a strong pair bond positively affects nest success (Trivers 1972). Head nodding (Meyerriecks 1960) is a rapid and enthusiastic up and down pointing of the bill and seems to signal recognition. This sign is most frequently given when an egret's mate is returning to the nest. Sometimes the head nodding signal is given to neighboring birds, potential mates and offspring. This signal becomes less pronounced toward the end of the breeding season. When head nodding is not reciprocated by the receiving party, aggression is often the response.

During the nesting cycle, Reddish Egrets spend an average of 27 days incubating. During nest building and egg-laying, there were generally two adults present. During the egg laying stage males appear to mate guard and show increased aggression toward other egrets approaching the vicinity of the nest. Throughout the incubation period, at least one adult is constantly at the nest leading to high attendance values (Fig. 5). During incubation, hot weather and disturbances were the only events that caused egrets to leave the nest. These absences were generally less than a minute or until the disturbance had passed and represented less than a 1% decrease in attendance during incubation (Fig. 5). Egrets appeared to stand more frequently during warmer periods of the day when eggs can remain warm without incubation. This could lead to an increase in vigilance. Observations were conducted during all daylight hours and in various weather conditions

to help minimize the effect of temperature. Incubating Reddish Egrets seem to spend 20-30% of their time vigilant (Fig. 5).

After approximately 27 days of incubation, hatching occurs. Since egrets appear to lay eggs approximately every other day (McMurry 1971), eggs are assumed to hatch approximately every other day, leading to a stage from three to twelve days in which a nest could have both eggs and hatchlings. During this hatching period, eggs are still being incubated and the hatched, semi-altricial young must still be brooded. Parents often stand and preen more during this stage, and seem to manipulate the nest or add material more often. This leads to an increase in vigilance (Fig. 5) since more time can be spent in the standing or up-right position.

Once all chicks are hatched, egret nests are considered to be in the Early Brood stage. During this stage adults stand at the nest more often, and seem to provide shade and at least some protection from predators like Great-tailed Grackles *Quiscalus mexicanus*, Black-crowned Night Herons *Nycticorax nycticorax*, and Laughing Gulls *Larus atricilla*. Vigilance, which is considered alertness while at the nest, is usually near 100% at this point (Fig. 5) as little time is spent with head down in the nest. Also, chicks become increasingly independent over the first two weeks after hatching and individual birds may decrease attendance in order to supply the growing demands of the hatchlings. This decrease is seen from day 35 to 48 (Fig. 5). The increase in independence coincides with behaviors of chicks this age. Chicks can help keep each other warm by huddling in patterns that maximize heat exchange (Fig. 6) or by providing shade for younger siblings.

However, the top position, often occupied by the largest chick, may be the optimal position when begging for food from the parent. Nestlings may regurgitate or snap at intruders. Later (at two weeks) they will scramble into adjacent vegetation. This behavior corresponds to a plateau in nest attendance at day 48 (Fig. 5). Near fledging, chicks will run or fly around colonies and adjacent shallow water. Egret fledging is less definite, since chicks will venture further from nests each day, and yet still may return to be fed at the nest 60 days after hatching. At this point observations become impractical for most focal nests and nest attendance is no longer correlated to parental care. The length of time parents feed young after leaving the colony is undetermined.

Figure 6 – Huddling formations of Reddish Egret hatchlings. Largest chick is usually on top with neck over-lapping to increase heat exchange.

While assortative mating, or at least pairing, is occurring, there seems to be minimal effect of morph on behavior and ecology. There is no temporal isolation of morphs from each other. Also, while morphs vary in proportion between colonies, both morphs are still well represented at each colony. At this scale, there appears to be no spatial isolation. There was some evidence of behaviors correlated to morph however. Returns to colony differed temporally. Also, attendance differed during brooding between

the two sites and morphs. These differences in behavior and the differences in proportion could be related to foraging. The underlying reason for these differences within the population in foraging returns, island proportions, and nest attendance, could be related to the mechanism that is causing the morph gradient on a range-wide scale. Future studies should replicate foraging return surveys for different colony islands across this gradient. Also, studies on foraging success of the two morphs during hour intervals are needed to either explain or reject the hypothesis of foraging efficiency affecting the differences in arrival time of the two morphs.

II. DIET

Reddish Egrets occur in an East-West gradient in terms of proportion of white to dark morph egrets. Bird counts in the 1950's revealed proportion of 89% white morphs in the southern Bahamas (Bolen and Cottam 1975), about 38% white morphs are currently in southern Texas (Amy Hanna, Texas Parks and Wildlife Department, unpublished data), and no white morphs have been reported in the Pacific coast colonies (Howell and Pyle 1997). Over this gradient, differences in weather patterns, water conditions, foraging habitat, nesting habitat, and prey species occur. The use of shallow, calm, estuarine water as foraging habitat, however, remains constant across the range (Lowther and Paul 2002). In this regard, the Reddish Egret is a habitat specialist. The prey of Reddish Egrets is predictably composed of shallow-water, schooling, euryhaline fish species (McMurry 1971, Simersky 1971, Paul 1991). The degree to which Reddish Egret diet changes over this polymorphism gradient is undocumented.

Dark-White polymorphism potentially affects prey selection in that plumage color can affect the foraging efficiency of Reddish Egrets in different habitats or on certain prey species (Green 2005, Green and Leberg 2005). Documentation of dark morphs spending more time foraging in shallower waters than white morphs (Green 2005) supports the hypothesis that differing foraging strategies are related to prey crypsis in Reddish Egrets. Pacific Reef Herons *Egretta sacra* also have foraging strategies that

differ between morphs. Rowher (1990) demonstrated a preference for deeper, turbid water by white morphs and selection of calmer, shallower waters by dark morphs.

About 38 feeding methods are used by the various species of heron (Kushlan 1978). The Reddish Egret has the most varied and active foraging techniques of any North American heron utilizing a majority of the foraging methods exhibited in herons (Meyerriecks 1960). Foraging techniques include stand and wait, wading, peering, wing-flicking, canopy feeding, and most commonly disturb and chase (Meyerriecks 1960, Rodgers 1983). Reddish Egrets may modify the use of these foraging strategies depending on habitat conditions (Rodgers 1983).

