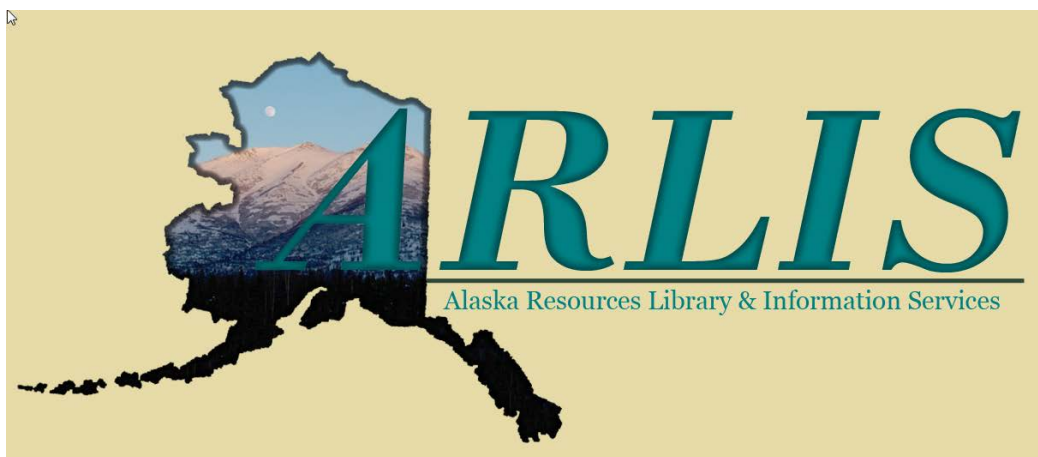


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THE BROOD-REARING HABITAT, BROOD HOME RANGE, AND FECUNDITY OF
THE SNOWY PLOVER (*CHARADRIUS ALEXANDRINUS*)
IN COASTAL SOUTHERN TEXAS.

A Thesis

by

JEFFERY R. RUPERT

Submitted to The University of Texas-Pan American
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE

December 1997

Major Subject: Biology

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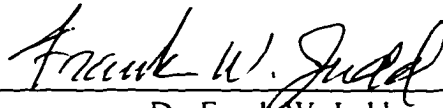
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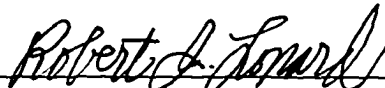
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The breeding biology of **Snowy Plovers (*Charadrius alexandrinus*)** was studied at **Laguna Atascosa National Wildlife Refuge in coastal southern Texas**. During **1995 and 1996** nests were found most often in high sand flat habitat and less frequently in low sand flat. Nest sites were dominated by open flat but had more rocks, pebbles and debris than control sites. Only **24% of the clutches hatched**, while **67% were eaten by predators and 9% were flooded**. Forty-three percent of Snowy Plover nests were within **Least Tern (*Sterna antillarum*) colonies** and these nests had a significantly greater chance of hatching than nests placed elsewhere. Radio telemetry and color-banding revealed that broods, like nests, were found only within high and low sand flat habitat. However, broods occurred in areas with significantly more vegetative cover and less open flat than nest sites. No other Snowy Plover study has described this habitat change. The mean brood area was 3.8 ha and broods moved an average of 84 m/day. Chick daily survival rate was estimated to be 0.951 during the brood-rearing (prefledge) period.

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INTRODUCTION

The Snowy Plover (*Charadrius alexandrius*) is a widespread species with a geographic range which includes much of North America, and portions of South America, Africa, Asia and Europe where it is named the Kentish Plover (Hayman et. al., 1986). Snowy Plovers inhabit sparsely vegetated beaches, flats and river channels along the Gulf Coast, the Pacific Coast and throughout the interior of western portions of the United States of America. Snowy Plovers both breed and overwinter in coastal southern Texas (Oberholser, 1974).

The American Ornithologists Union (1957) recognizes two Snowy Plover subspecies in the United States. The geographic range of the Western Snowy Plover (*C. a. nivosus*) includes the West Coast, Great Basin, Great Plains, and western Gulf Coast breeding populations (Fig. 1). This subspecies is distinguished by its plumage coloration. The upper parts are generally light brownish gray or grayish brown and the crown and occipital region often vary to light buff (Ridgeway, 1919). The geographic range of the Cuban Snowy Plover (*C. a. tenuirostris*) includes the eastern Gulf Coast breeding populations and extends from Louisiana to Florida (Fig. 1). This subspecies can be distinguished by plumage coloration. The upper parts are pale drab-gray, but sometimes approach grayish white in mid-summer, and the feathers darken centrally.

The subspecies identity of Snowy Plovers occurring in the Great Plains and along the western Gulf Coast has been questioned. Several authors have indicated that birds breeding in the Great Plains and along coastal Texas are Cuban Snowy Plovers (Oberholser, 1974; Johnsgard, 1981). Conversely, Oberholser (1974) indicated that birds wintering along the Texas

coast include both Cuban and western Snowy Plovers. Hayman et al. (1986) does not recognize the Cuban subspecies as a valid taxon.

Concerns have been raised over the current status of Snowy Plover populations in the United States. Page et. al (1995) showed that the Pacific Coast population of western Snowy Plovers suffered a 20% decline from 1977 to 1989. In response, the U. S. Fish and Wildlife Service listed the Pacific coast population of *C. a. nivosus* as threatened under the Endangered Species Act (Federal Register, 1993). Other populations of this subspecies are not specifically protected, although they have been implicated to be in decline (Boyd, 1991). No specific considerations for protection under the Endangered Species Act are currently afforded *C. a. tenuirostris*, even though it has a smaller range than does *C. a. nivosus*.

Considerable knowledge of the nesting ecology of Snowy Plovers in the United States exists. Snowy Plovers are usually associated with salt water and are reported as relatively uncommon adjacent to fresh water sites (Hayman et al., 1986). This association with saltwater is consistent with Purdue's and Haine's (1977) finding of specific physiological mechanisms in Snowy Plovers that reduce the internal effects of saltwater contact; as well as the ability to satisfy water requirements through metabolic water production. Conversely, Paton and Edwards (1996) speculate that fresh water is critical for Snowy Plover chicks.