The objective of this study was to investigate prey selection of Reddish Egrets, potential differences between color morphs, and the influence of colony location on prey selection. I hypothesized that white morph egrets would more likely capture prey common in intermediate depths of water, and dark morph egrets would more likely capture prey common to shallower waters; these differences in prey selection will be reflected in their prey diet. I also hypothesized that differences in local foraging areas will result in differences in prey species captured during the nesting season.

Methods

Four colonies of Reddish Egrets within the Laguna Madre south of the Kennedy Causeway Bridge were sampled opportunistically during banding excursions (Fig. 1). In addition, colonies on Great Inagua, Bahamas, and in Baja, Mexico were sampled. When chicks are approached or handled for banding, some will regurgitate all or a portion of their last meal. The content of these boluses were gathered and put in bags. The color morph of the nestlings, colony location and date were labeled on each bag. Nestlings that came from mixed broods were assumed to have dark morph parents. Later, fish were identified and weighed for each bag, and the proportion of each species was tallied and the percent mass of each species represented was determined. Samples were compared between colony sites and parental morph using a MANOVA (Zar 1996) on the proportions of prey items in each collection bag by frequency. A separate MANOVA (Zar 1996) was used to compare weight of each species between colony sites and parental morph.

Results

Most regurgitant collected was dominated by one species of fish (>80%) (Fig. 7).

In Texas and Bahamas, that species was Sheepshead Minnow *Cyprinodon variegatus*. In

the Bahamas, this was the sole component of Reddish Egret regurgitant (n=6).

Regurgitant samples from Texas contained a larger diversity of prey items, but

Sheepshead Minnow (85%) and Tidewater Silverside *Menidia peninsulae* (7%)

dominated, composing 92% of the diet (n=65) (Fig. 7). Though no species and only one

family was shared between Texas and Baja, Baja had a similar species distribution with

82% of regurgitant belonging to one species, Pacific Sleeper *Gobiomorus maculatus*, and

10% containing Sargassum Blenny *Exerpes asper* totaling 92% of the diet (n=16) (Fig.

7). Other prey species present in Reddish Egret samples typically composed less than 3%

of the total diet.
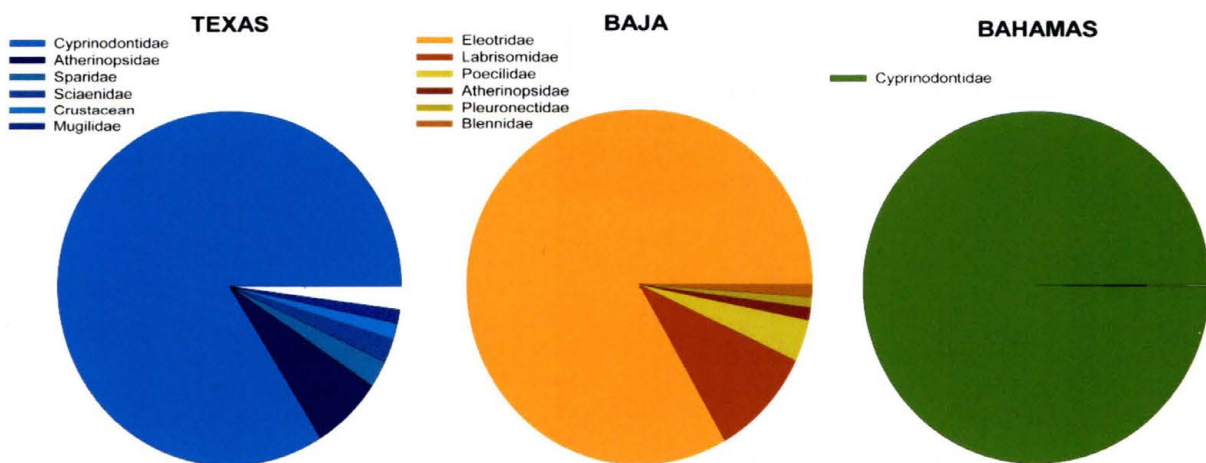
Figure 7 – Reddish Egret chick diet obtained from regurgitant across Reddish Egret range. Each slice represents cumulative frequency of each prey species found in each chick's boluses. Texas, n= 65; Baja, n = 16; Bahamas, n = 6.

Within the Laguna Madre of Texas, we were interested in the differences in regurgitant between morphs and between colony sites which were generally over 20 km apart. Reddish Egret morphs did not differ in the composition of prey items $(F_{(1,61)}=1.362, P= 0.224)$ (Fig. 8). Also, there was no interaction between morph and colony site $(F_{(1,61)}=0.55878, P=0.8394)$. Diet composition as a whole did not significantly vary between colony sites $(F_{(1,61)}=1.457, P=0.182)$ (Fig. 8). The only significant difference detected for any species of prey was in shrimp between colony sites $(F_{(1,61)}=6.861, P= 0.011)$. There were differences in the weight distribution of prey items between islands however $(F_{(1,60)}=2.683, P=0.010)$. Differences occurred between Tidewater Silverside $(F_{(1,60)}=4.720, P=0.034)$, Pinfish *Lagodon rhomboides* $(F_{(1,60)}=4.139, P=0.046)$, Mullet *Mugil* sp. $(F_{(1,60)}=4.139, P=0.046)$, shrimp $(F_{(1,60)}=5.705, P=0.020)$ and Spot *Leiostomus xanthurus* $(F_{(1,60)}=5.404, P= 0.023)$. Tidewater Silverside, Pinfish, Spot and shrimp were all a larger proportion of the total mass of Reddish Egret chick diet in the lower Laguna Madre. Mullet weighed proportionally more in the middle Laguna Madre (Fig. 8).

Figure 8 – Histogram with SE bars of proportion of prey items found in regurgitant from Reddish Egret colonies in the lower Laguna Madre and middle Laguna Madre. Bars express proportion by mean weight of prey items and mean number of prey items.