Timing of breeding varies in different geographic areas of the United States. Breeding along the Pacific Coast begins in mid-March, with the first eggs appearing in late March (Warriner et al., 1986). The Texas breeding season begins approximately one month later, in mid-April, with eggs first appearing in late April (Oberholser, 1974). The Great Plains breeding season begins in mid-May, with eggs first appearing in late May (Boyd, 1972). Page et al.

(1995) reported that Snowy Plover courtship initiation varies geographically. Puerto Rican Snowy Plovers pair and nest in January, coastal Florida birds pair in January, followed by coastal California birds in February, and, finally, by Great Basin and Great Plains birds in late March to April.

Nest site characteristics have been described by Boyd (1972), Oberholser (1974), Purdue (1976), Grover and Knopf (1982), Page et al. (1985), Warriner et al. (1986), and Hayman (1988). Nesting occurs in or along the margins of barren areas. These may be shorelines, or saline or alkaline flats adjacent to bodies of water. Nests are often located with respect to conspicuous objects such as driftwood or cow droppings. They may be placed on small rises, or in areas of peculiar substrata such as broken glass or pebbles. A study along the Oregon Coast (Wilson-Jacobs and Meslow, 1984), quantified nest site habitat as having a mean of 28% ($s = 24.1$, $n = 65$) vegetative cover.

Page et al. (1995) found that Snowy Plovers maintain nest territories of varying sizes. They are as small as 0.1 ha in the Great Basin, between 0.5-1.0 ha in the Great Plains, always less than 0.5 ha within a salt pan along the Pacific Coast, and larger than 0.5 ha on the beach along the Pacific Coast. Snowy Plover territoriality has not been studied along the Gulf Coast.

Incubation is performed by both sexes of a pair and is initiated upon laying of a three (occasionally two) egg clutch. The incubation period ranges from 24-32 days (Boyd, 1972; Page et al., 1983; Warriner et al., 1986). In the Great Plains, females are responsible for most of the incubation, both day and night, with males relieving females for only short periods in the early evening and early morning. Along the Pacific Coast, females incubate during daylight hours, while males incubate during the early evening and throughout the night.

The annual mean nest success rate describes the percent of nests which hatched at least one chick. This rate has been shown to vary during studies of Snowy Plover breeding populations between single seasons, but is similar over time. Over a six year period along the West Coast, clutch hatching success ranged from 38-85%, with a mean rate of 58% (Warriner et al., 1986). Over a two year period in the Great Plains, clutch hatching success ranged from 38-73%, with a mean rate of 55% (Grover and Knopf, 1982). Page et al. (1995) compiled the results of 17 North American studies and found a mean hatch rate of 53% for all studies combined.

Many causes of clutch failure have been identified. When ranked in order from the greatest to the least at a coastal site in central California, they are: human perturbation; natural predators, including various mammals, unidentified gulls (*Larus* sp.), and American Crows (*Corvus brachyrhynchos*); wind; tidal flooding; and rain (Warriner et al., 1986). The greatest cause of clutch failure identified in the Great Plains was predation by coyotes (*Canis latrans*) followed by flooding (Grover and Knopf, 1982). Most Snowy Plovers respond to clutch failure occurring before mid-July by maintaining the pair-bond (71-85% of the time) and then renesting (Page et al., 1995).

Chicks are able to feed themselves immediately after hatching. During brood-rearing the adults do not feed the chicks, but lead them to appropriate feeding areas (Page et al., 1995). The pattern of brood-rearing varies between regional Snowy Plover populations. In the Great Plains, both adults typically maintain the pair bond and continue to rear broods through fledging, and consequently are characterized as primarily monogamous (Boyd, 1972). The Pacific Coast population, however, exhibits serial polyandry which has a profound effect on brood-rearing

(Warriner et al., 1986). Females typically abandon their broods after approximately one week, at which time they reneest with another male, leaving the brood to be raised by the original male. In this manner, a single female can produce as many as three broods in a single season (Page et al., 1995).

The fledging period for Snowy Plovers is between 27 and 33 days (Boyd, 1972; Cramp, 1983; Warriner et al., 1986). A study in California found that 296 chicks had a chick-fledging rate (percent of chicks fledged) of 39-42% (Warriner et al., 1986). Brood rearing habitat has not been identified as distinctive from nesting habitat and brood home range has not been quantified.

The Pacific Coast Snowy Plover population suffered a 20% decline during a ten year period from the late 1970's to the late 1980's (Page et al., 1995). Several causes were implicated as driving this decline: direct human disturbance, permanent or long-term loss of nesting habitats due to encroachment of introduced European beachgrass (*Ammophila arenaria*), and urban development were identified as primary factors. Both natural predation and inclement weather were identified as significant contributors (Federal Register, 1993). Several authors suggested that Gulf Coast populations have declined as well (Page et al., 1995). However, no quantitative evidence of a Gulf Coast decline is available, and any effect that factors driving the Pacific Coast decline may have on the coastal southern Texas Snowy Plover population is unclear because the Gulf Coast populations remain largely unstudied.

The major objectives of this study were to: 1) identify factors influencing fecundity, 2) quantify differences between nesting and brood-rearing habitat, 3) determine the presence or absence of brood territoriality, and 4) determine home range size during the brood-rearing phase of the breeding season of Snowy Plovers in coastal southern Texas.

METHODS AND MATERIALS

The study was located at Laguna Atascosa National Wildlife Refuge and Buena Vista Ranch, Cameron County, Texas (The approximate center of the study area lies at 26°16' latitude and 97°22' longitude). The local climate is characterized as semiarid (Thornwaite, 1948) and subtropical (Judd and Lonard, 1985). The average annual rainfall is 60.9 cm and peaks occur in September and October. Beginning late February, winter low temperatures (10 to 11°C) are gradually replaced by mild spring temperatures, commonly approaching 25 to 30°C. Summer begins in May and stretches through September. Temperatures generally range from 32 to 35°C during the day, and 23 to 25°C at night. The study period extended throughout two breeding seasons, i.e. from 1 March to 31 August, in 1995 and 1996. I visited the study sites 4 times per week in 1995 and twice per week in 1996.