Discussion
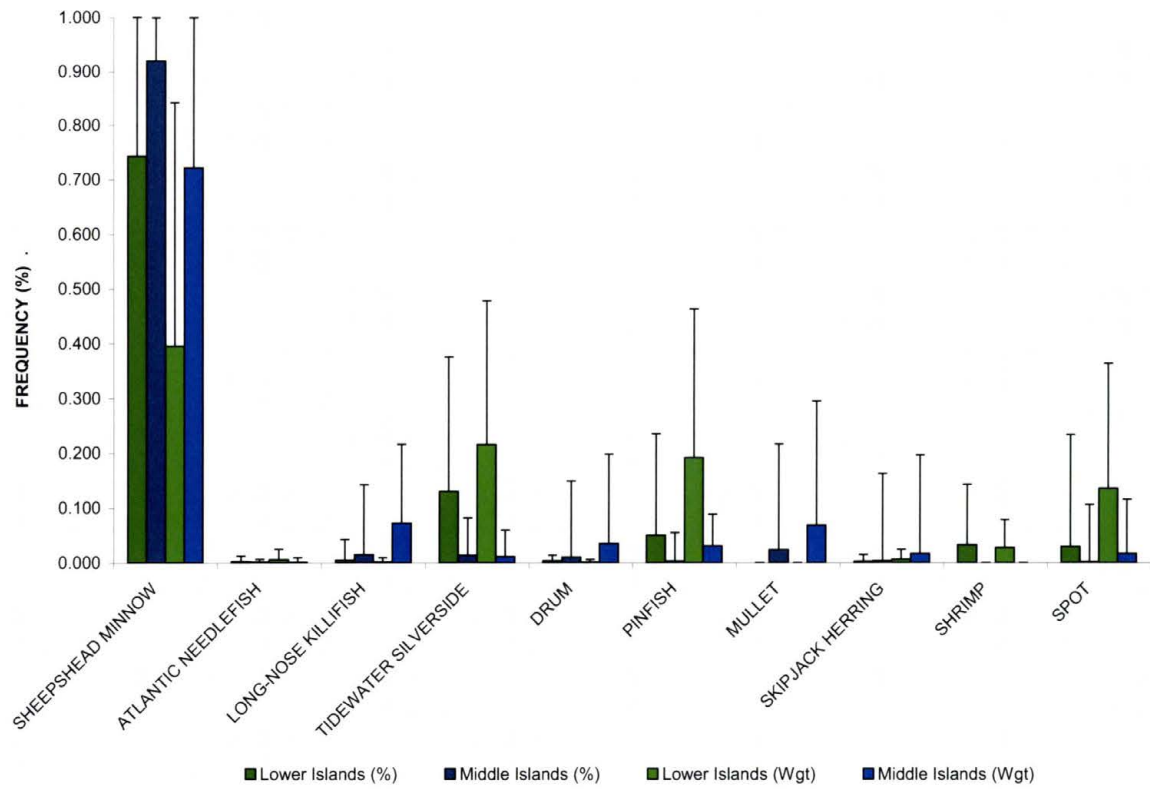
If foraging is an important factor in egret polymorphism, then Reddish Egret regurgitant could reflect these differences. Also, colony site would be predicted to affect prey frequency due to spatial variation in fish species and aquatic habitat. The variation of habitat and fish species utilized over the entire range of Reddish Egrets is still undocumented.

As seen in previous studies, Sheepshead Minnow represents the primary prey item in the diet of Reddish Egret chicks in Texas. Regurgitant samples from this study contained Sheepshead Minnow (84%), Long-nosed Killifish (1.1%), Tidewater Silverside (6.8%), Pinfish (2.4%), Mullet (1.3%), shrimp (1.5%), Spot (1.2%) and less than 1% each of Atlantic Needlefish *Strongylura marina*, drum *Umbrina coroides/Larimus fasciatus*, Skipjack Herring *Alosa chrysochloris*, Sea Trout *Cynoscion arenarius*, and Menhaden *Brevoortia sp*. McMurry and Simersky (1971) assessed fish species composition of 14 Reddish Egret chick boluses collected from the Laguna Madre, TX, colony and found Sheepshead Minnow (83%), Long-nosed Killifish *Fundulus similis* (9%), Pinfish (5%), Striped Mullet *Mugil cephalus* (<1%) and Ladyfish *Elops saurus* (<1%) to represent a majority of the Reddish Egret's diet (McMurry 1971, Simersky 1971). From over 1,500 regurgitated boluses collected from nestlings in Aransas Bay, TX, similar frequencies were obtained: Sheepshead Minnow (69.6%), Mullet *Mugil curema/M cephalus* (10.6%), Pinfish (5.4%), Long-nosed Killifish (4.3%), Tidewater Silverside (3.3%), and shrimp *Penaeus aztecus* (<1%) (Paul 1991).

The life history of Sheepshead Minnows makes it an ideal prey species for Reddish Egrets given the egret's foraging habitat. Sheepshead Minnow is a coastal species found in shallow estuarine water (Johnson 1980). In the Laguna it can be very abundant where the bottom is at least partially sandy, emergent vegetation is lacking, and the water is calm (Johnson 1980). During spawning peaks from April through July (Gunter 1950), large numbers of *C. variegatus* may accumulate in the shallower waters of the Laguna Madre (Allen 1942). These dates roughly correspond with Reddish Egret hatch dates (Fig. 2). Gunter (1945) found that in very shallow water this species is one of the predominant species, along with Tidewater Silverside. Sheepshead Minnow also have a high tolerance to variation in both temperature and salinity (Kilby 1955, Bennett and Beitinger 1997). The natural history of the Sheepshead Minnow, a species that lives and reproduces in large numbers in these calm, coastal flats, presumably explains why this species consistently represents over 80% of the Reddish Egrets diet during the breeding season.

In the limited samples from the Bahamas, the only fish species found in regurgitant samples has been Sheepshead Minnow. This monotypic sampling of Sheepshead Minnow is likely due to the habitat on Great Inagua, which is a large, hypersaline lake that concentrates fish, oxygen and salt. Sheepshead Minnow may be one of the few fish that can tolerate these environmental extremes (Kilby 1955, Bennett and Beitinger 1997).

In Baja California, Sheepshead Minnow are absent and over 80% of the Reddish Egret's breeding season diet is composed of Pacific Sleeper. Though the ecology of the Pacific Sleeper is poorly studied, most sources indicate that the young are very abundant near the coast and that reproduction is assumed to occur in estuarine waters. The possible similarities in life histories between *Gobiomorus* and *Cyprinodon*, suggest the species are ecological equivalents and *Gobiomorus* represents a suitable alternative prey species for Reddish Egrets during the breeding season on the Pacific Coast. Other fish of the shallow estuarine waters seem to compose a small portion of the diet and are potentially taken opportunistically according to local abundance within foraging habitats.