I monitored nest and brood success to identify fecundity and factors limiting fecundity. Nests were located by scanning appropriate habitat with a 20-60X telescope. Once located, I mapped nests on "field updated" U.S. Geological Survey 7.5' quadrangle map and aerial photographs. Nests were then monitored to determine clutch fate. A clutch was determined to have failed if I found no eggs and evidence, such as predator tracks, feces, or egg remains at the nest site.

Clutches were aged by floating the eggs. As eggs mature the liquid volume (primarily yolk and albumen) is converted to solid tissue or is lost through evaporation. As a consequence, the volume of air within the egg and its visible buoyancy increases. A freshly laid egg exhibits no buoyancy, and will sink to the horizontal position when placed in a water container. With further development of an embryo, the egg density drops below the water density and the egg

floats vertically at the surface. After additional development the vertical floating egg begins tilting toward horizontal and breaks the water surface. A few days prior to hatching the egg protrudes well above the surface and floats horizontally. When the eggs reached the horizontal floating position (approximately 20-22 days old), I captured one or both of the adults (while at the nest incubating) by using a swing door trap or a funnel trap constructed of hardware cloth. Each captured bird was fitted with a U.S. Fish and Wildlife Service numbered metal leg band and three plastic color leg bands arranged in a unique order. A 1.5 g radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota) was also attached to the upper spinal tract feathers. This technique was successfully used for a study of Mountain Plovers (*Charadrius montanus*) in Colorado (Knopf and Rupert, 1996). The transmitter was attached to each bird by applying waterproof adhesive (Titan Corp., Lynwood, Washington) and sliding it under, and attaching it to, the feathers. This method assures that the transmitter will be dropped during the subsequent molt.

After hatching, juvenile birds were fitted with a U.S. Fish and Wildlife Service numbered metal band and a single color band. By following radio signals with a three element yagi antenna and radio receiver (Wildlife Materials Inc., Carbondale, Illinois) and by observing color band combinations, I was able to positively identify and track brood-rearing adults and determine the fate of each brood. After the first season it was apparent that brood-rearing habitat was limited and selected for in such a specific manner by adult Snowy Plovers so that telemetry was unnecessary and color banding alone was sufficient to maintain contact with broods. I calculated Heisey-Fuller (1985) daily survival rates for the monitored broods. The daily survival

rate is the probability that an animal alive at the beginning of a day, during a given time interval, will survive to the end of that day.

I recorded and mapped daily brood movements and locations. These locations were used to determine each brood's minimum area of use as an adaptation of the grid cell home range (Siniff and Tester, 1965). This method was used for a study of Mountain Plovers in Colorado (Knopf and Rupert, 1996). The area used was estimated by superimposing a grid over the map of daily locations and counting the number of new cells (25 m x 25 m) visited over time. The tendency of telemetry data to be discontinuous often leaves successive locations several cells apart. This estimate conservatively assumes that birds travel in a straight line between successive locations.

I identified habitat selection by comparing observed nest and brood habitat to that available using a chi-square test. Available habitats were quantified from maps of the Texas Submerged Wetlands (Bureau of Economic Geology, 1986), which identified 17 specific submerged wetland habitat types occurring along the Texas Coast.

Microhabitat was characterized following Knopf and Miller's (1994) methodology. I centered a half meter (1.0 x 0.5 m) rectangular frame over nest and brood sites in a north to south orientation and photographed them. Control sites (also 0.5 m²) were located by stretching a fiberglass tape to the north of nest or brood sites. The 0.5 m² frame was oriented north to south at intervals of 10, 20, and 30 m and then photographed. A grid was superimposed over each photograph. I characterized all nests which successfully hatched chicks, and the subsequent initial brood location following hatching. I identified the frequency of occurrence of three microhabitat features within the frame of each sample site: bareground; vegetation; and rocks,

pebbles, and/or debris (as a single category). Nest, brood, and control sites were compared using a Kruskal-Wallis one-way analysis of variance and Mann-Whitney U tests (H_0 = nest = brood = control).

RESULTS

Snowy Plovers were first observed exhibiting courtship behavior, paired and unflocked, on 10 February 1995 and 19 January 1996. In 1995, the first located nest was initiated on 26 March (based on the assumption of 28 days of incubation prior to hatch date) and hatched on 24 April. In 1996, the first nest was initiated on 1 April and hatched 28 April. In 1995, the latest nest was initiated on 10 July 1995 and in 1996 the latest nest was initiated between 1-5 July.

Fecundity. I monitored 67 nests, 43 in 1995 and 24 in 1996. Predators had the greatest impact on nest success. In 1995, 63% of the nests were depredated and in 1996, 75% of the nests were lost to predators. Nests fell prey to three known predators: coyotes (*Canis latrans*), based on tracks at the nest; raccoons (*Procyon lotor*), also based on tracks; and Chihuahuan Ravens (*Corvus cryptoleucus*), observed directly (Table 1). In 1995, 14% of the nests were flooded. All six of the flooded nests occurred in low mudflat habitat and were lost during a single isolated thunderstorm on 19 May 1995. In 1996, no nests were flooded. Nest success was similar over the two seasons: 23% of the 1995 nests and 25% of the 1996 nests hatched. Brood success was lower in 1995 than in 1996. In 1995, 40% of the broods from the 10 successful nests fledged. In 1996, 83% of the broods from the six successful nests fledged.

Snowy Plovers commonly nested within the boundaries of Least Tern (*Sterna antillarum*) colonies. Forty-three percent of all Snowy Plover nests, over both years, occurred within Least Tern colonies. The hatch success rate of Snowy Plovers nesting within Least Tern colonies was 42%; while 14% of the nests which occurred outside of tern colonies hatched. The Snowy Plovers which nested within tern colonies, both spatially and temporally, had a significantly greater chance of success ($\chi^2 = 6.07$, $df = 1$, $P = 0.014$).

In 1995, I monitored 23 chicks (of which eight survived to fledge) from ten broods for a total of 241 days and calculated a daily survival rate of 0.938. In 1996, I monitored 16 chicks (of which 11 survived to fledge) from six broods for a total of 171 days and calculated a daily survival rate of 0.971. The combined 1995-96 chick daily survival rate was 0.951 (Table 2).

The adult females from 10 of the 16 broods abandoned their broods a mean of 10.4 days ($s=2.27$) after hatch. Only two females remained to brood-rear for greater than 14 days. One of these broods suffered mortality at 17 days and the second fledged at 30 days. The four remaining broods failed at less than 14 days with both male and female present.

Brood Area Movements. I captured a total of 36 adult Snowy Plovers. Fifteen of these adult birds successfully hatched chicks and participated in brood-rearing, and one additional brood from an unknown nest was monitored (Table 3). Aggression between adjacent brood-rearing adults was common, indicating the existence of actively defended brood territories. I monitored broods for periods ranging from four to 44 days ($\bar{X} = 27$ days, $s = 14.6$, $n = 16$). The mean brood area over both seasons was 3.8 ha ($s = 2.4$), with a 4.3 ha mean ($s = 2.7$) brood area in 1995, and 2.9 ha mean ($s = 1.3$) brood area in 1996. Broods moved a mean of 84 m per day ($s = 87.7$) with the single greatest daily move being 775 m. The greatest distance from the nest site that I located a brood was 875 m.

Macrohabitat selection. Using the submerged wetlands map compiled by the Bureau of Economic Geology (1986), I determined that 5,193 ha of the 15,939 ha study area consisted of ten submerged or periodically submerged wetland habitat types: high sand flat, low sand flat, sand or mud flat/marsh undifferentiated, high brackish marsh, low brackish marsh, proximal

saltmarsh, distal saltmarsh, wetland/upland area undifferentiated, transitional area A, transitional areas.

I found that Snowy Plovers nested in only two of these habitat types, high sand flat ($n=47$), and low mud flat ($n=12$). All 12 of the low mud flat nests occurred in 1995 and none of these nests successfully hatched. Broods were likewise found only within the same two habitats, high sand flat ($n=12$) and low mud flat ($n=4$). One additional point of interest is that over the two years of my study 51% of the 67 total nests occurred within coves that did not maintain standing water throughout the nesting season. Overall, 10 broods were monitored under this circumstance and four of those broods successfully fledged.

Microhabitat selection. The control sites best describe the mean composition of the microhabitat features for the flats in which I found Snowy Plovers successfully nesting (Table 4). Unvegetated flat was the dominant feature ($\bar{X}=69\%$, $s=35.2$, $n=88$). Vegetation was the second most common feature ($\bar{X}=30\%$, $s=35.4$, $n=88$). Three plant species accounted for all of the vegetative cover: coastal saltgrass (*Distichlis spicata*), sea purslane (*Sesuvium erectum*), and glasswort (*Salicornia bigelovii*). Rocks, pebbles, and/or debris were the least common features of the control sites ($\bar{X}=1\%$, $s=10.9$, $n=88$).

Unvegetated flat was the dominant feature of successful nest sites ($\bar{X}=85\%$, $s=14.6$, $n=15$), (Table 4). The second most common feature at the nest was vegetation ($\bar{X}=11\%$, $s=14.2$, $n=15$), with the same vegetative species composition as the control sites. Rocks, pebbles, and/or debris were the least common feature at the nest ($\bar{X}=4\%$, $s=14.2$, $n=15$).

Brood sites were dominated by vegetation ($\bar{X}=54\%$, $s=28.6$, $n=15$), (Table 4) and again the plant species composition was the same as the control and nest sites. The second most

common feature was unvegetated flat ($\bar{X}=40\%$, $s=25.1$, $n=15$). The least common brood feature was rock, pebbles, and/or debris ($\bar{X}=6\%$, $s=15.8$, $n=15$).

The results of the Kruskal-Wallis one-way analysis of variance revealed significant differences between control, nest, and brood site microhabitat (Table 5). The nest sites had significantly more rocks, pebbles, and/or debris ($U=845.5$, $P=0.027$) than the control sites, but similar quantities of unvegetated and vegetated flat. The brood sites had significantly less unvegetated flat ($U=341.5$, $P=0.003$) and more vegetation ($U=914.5$, $P=0.017$) than control sites, but similar amounts of rock, pebble, and/or debris. The nest sites had significantly more unvegetated flat than the brood sites ($U=206.5$, $P<0.001$) while brood sites had significantly more vegetation than nest sites ($U=24.5$, $P<0.001$). Both had similar quantities of rock, pebble, and/or debris.

DISCUSSION

The earliest nest I found on 26 March 1995 suggests that Snowy Plovers begin nesting three to four weeks earlier than Oberholser (1974) reported. Oberholser does not specify the beginning of pair formation, however I observed that Snowy Plovers were paired by mid January to mid February. The breeding phenology I observed conforms to the trend reported by Page et al. (1995) of latitudinal variability in the timing of pair formation and nest building (Table 6). For example, in coastal Florida where the latitude is similar to that in southern Texas (25-31° N) the timing of pairing and nesting (Chase and Gore, 1989) coincided.

Fecundity Habitat. The hatch rates I found over the two years of the study were well below the mean hatch rate of 53% that Page et al. (1995) compiled from 17 North American studies. However, the southern Texas hatch rates fall within the range, 12.5 to 86.8%, of those compiled studies. Grover and Knopf's (1982) study of three Charadriiform species illustrate the variability which can occur in hatch rates between seasons. During the first year, 1977, of their study they found 73.1% of the Snowy Plover nests were successful. The following year, 1978, they found only 37.6% of Snowy Plover nests were successful. They speculated that climatic conditions were responsible for the decline in nest success between the two years.

The main factor responsible for nest failure and presumably brood failure in southern Texas was a high rate of predation, which may have been exacerbated by drought. Southern Texas experienced drought throughout the summers of 1995 and 1996. The mean six month rainfall total, March through August 1984-94 in nearby Port Isabel, was 30.4 cm ($s=14.9$). During the same six month period in 1995 only 16.3 cm fell and in 1996 only 13.9 cm, less than half the normal amount (NOAA, Brownsville, TX). While any direct effect the drought may

have had on Snowy Plovers breeding in the area is unclear. It seems possible that during the breeding season of both years the drought may have caused an increase in predation pressure. The predators I was able to identify were mostly omnivorous. Many of the common food sources for these predators were likely negatively affected by the drought. In light of my findings that standing water (fresh or saline) was not a necessary factor for Snowy Plover maintenance, growth, or reproduction, Snowy Plovers eggs and chicks may have represented a relatively available food source during a time of scarcity. While it is possible that these predation rates are indicative of some longer term trend, a more conservative assumption would be that they result from a shorter term climatic cycle.