Differences between morphs in diet composition were small and insignificant. Pinfish and shrimp were found in larger numbers in white morphs, but samples containing shrimp and Pinfish were so few it was not statistically significant. Both Pinfish (Muncy 1984) and shrimp are species that tend to be deeper in the water column. This may reflect preferences in foraging depth (Green 2005). However, the insignificant differences seen would indicate that morphs are not feeding in different microhabitats or that differences in fish composition do not vary greatly within the range of egret feeding depths.

Differences in diet between islands were more apparent. Shrimp was the only food item that significantly differed in composition between island groups in frequency. Mullet, Tidewater Silverside, Pinfish, Spot and shrimp all differed by mass between island groups. This may indicate that Mullet were more abundant in the Middle Laguna

Madre foraging areas that might be shallower or closer to shore. Lower Laguna Madre island colonies may have deeper water or habitat otherwise more suitable for Pinfish, shrimp, Tidewater Silverside, Spot and generally more diversity in prey items. Differences may also be related to differences in water quality, salinity, disturbance, and aquatic vegetation between the two colony sites.

Large differences in Reddish Egret diet occur over the species range. No prey species are shared between the Pacific and Atlantic populations. However, the distribution of species was remarkably similar. Within the Bahamas population on Inagua, the sole food source discovered thus far for Reddish Egret nestlings are Sheepshead Minnows. Within the Texas population, morph seems to have an insignificant effect on prey composition. Colony site within Texas does however significantly affect the mass of prey species that are captured. Reddish Egrets do not seem pre-adapted to certain prey species, but rather to shallow water habitat types that attract similar species.

III. NEST SITE SELECTION

Nest sites are not chosen randomly by birds (Clark et al. 1983). Birds often select nest sites in terms of the amount of cover the location provides (Fasola and Alieri 1992). Cover can provide protection from predators (Fasola and Alieri 1992) and adverse weather. Within nesting colonies, nesting sites vary in cover (Fasola and Alieri 1992). Sites more suitable for reproduction should be selected first. Thus, within colonies, differences in preference and in temporal variation would affect the distribution of nests.

Plumage may be used to communicate with conspecifics (Butcher and Rohwer 1988). It is hypothesized that conspecifics assess each others morph (Roulin 2004) and this knowledge may affect interactions between individuals. If so, it is plausible that same-plumaged birds are more likely to be associated with one another.

Birds of the same-color morph would also be expected to have similar advantages and disadvantages. White morph Reddish Egrets are likely to have increased predator detection due to conspicuous plumage (Caldwell 1986). Reddish Egrets generally nest in colonies and in habitat where predators are less abundant, thus predation is likely an important factor in influencing nest site selection and therefore reproductive success of Reddish Egrets. If selection is influenced by predation, less cryptic white morph Reddish Egrets should nest in close proximity to one another to enhance predator detection

through shared vigilance (Pulliam 1973). Conversely, "spacing out" may create a scattered target that is difficult for aerial predators to pinpoint and attack, as well as decrease the ability of detecting aggregations of birds from a distance (Vine 1973). If the first response is true, the distance between white morph Reddish Egret nests within a patch will be closer to one another than dark morph Reddish Egret nests. If the second response is more indicative of Reddish Egrets, than differences in mean nesting distance will be greater for white morph Reddish Egrets than dark morph Reddish Egrets.

Other variables may result in differential nest site selection between white and dark morph Reddish Egrets. In Texas, it would appear that all Reddish Egrets prefer the protection of dense, spinous vegetation when available, but they may choose different sites within habitat patches due to different effects associated with plumage color. Thermal stress is one effect that may influence nesting adult success and chick mortality (Ellis 1980). In nesting situations, white plumage may confer a thermal advantage in the warm sub-tropical climes that Reddish Egrets inhabit (Ellis 1980). Dark plumage birds are presumably more prone to thermal stress and would therefore confer more of a disadvantage at nest sites within cactus patches that do not minimize direct solar radiation during the hottest parts of the day. Conversely, white plumaged Reddish Egrets would be more likely to find available nest sites in edge or open areas that have less cover and higher direct solar radiation. This effect may contribute to nest distribution among dark and white morph Reddish Egrets.

The objectives of this study are to determine if Reddish Egrets select nesting habitat within colony islands and if morphs distribute themselves differently in relation to one another. Furthermore, habitat will be compared between islands, morphs and random sites for microhabitat differences in cover to see if Reddish Egret morphs are selecting different microhabitats for nest sites given the differing physical pressures their plumage or colony site may incur. I hypothesized that Reddish Egrets are selecting prickly pear patches as nesting substrate when available. Also, white morph Reddish Egret nearest-neighbor distances should be different than nearest neighbor distances of dark morph birds.

Methods

Data for nest site selection were collected from islands in the Laguna Madre near Corpus Christi, TX (27° 46' N, 97° 30' W). Dark and white morph Reddish Egret nests were determined by brood coloration within two weeks of hatching. Garmin© handheld GPS units were used to mark coordinates (Universe Transverse Mercator-UTM) of nests and circumscribe cactus patches. These points were then exported to ArcGIS for spatial analyses. Overlay maps were Digital Orthoquads (DOQQs) accurate to 1 meter were downloaded from the Texas Natural Resources Information System website (www.tnris.state.tx.us).

GPS points of known nests of the two morphs of Reddish Egrets were overlaid with a DOQQ raster file. Randomly generated nest points and circumscribed cactus

patches were also overlaid on the DOQQ raster. Infrared vegetation images were compared with plotted cactus patches. I used Hawth's Tools (Beyer 2004) to randomly generate points within island and patch polygons. The frequency of random points that fell within patches was compared to the frequency of nest points that fell within patches. Chi-squared test (Zar 1996) was conducted to compare observed frequencies inside and outside of designated patches to frequencies of random points inside and outside of designated patches.

Since Reddish Egret colonies are biased toward the dominant dark morph, comparisons of nearest-neighbor distances between morphs might be biased. To correct this bias, I used the Spatial Analyst extension to generate expected null distances for each morph and patch. These nulls were based on randomized points equivalent to the number of birds within a patch or colony. Mean random distances were then generated between these points. A paired t-test was used to evaluate these mean distances to determine if spacing between a nest and nearest neighbor are different than what would be predicted by chance alone (Zar 1996, Green and Leberg 2006).