Flooding contributed to the overall low hatch rate in 1995, but when all of the circumstances surrounding the flooded nests are considered it seems unlikely that, to date, flooding has played a major role in any long term population trends. First, the only flooded nests occurred in low flat habitat and I found birds nesting in high sand flats nearly four times more often than in low sand flats. Second, most summer storms in southern Texas are isolated events and are likely to impact only a single colony, and not the entire regional breeding population of Snowy Plovers. Conceivably, a proportional shift of nest occurrence from high to low sand flat could result in flooded nests contributing more significantly to longer term population trends.

At the time of hatch a chick still must survive for at least four weeks before it gains the competitive advantage of flight over potential predation. After hatching an individual juvenile plover does, however, gain the advantage of some mobility and a degree of independence from predation pressure. Prior to hatch, any nest that was discovered by a predator resulted in all of the eggs being eaten (I found no examples of partial predation). Eggs in a nest are all in close

proximity and they can't move to escape a predator. Chicks relying on crypticity or running ahead of predators (Page et al., 1995) as predator escape mechanisms, are relatively scattered compared to a clutch of eggs in a nest. The discovery, by a predator, of one chick does not guarantee the loss of the entire brood. After hatching an individual chick had a 26% chance of surviving to fledge, or said differently a 0.951 probability of surviving to the next day for a 28 day period. The likelihood that an individual chick would survive to fledge was not much greater than the likelihood that a nest would be successful. This suggests that predation pressure was relatively consistent throughout the entire incubation and brood-rearing cycle. If the fate of an entire brood is considered, the likelihood that at least one chick per brood would fledge increased to 56%.

In addition to the three known predators I was able to identify, I regularly saw juvenile Aplomado Falcons (*Falco femoralis*) perched or overflying nest and brood areas. Avian predation has been known to severely impact Snowy Plover breeding colonies in California (Warriner et al., 1986). They found that Loggerhead Shrikes (*Lanius ludovicianus*) took at least 14 pre-fledge chicks from a single colony. Additionally, there was a great deal of circumstantial evidence that implicated snakes (Order Squamata) as potential predators, particularly of juveniles. I commonly found snake tracks on the flats proper. Although, I never found tracks near a depredated nest, I found them extensively throughout the vegetated brood-rearing portions of the flats. The tracks usually passed one-way in a more-or-less straight line when occurring on open flat, but, literally blanketed entire portions of vegetated flat criss-crossing and meandering from plant to plant. The only snake species I observed on the flats proper was the western diamondback rattlesnake (*Crotalus atrox*). Birds are known to comprise an appreciable part of

the western diamondbacks diet where ground nesting is plentiful, but, eggs are considered to be a rare food item for rattlesnakes (Klauber, 1956)

Serial polyandry is apparently common in southern Texas. Eighty-three percent of broods which survived to at least 15 days ($n=12$) were abandoned by the female. This behavior was documented for Snowy Plovers in California where females typically abandoned broods by day 6 (Warriner et al., 1986). In Utah, females were seldom seen with broods more than two days after hatching (Paton, 1995).

One interesting and potentially significant finding of this study was the increased hatch success rate Snowy Plovers experienced when nests occurred within Least Tern colonies. Interestingly, a study of Piping Plovers (*Charadrius melodus*) in Massachusetts found that nest predation increased when nests were associated with Least Tern colonies and human disturbance (Strauss, 1990). The advantage to Snowy Plovers associated with Least Terns in South Texas seemed intuitively obvious to me: the increased aggression of Least Terns toward predators entering the colony afforded the associated Snowy Plover nest the same benefit. Presumably, it was the human disturbance factor in Massachusetts that contributed most significantly to the observed increase in Piping Plover nest predation. Page et al. (1983) suggested that density-dependent rates of predation could be a factor limiting population size. It remains to be seen how commonly the Least Tern-Snowy Plover association occurs along the Texas Coast (43% of all Snowy Plover nests which I located were associated with Least Terns). Clearly, the association represents an opportunity for Snowy Plovers to nest successfully at higher densities.

Snowy Plovers usually breed during their first year of life (Warriner et al., 1986) and the most recent predictions place their life expectancy at 2.7 years (Paton, 1994). This would allow

most females to make three seasonal breeding attempts during their lifetimes. In southern Texas, with a 15 week nesting season, females could conservatively make two breeding attempts per season (24-32 d incubation and 1-2 wk brood-rearing before abandonment). As a consequence over a life span a female must average a 33 % fledge rate (produce at least one fledgling per nesting attempt, twice over her life span) for the local population to sustain itself. If hatch and fledge rates in southern Texas continue at the low level I observed for several seasons I expect a noticeable decline in the southern Texas population. Future and ongoing inquiries into local Snowy Plover fecundity will reveal this.

The chi-square test which considered habitat selection between the Bureau of Economic Geology's (1986) submerged habitats showed no overall statistical preference for macrohabitat. A closer examination of five of the ten categories, mud flat marsh, brackish high marsh, brackish low marsh, proximal saltmarsh, and distal saltmarsh revealed little to no open substratum associated with any of these habitat types and therefore these habitats are likely unavailable to Snowy Plovers. Both transitional A and transitional B habitats, and dredgewaste-mudflats contain some open substratum, but, only high flat and low flat are specifically characterized by large amounts of open substratum. When just these two habitats were compared, I detected no significant preference for high flat ($\chi^2=2.77$, 1 df, $P=0.096$). Snowy Plovers which nested on high flats had an apparent advantage over low flat nesting birds when loss to flooding was considered. All six of the flooded nests occurred within low flat habitat and no high flat nests were ever flooded. Considering that nests only occur in two habitat types, and the relative ease of identifying these habitats using the BEG submerged habitat maps, future investigations into

the nesting distribution of Snowy Plovers in southern Texas should benefit by first examining these maps for occurrence of appropriate habitats.

Many authors have commented on the propensity of Snowy Plovers to nest near a conspicuous object (Boyd, 1972; Purdue, 1976; Hill, 1985; Page et al., 1985). Only one study from Mono Lake, California (Page et al., 1985), quantified the tendency for nests to be placed in the open versus under or within 15 cm of an object. Findings from that California study indicated that 40% of 211 nests occurred in the open and that the other 60% were under or within 15 cm of an object. Although a direct comparison between the California study and my own are impossible because of differing methodologies, my findings support this trend because I found significantly more rock, pebble and debris coverage at the nest sites than within the control sites. That is not to say that all nests were near an object, since two of the 15 successful nests from which I collected microhabitat data had neither vegetation nor debris present.

My description of nest and brood macrohabitat clearly illustrated the necessity for open substratum during both incubation and brood-rearing phases of the breeding cycle (particularly the incubation period). After hatching there was a shift in habitat to areas with more vegetative cover. No other Snowy Plover study has described this habitat change. The reason for this may be partially explained by Paton (1994) who indicated that he simply did not have enough nestling resightings to estimate survival. If juvenile locations are not specifically targeted methodologically, by increasing observation distances and decreasing disturbance, then broods are probably led away to an unobservable location. Other shorebird studies document brood habitat shifts. An American Golden-Plover (*Pluvialis fulva*) and Pacific Golden-Plover (*Pluvialis dominica*) study found that broods moved to wetter tundra, presumably in search of

cover and food (Johnson and Conner, 1996). Wilson's Phalarope (*Phalaropus tricolor*) broods were also found to move to wetter habitats (Calwell and Jehl Jr., 1994). Brood habitat shifts may prove a common feature of shorebird behavior.

The shift from relative open substratum to relative heavy vegetative cover in Snowy Plovers may serve two purposes. First, cover undoubtedly helps to avoid initial detection by predators; or once detected, vegetation provides better hiding places. It was clear that on occasions when I approached broods for banding or on a few occasions during field observations, despite my best efforts to maintain an adequate distance, I caused broods to actively seek vegetation for cover. Second, and for at least some Snowy Plover broods more importantly, vegetated flat served as primary foraging areas. Over the two years of my study 34 of the 67 nests occurred within coves which did not maintain standing water throughout the nesting season. I found no evidence that the broods which occurred within these dry coves ever foraged in the open flats, rather they were always observed foraging very near, and often directly from, standing vegetation. Probing in sand at the base of low growing plants has been previously observed in this species when foraging above the high tide line in California (Page et al., 1995). Those observations, as well as my own, indicated that Snowy Plovers readily exploited food resources not directly identifiable as tidally related, aquatic, or semi-aquatic invertebrates. The vegetated flats were clearly an important feature for foraging juveniles.

Paton and Edwards (1996) speculate that freshwater is critical to nesting Snowy Plovers because chicks cannot tolerate high salt concentrations citing Purdue's and Haine's (1977) study. It should be noted that Purdue and Haines (1977) found that on a dry diet with drinking water at 0.3 M NaCl, Snowy Plovers could not maintain body weight. More importantly, however, their

findings indicated that on a diet of mealworm larvae and no water, Snowy Plovers could maintain body weight and that after an initial weight loss the birds actually gained weight. As mentioned previously, I monitored broods in areas without standing water. I also monitored broods in areas with standing hypersaline water (<0.6 M). This indicates that chicks are capable of growth and development using dietary-derived water only and that freshwater is unlikely a necessary factor of brood habitat.

Brood Area Movements. No quantitative Snowy Plover brood movement information was available for comparison with my findings. There were however, several observational notes included in two published reports. A California study notes that "broods rarely remained in the nesting territory until fledging, although they sometimes remained in the general area" (Warriner et al., 1986). My findings support the trend of movement from the nesting territory and additionally, I saw no evidence of pre-fledge broods moving beyond the boundaries of their particular tidal cove (presumably this falls under the description of the general area). Page et al. (1995) reports that two California broods moved six and seven kilometers as early as two days after hatch. The greatest distance from the nest that I ever found a brood was 875 m. One reason that I may not have seen broods move distances on the scale seen in California could possibly be explained by differences in human disturbance present near the nest sites. One major goal of this project was to reduce the amount of human disturbance present within the nesting colonies. Consequently, I generally monitored broods from distances of greater than 200 m, which may have reduced the likelihood that broods would move to more distant areas.

Findings from other Charadriiformes studies showed variation within a pattern of generally local brood dispersal. Semipalmated Sandpipers (*Calidris pusilla*) broods moved up to

3 km away from the nest site (Gratto-Trevor, 1992). Black-bellied Plover (*Pluvialis squatarola*) broods were found to usually stay within 1.5 km (occasionally up to 3 km) of the nest site (Paulson, 1995). A Buff-breasted Sandpiper (*Tryngites subruficollis*) study found that broods usually moved 50 m on day 1 after hatching (Lancot and Laredo, 1994). After day 1, the Buff-breasted Sandpiper broods then moved about 0.5 km or more per day. Snowy Plover average daily brood moves of 84 m per day were generally much smaller than these reported values.

Based upon my findings and the little information currently available for other Charadriiform species this observable nest to brood habitat shift may be important when considering the breeding ecology of Snowy Plovers. To simply manage for appropriate nesting habitat without consideration for providing alternate brood habitat may leave Snowy Plovers without a very necessary habitat component and therefore susceptible to low breeding success rates.

The sites I selected to study Snowy Plovers may represent an ideal set of circumstances under which Snowy Plovers in coastal Texas breed, especially with regards to human disturbance. Brood habitat generally occurred along the most elevated portions of high sand flats and most Snowy Plover nests occurred within that same macrohabitat. High sand flats in other areas, such as South Padre Island and Port Isabel, represent some of the most developable and accessible recreational land along the Laguna Madre. Further studies leading to greater understanding and recognition of the threat of human disturbance to high sand flat habitat will likely be a key ingredient to long-term conservation of the Snowy Plover along the Texas Gulf Coast.

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Figure 1. Continental U. S. range of the Snowy Plover (*Charadrius alexandrinus*). Shaded areas indicate *C. a. nivosus* range, hatched area indicates *C. a. tenuirostris* range (Page et al., 1995).