Microhabitat measurements were collected using line intersects to determine cover percentages. Vegetation classes were defined as tall (>40cm) and low (<40cm) Prickly Pear Cactus *Opuntia sp.*, Sea-Oxeye *Borrichia sp.*, tall (>20cm) and low (<20cm) grass, bare ground, low vegetation (evergreen, prostrate vegetation), annuals, shrubs, and trees. Each sample plot consisted of two perpendicular ten meter tapes that intersect at five meters at location of nest or random point. Orientation of sample plot was

predetermined using bearings assigned by the random number generator in Excel©.

Percent of each plant species that came in contact with the measuring tape was recorded

for each meter along each axis of a sample plot. Nest number and morph was recorded

for each sample plot as well. The PCA function in R version 2.5.1© (R Development Core

Team 2008) was used to discern general differences in cover composition between sites

and morphs. The correlation matrix was used in conducting the PCA.

Results

The presence of observed nests inside versus outside Prickly-pear *Opuntia engelmannii* patches was compared to that of randomly sampled points. Pearson's Chi-squared test with Yates' continuity correction revealed that a larger proportion of nests were found within cactus patches than what would be expected if Reddish Egret selected nest sites proportional to habitat availability within a colony (χ^2=101.344, df=1, P< 0.001). Reddish Egrets select Prickly-pear Cactus for nest sites over other available habitat (Fig. 9).
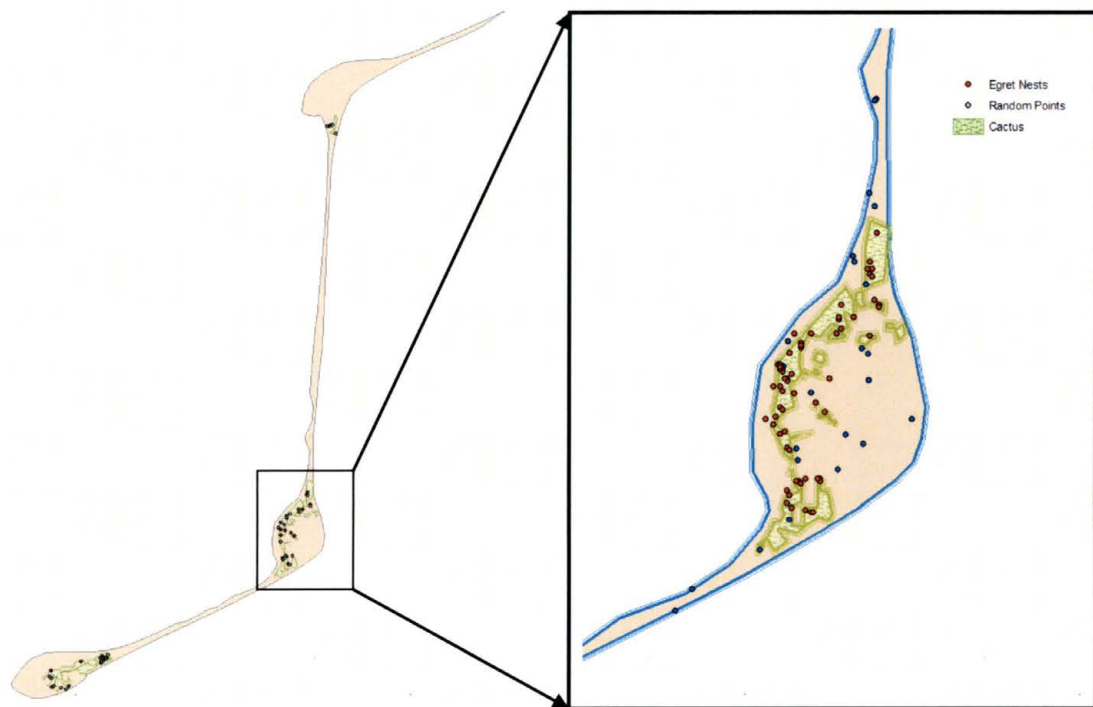
Figure 9 – Distribution of Reddish Egrets within a nesting colony containing Prickly Pear Cactus *Opuntia engelmanii*.

Spatial analysis revealed that white morphs were closer to other white morphs

than what would be expected given their density at both sites (Zigzag t-test=-3.28,

df=51,P=0.002; Rabbit t-test=-2.06,df=32,P=0.047) (Fig. 10). Spatial analyses also

revealed that there was not a significant difference between the observed distances

between dark morph nests and that which would be expected if the nests were randomly

distributed (Zigzag t-test=0.65, df=36, P=0.519,; Rabbit t-test=-0.85, df=75, P=0.400)

(Fig. 10).
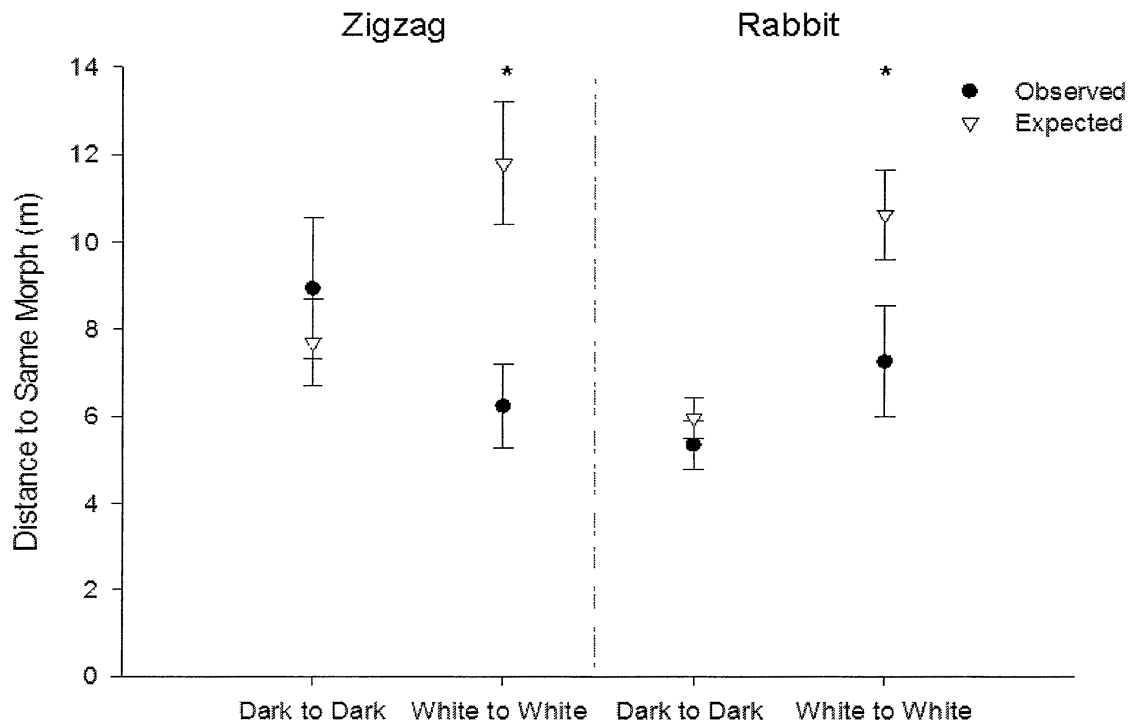
Figure 10 - Comparison of observed same morph nest distances to random points within cactus patches at Zigzag Island and without cactus patches at Rabbit Island. Site 1: Zigzag Island, (n=23, n=30); Site 2: Rabbit Island (n=40,n=18). Black circles are observed mean distance and hollow triangles are randomly-generated distance between like-morphs; bars represent ±1 SE.