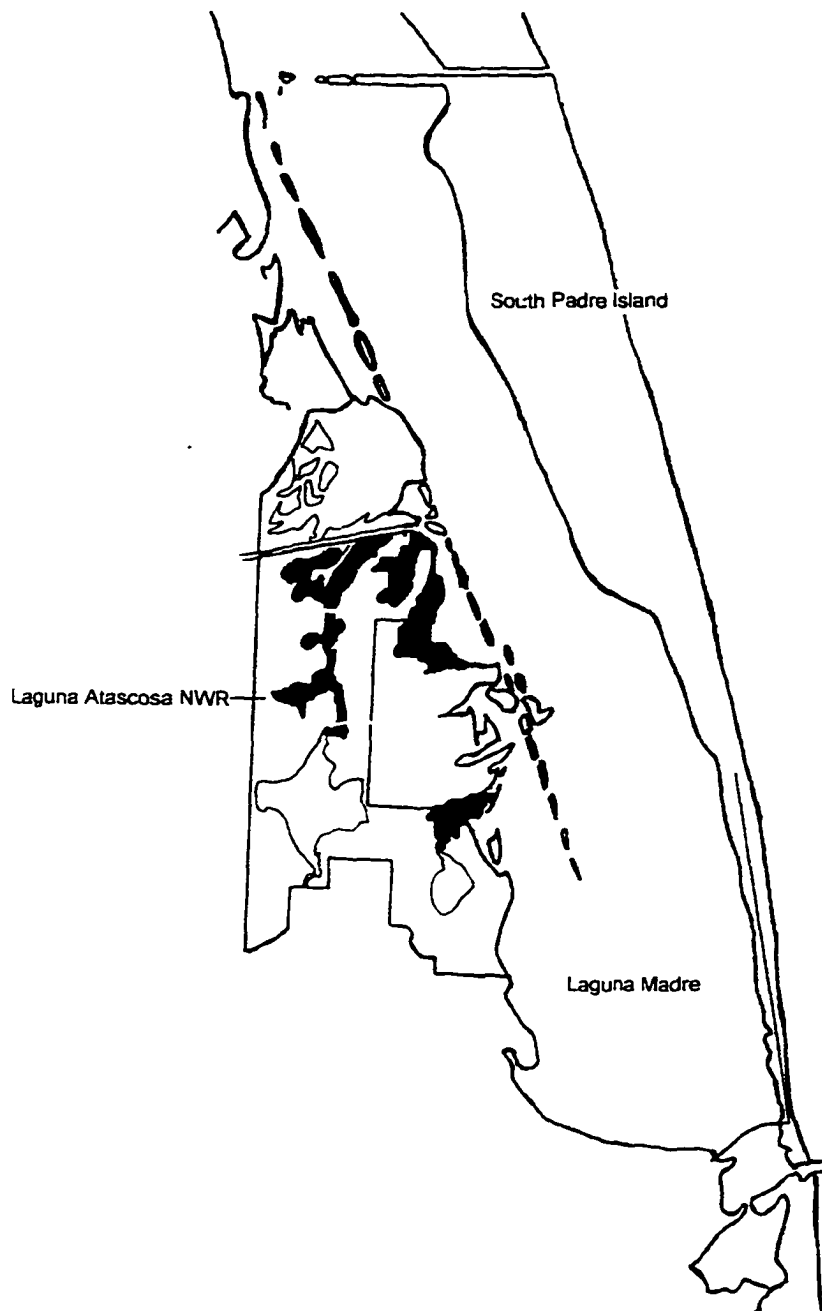


Figure 2. Map of the Lower Laguna Madre, outlining the boundaries of Laguna Atascosa National Wildlife refuge. Solid areas indicate sites with the greatest tidal influence and the focal study areas.

Table 1. Sources of Snowy Plover nest predation, 1995, 1996, and combined.

Number of nests, % (% of known outcomes).

Source	1995	1996	1995&96
Coyote	15, 56% (60%)	2, 11% (50%)	17, 38% (59%)
Raccoon	7, 26% (28%)	2, 11% (50%)	9, 20% (31%)
Chihuahuan Raven	3, 11% (12%)	0	3, 7% (10%)
Unknown	2, 7%	14, 78%	16, 35%

Table 2. Results of chick monitoring, by brood, for 1995-96. The year the brood was monitored is indicated by the brood number prefix..

Brood No.	No. of Days Monitored	No. of Juv. in Brood	No. of Mortalities
95-1	4	2	2
95-2	3	1	1
95-3	31	3	3
95-4	44	3	1
95-5	12	3	3
95-6	31	2	0
95-7	43	3	0
95-8	26	3	3
95-9	17	2	2
95-10	30	1	0
total for 95	241	23	15
96-1	37	3	0
96-2	30	3	1
96-3	30	2	1
96-4	31	3	1
96-5	29	3	0
96-6	14	2	2
total for 96	171	16	5
Total for 95&96	412	39	20

Table 3. Results for individual broods estimated brood area (ha), mean move per day (m), and greatest single move (m), for 1995 and 1996. The year the brood was monitored is indicated by the brood number prefix. \bar{X} gives the mean, s the standard deviation of the mean.

Brood No.	No. of Days Monitored (start date)	Minimum Brood area	\bar{X} Move/Day	Greatest Single Move
95-1	4 (26 Apr)	2.7	350	600
95-2	3 (2 May)	1.7	242	400
95-3	31 (15 June)	8.6	151	600
95-4	44 (21 June)	6.3	65	650
95-5	12 (25 June)	2.8	92	110
95-6	31 (11 June)	5.1	73	450
95-7	43 (19 June)	8.4	83	350
95-8	26 (7 July)	2.8	53	475
95-9	17 (14 July)	0.7	44	275
95-10	30 (23 June)	4.5	68	775
\bar{X} for 95	24 ($s=14.7$)	4.3 ($s=2.7$)	122 ($s=100.0$)	453 ($s=190.7$)
96-1	41 (13 Apr)	3.1	34	95
96-2	38 (2 June)	5.1	56	69
96-3	42 (4 June)	1.6	20	70
96-4	33 (9 June)	1.9	33	68
96-5	35 (10 June)	3.4	49	183
96-6	4 (10 June)	2.0	13	13
\bar{X} for 96	32 ($s=14.2$)	2.9 ($s=1.3$)	34 ($s=16.4$)	83 ($s=55.9$)
\bar{X} for 95&96	27 ($s=14.6$)	3.8 ($s=2.4$)	84 ($s=87.7$)	314 ($s=239.1$)

Table 4 Results of microhabitat plot survey. The initial number under each category indicates the frequency of occurrence (out of 231 possible) for microhabitat type, followed by coverage, in that plot. \bar{X} gives the mean, s the standard deviation of the mean.