Within cactus patches, both white and dark morph Reddish Egrets were more closely associated with each other than expected by random dispersal within cactus patches given densities of both morphs (t-test=-1.75, df=43, P=0.008; t-test=-2.81, df=50, P=0.007) (Fig. 11). In the absence of cactus patches though, dark and white morph Reddish Egrets were not more closely associated than expected (t-test=-1.59, df=77, P=0.117; t-test=-0.64, df=31, P=0.527) (Fig. 11).

Figure 11 – Comparison of observed opposing morph distances and randomly-generated distances from observed nests. Zigzag Island (n=23, n=30); Rabbit Island (n=40, n=18). Black circles are observed mean distance and hollow triangles are randomly-generated distance between opposing morphs; bars represent ±1 SE.

Distances between observed nests and between random points were also analyzed. On Rabbit Island, observed white morph egrets were not closer to one another than based on random chance (t-test=-1.50, df=30, P =0.145). However, dark morph birds were more concentrated than a randomly dispersed sample of equal size over the entire island (t-test=-2.52, df=76, P=0.014). On Zigzag Island, neither dark nor white morphs appeared more concentrated within cactus patches than that of a randomly distributed sample (White morph: t-test=-0.78, df=55, P=0.440; Dark morph: t-test=-0.26, df=43, P = 0.795).

Cover within one meter of Reddish Egret nests was considered "nesting cover". Principal component analysis (PCA) included ten vegetation variables as input data, and demonstrated differences between sites (Table 1, Fig. 12). Within one meter of nests, *Opuntia* and Low Vegetation contributed most to principal component 1. Short *Opuntia*, Shrubs and *Borrichia* were the important factors in principal component 2. The first two components constitute 33% of the variance between sites (Table 1). On Zigzag Island, the selection of cactus patches was detected with nests having higher values in principal component 1 (Fig. 12), which is associated with percent cover of *Opuntia englemannii*, than random points. Rabbit Island nests seemed to have higher scores associated with low vegetation compared to random points along principal component 1 (Fig. 12). Variation between morphs within sites was not apparent from this analysis (Fig. 12). Mixed morph nests may have separate from other nests in nest vegetation cover, however sample size was low (n=2, Fig. 12).

Figure 12 – PCA scatter plot comparing nest vegetative characteristics within 1 meter of nest between morphs and colonies. Axes represent Eigen values with labels referring to highest loading scores.

Cover within ten meters of Reddish Egret nests was also measured and compared. This was considered "peripheral cover". Principal component analysis (PCA), included the same ten vegetation variables as input data, and correlated to differences between sites (Table 1, Fig. 13). Outside of a meter from nests, *Opuntia* and Low Vegetation accounted for most of principal component 1. Short Grass and *Borrichia* were the important factors in principal component 2. The first two components constitute 37% of the variance between sites (Table 1). On Zigzag Island, the selection of cactus patches was detected with nest scores having high values for principal component 1 (Fig. 13), which is associated with percent cover of *Opuntia englemannii*, than random points. Rabbit Island nests seemed to have higher scores associated with low vegetation in the

nest periphery compared with random points (Fig. 13). Variation between morphs within

sites was not apparent from these analyses (Fig. 13). Mixed morph nests may have

separate from other nests in peripheral vegetation cover, however sample size was low
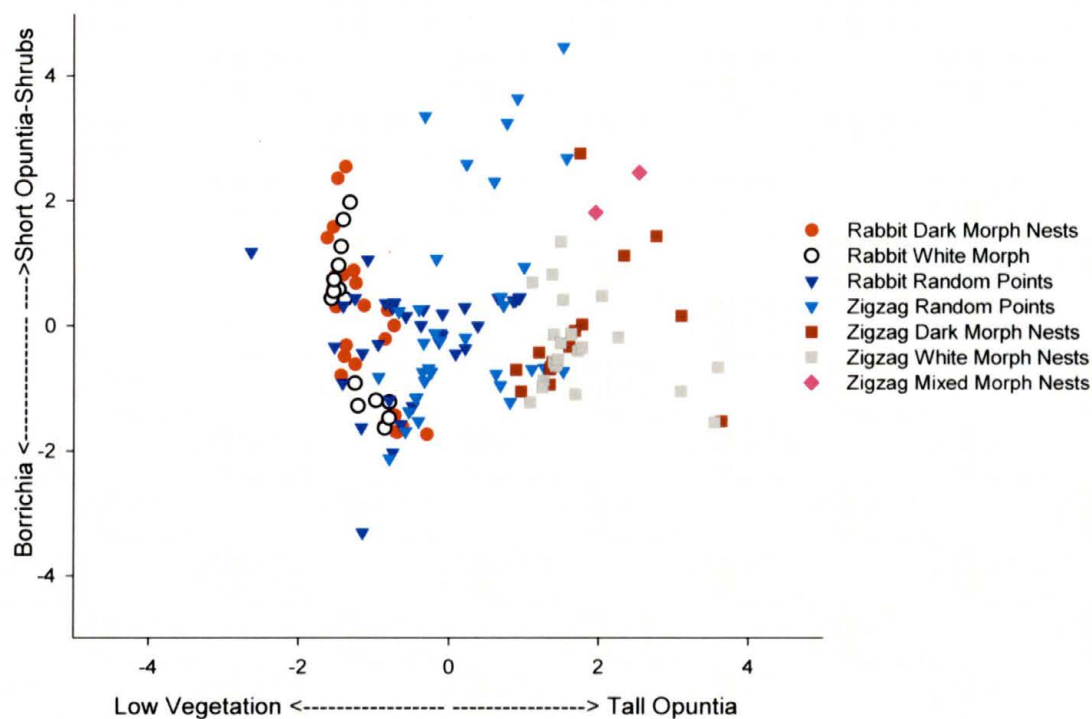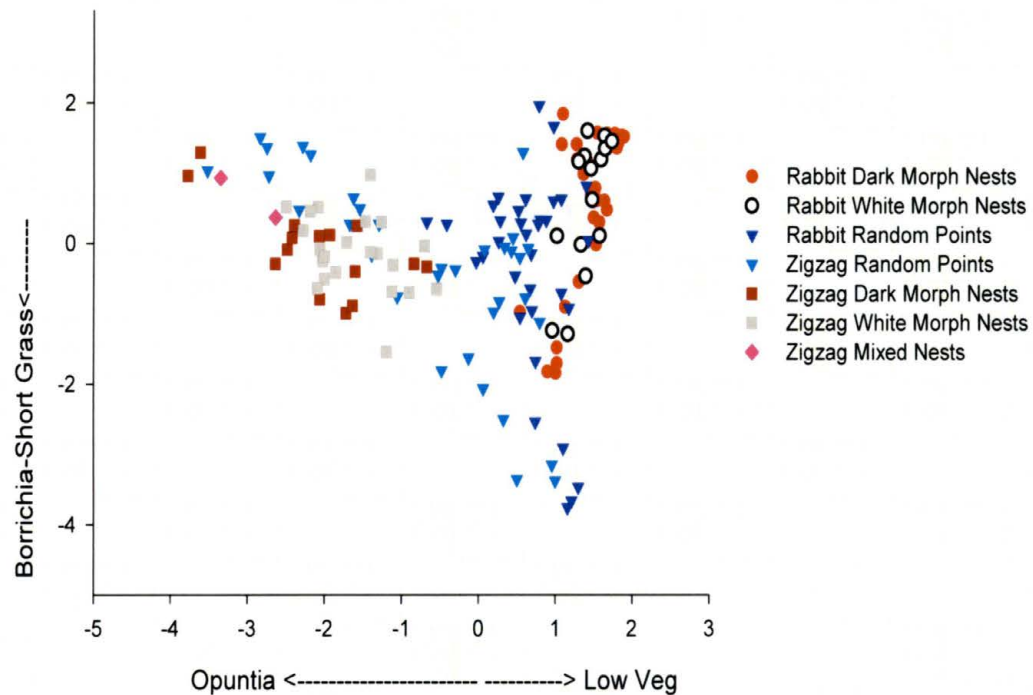
(n=2, Fig. 13).

Figure 13 – PCA scatter plot comparing peripheral vegetative characteristics within 10 meter radius of nest between morph and colonies. Axes represent Eigen values with labels referring to highest loading scores.

Table 1 - Loadings of vegetation variables on the first two principal components and the proportion of variance explained by each component. Bold-faced loadings >0.40 were used as axes labels in Figure 12 and Figure 13.

	NESTING COVER		PERIPHERAL COVER	
	PC 1	PC 2	PC 1	PC 2
Tall *Opuntia*	**0.552**	-0 154	-0 371	-0 131
Short *Opuntia*	0 359	**0.414**	**-0.548**	0 093
Borrichia	-0 16	**-0.453**	0 11	**-0.583**
Tall Grass	0 373	-0 166	-0 324	-0 036
Short Grass	-0.097	-0.31	0 091	**-0.563**
Bareground	-0 127	0.087	0 026	0 189
Low Vegetation	**-0.556**	0 226	**0.468**	**0.46**
Annuals	0.232	0 137	-0 225	0 045
Shrubs	-0 036	**0.598**	-0 294	0 212
Trees	0 113	0 201	-0 282	0 148
Variance Explained (%)	**0.18**	**0.15**	**0.23**	**0.14**

Discussion

Although Reddish Egrets nest on a variety of substrates, within any given colony they appear to select whichever substrate would seem to give them the most thermal and predator protection. On the Zigzag Island colony there exist discrete Prickly Pear patches that Reddish Egrets significantly selected. This selection of nesting sites by Reddish Egrets should also occur where discrete patches of *Borrichia*, mangrove, yucca or other vegetation or substrates exist in other colonies.

Another interesting component to colony composition is how the different plumaged individuals of this polymorphic species nest in relation to each other. Since similar species tend to nest with similar species, and same species with same species, it

seems logical that same morphs would tend to nest near same morphs. It would appear that within Reddish Egret colonies, white morphs tend to nest near other white morphs while dark morph Reddish Egrets distribute themselves randomly within defined colonies.

However, egrets do not seem to distribute themselves randomly over the whole colony. On Rabbit Island, dark morphs appear to be closer to one another than is expected from a random distribution. White morphs also had a high likelihood of being closer to one another than expected by random distribution, but the difference was notconsidered significant, which may be a result of a small sample size. The results were not significant on the other study site, Zigzag Island. The differences in significance may have resulted in the way the spatial analysis was done for each island. Since it was known that colonies were strongly associated with cactus patches, analysis was confined to within patches on Zigzag Island. On Rabbit Island, analysis was not confined to patches. Though patches of higher quality habitat such as *Borrichia* and high elevation areas may have occurred on Rabbit Island, these features were not examined and the study site was assumed relatively homogenous. At this site, the egrets may have concentrated in sub-colonies similar to what were observed on Zigzag Island within cactus patches, while random points were not constrained within these patches.

Having a conspecific neighbor close by may be important in communication of vital information within a colony. Conspecifics can assess danger or acquire information about food sources from a neighbor's behavior or vocalizations. Also, fitness advantages may be achieved by extra-pair copulations with neighbors. These same factors can cause

disadvantages such as competition for resources and mates, and increased predation

encounters (Wittenburge and Hunt 1985). If morphs are more different than just plumage

color, information from a conspecific with similar plumage color would be more

advantageous. However, the closeness of your neighbor reflects a balance between the

advantages and disadvantages of colonial nesting. White morphs may situate themselves

closer to one another to increase predator detection as result of their conspicuous

plumage, or due to the notion that white plumage creates a higher degree of sociality.

Conclusions from this study support previous studies that found white Ciconiiformes

oriented more closely in proximity to one another than darker Ciconiiformes (Green and

Leberg 2006).

PCA analyses indicated that while differences in microhabitat selection were

apparent between sites, and between random points and nest sites, differences between

morphs were not. Though egrets are selecting certain cover types for nesting, the two

morphs are not selecting these characteristics differently. Factors influencing egret nest

site choice may be related to accessibility to predators (or human disturbances), line of

sight, and occupancy of more dominant Ciconiiformes. Reddish Egret nests are often

lower in colony or closer to the periphery than Great Blue Herons, Great Egrets, or

Roseate Spoonbills (Burger 1979). There are also perceivable differences in habitat

between the two colony sites. Though vegetation varies considerably among colonies,

egrets seem to prefer those sites that have dense, thorny vegetation or vegetation that can

conceal nests.

This study should be expanded to include colonies in the Bahamas which are roughly 80% white morph (Bolen and Cottam 1975), and in Baja California which are considered 100% dark morph (Howell and Pyle 1997), to assess whether Reddish Egret colonies are denser when composed of high proportions of one morph. Also, the effect of nesting substrate patches (i.e. *Opuntia*, *Borrichia*, Mangrove, *Yucca*, and Taumalipan thornscrub) on nest-site selection and nesting densities of the two morphs could be examined. This information combined with nest success data could be used when designing heron nesting rookeries with special consideration for Reddish Egrets and maintenance of local population genetic structure. Also, findings may provide insights into the role of plumage polymorphism in birds and natural selection in Ardeids.

CONCLUSION

Investigations into ecology of polymorphism are increasing (Gray and McKinnon 2006). The existence of different phenotypes within the same population is an intriguing riddle. Most species have a single form, and that form is assumed to be maintained by natural selection. Conversely, if a species has two or more persisting forms then natural selection may be acting on the forms differently. The factors that lead to dark-white polymorphism in birds and the effects it has on individuals are not yet resolved. Apostatic selection has also been suggested, where prey avoid the most common morph. However, this would not explain constant gradients and stable polymorphism proportions. It is possible that dark-white polymorphism is just a balance of recessive-dominant genes. However, this does not seem to explain geographical gradients in proportions seen in some polymorphic species and would assume random mating.

Conversely, Reddish Egret polymorphism could be a balance of advantages and disadvantages derived from difference in color. If this is true, then each morph should theoretically do better in conditions that have the advantages, but lack the disadvantages. These differences may be subtle or hard to identify, but may be important in the evolutionary trajectory of the species. Since morphs are variations within the population and species level, these variation may provide a stepping stone for speciation if isolated.

However, factors differing between morphs must be strong enough to isolate the morphs from each other.

One mechanism that may isolate Reddish Egret morphs is non-random mating. If mating is random, then pairings between morphs would be proportional to the frequency of each morph within that population. This does not seem to be the case in Reddish Egrets. Egrets far more often nested and mated with birds of similar morph, and only rarely with mates of opposing morphs. Assortative mating demonstrates that birds perceive the difference between morphs. However, assortative mating alone may be too weak of a mechanism to restrict gene flow sufficiently enough to cause speciation. Egret morphs do not differ from each other either spatially or temporally in nesting, making gene flow between the two morphs easier. Unless morphs in a colony are of equal number and quality of males and females, morphs will still occasionally mate with each other rather than suffer the fitness costs of not mating at all.

Another difference detected between morphs related to colony return times. Returning to the nest during the nestling stage is an indicator of foraging success. Dark morphs returned most frequently during the morning hours between 08:00 and 11:00. White morphs returned to nest more consistently throughout the day. If these observations at Rabbit Island can be extrapolated to the entire Texas population, it would indicate that dark morph Reddish Egrets are more successfully foraging at crepuscular hours. This may have to do with either fish availability in shallower water or crypsis to

prey with varying background lighting. Counts expanded to other sites and lasting later into the evening would reinforce this data set.

The proportional gradient of white to dark morph Reddish Egrets from East to West is also interesting. Studies with Pacific Reef Herons have shown this gradient to be influenced by foraging substrate and correlated with differences in feeding styles. The Reddish Egret gradient may be a result of dispersal and may have been affected by the plume trade. However, the Reddish Egret's ability to migrate and disperse does not seem like it would be limiting. Habitat for foraging and nesting differs greatly from region to region. The Bahamas populations seem to feed on a subset of the prey items found in Texas, probably due to limitations in availability. Baja populations, however, have diets consisting of completely different prey species. The proportion of the prey species is very similar to Texas though. Birds in both regions seem to feed heavily on abundant, r-selected, euryhaline fish and potentially coincide the nesting season to the breeding seasons of these fish. In this manner, the Reddish Egrets appear to be habitat specialists in shallow, sparsely vegetated flats and not prey specialists.

Reddish Egrets are most vulnerable to predation and thermal stress while they are tied to the nest as eggs, hatchlings and even as adults. The color of adults and chicks alike could draw the attention of aerial predators. Likewise, as Ellis (1980) describes, different colored feathers carry different heat loads. The only ways to compensate for these differences would be in behavior or nest site selection. Nest sites are selected that considerably decrease confrontations with mammalian predators. Nest sites do not seem

to be selected differently between morphs in relation to detectability by predators (i.e. cover) or in regards to thermal cover. Variation in vegetative cover occurred between nesting colonies and even more so over the Reddish Egret's range. Vegetation does not seem to limit egret nesting as much as isolation of the colony from mammalian predators and disturbance, and proximity to adequate foraging grounds.

Though Reddish Egrets have recovered from the plume trade and the use of DDT, their population size is still very small compared with historical numbers. This species is one of only two species that is a dark-white polymorphic Ardeidae as adults over a majority of its range, yet few formal studies have been conducted examining the frequency of the morphs over time and space, the comparative ecology of the species or the basic life history characteristics of the species, especially those involving dispersal and migration. The differences found in this study may be expanded on and used for management of Reddish Egret morphs. While morph does not seem to affect nest site habitat, differences may be related to foraging. Management of aquatic resources and their quality adjacent to colonies may be vital in preserving morph ratios and thus genetic diversity. While this study may not have resolved the issue of the function of polymorphism in egrets, I believe it has provided evidence of possible difference between Reddish Egret morphs, provided some new information on the reproductive ecology of this rare species and help to produce data that can more accurately give direction on where to focus future studies on dark-white polymorphism in birds.

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