Brood/Nest #		Unvegetated Flat		Vegetation		Rock, Pebble, Debris	
95-1	brood	162	70%	68	29%	1	<1%
95-2	brood	223	97%	8	3%	0	0%
95-3	brood	87	38%	44	62%	0	0%
95-4	brood	27	12%	204	88%	0	0%
95-5	brood	104	45%	127	55%	0	0%
95-6	brood	22	10%	209	90%	0	0%
95-7	brood	109	47%	122	53%	0	0%
95-8	brood	119	52%	112	48%	0	0%
95-9	brood	58	25%	173	75%	0	0%
95-10	brood	32	14%	199	86%	0	0%
96-1	brood	78	34%	143	62%	10	4%
96-2	brood	51	22%	168	73%	12	5%
96-3	brood	55	24%	139	60%	37	16%
96-4	brood	173	75%	58	25%	0	0%
96-5	brood	91	39%	0	0%	140	61%
\bar{X}		92.7 (s=57.9)		124.9 (s=66.0)		13.3 (s=36.4)	
95-1	nest	231	100%	0	0%	0	0%
95-10	nest	209	90%	22	10%	0	0%
95-2	nest	204	88%	0	0%	27	12%
95-3	nest	217	94%	0	0%	14	6%
95-4	nest	231	100%	0	0%	0	0%
95-5	nest	188	81%	43	19%	0	0%
95-6	nest	223	97%	6	3%	2	1%
95-7	nest	183	79%	48	21%	0	0%
95-8	nest	145	63%	86	37%	0	0%
96-1	nest	216	94%	14	6%	1	<1%
96-2	nest	213	92%	2	1%	16	7%
96-3	nest	127	55%	104	45%	0	0%
96-4	nest	139	60%	23	10%	69	30%
96-5	nest	219	95%	0	0%	12	5%
\bar{X}		196.3 (s=33.7)		25.3 (s=32.7)		9.4 (s=18.5)	
<i>Control -</i>							
1	control	215	93%	15	6%	1	<1%
2	control	227	98%	3	1%	1	<1%
3	control	221	96%	10	4%	0	0%
4	control	227	98%	4	2%	0	0%
5	control	231	100%	0	0%	0	0%
6	control	229	99%	2	1%	0	0%
7	control	231	100%	0	0%	0	0%
8	control	231	100%	0	0%	0	0%
9	control	229	99%	2	1%	0	0%
10	control	227	98%	4	2%	0	0%
11	control	225	97%	4	2%	2	1%
12	control	223	97%	8	3%	0	0%

Table 4. Continued.

Control #		Unvegetated Flat		Vegetation		Rock, Pebble, Debris	
13	control	228	99%	0	0%	3	1%
14	control	228	99%	3	1%	0	0%
15	control	231	100%	0	0%	0	0%
16	control	231	100%	0	0%	0	0%
17	control	166	72%	65	28%	0	0%
18	control	64	28%	167	72%	0	0%
19	control	207	90%	24	10%	0	0%
20	control	210	91%	20	9%	1	<1%
21	control	217	94%	4	2%	0	0%
22	control	222	96%	8	3%	1	<1%
23	control	227	98%	3	1%	1	<1%
24	control	231	100%	0	0%	0	0%
25	control	226	98%	4	2%	1	<1%
26	control	231	100%	0	0%	0	0%
27	control	231	100%	0	0%	231	100%
28	control	220	95%	10	4%	1	<1%
29	control	190	82%	41	18%	0	0%
30	control	225	97%	5	2%	1	<1%
31	control	221	96%	9	4%	1	<1%
32	control	224	97%	4	2%	3	1%
33	control	231	100%	0	0%	0	0%
34	control	231	100%	0	0%	0	0%
35	control	86	37%	145	63%	0	0%
36	control	88	38%	143	62%	0	0%
37	control	96	42%	135	58%	0	0%
38	control	100	43%	131	57%	0	0%
39	control	130	56%	101	44%	0	0%
40	control	231	100%	0	0%	0	0%
41	control	144	62%	87	38%	0	0%
42	control	163	71%	51	22%	17	7%
43	control	159	69%	72	31%	0	0%
44	control	167	72%	64	28%	0	0%
45	control	190	82%	41	18%	0	0%
46	control	115	50%	115	50%	1	<1%
47	control	208	90%	23	10%	0	0%
48	control	130	56%	101	44%	0	0%
49	control	79	34%	152	66%	0	0%
50	control	102	44%	129	56%	0	0%
51	control	208	90%	23	10%	0	0%
52	control	185	80%	46	20%	0	0%
53	control	141	61%	90	39%	0	0%
54	control	228	99%	3	1%	0	0%
55	control	217	94%	14	6%	0	0%
56	control	76	33%	155	67%	0	0%
57	control	228	99%	3	1%	0	0%
58	control	199	86%	32	14%	0	0%
59	control	231	100%	0	0%	0	0%
60	control	85	37%	146	63%	0	0%

Table 4. Continued.

Control #		Unvegetated Flat		Vegetation		Rock, Pebble, Debris	
62	control	166	72%	65	28%	0	0%
63	control	2	1%	229	99%	0	0%
64	control	20	9%	211	91%	0	0%
65	control	30	13%	201	87%	0	0%
66	control	0	0%	231	100%	0	0%
67	control	0	0%	231	100%	0	0%
68	control	8	3%	231	100%	0	0%
69	control	2	1%	231	100%	0	0%
71	control	53	23%	178	77%	0	0%
72	control	23	10%	208	90%	0	0%
73	control	26	11%	200	87%	5	2%
74	control	34	15%	190	82%	12	5%
76	control	47	20%	184	80%	0	0%
77	control	173	75%	58	25%	0	0%
78	control	0	0%	231	100%	0	0%
79	control	0	0%	231	100%	0	0%
80	control	227	98%	4	2%	0	0%
81	control	224	97%	5	2%	2	1%
83	control	222	96%	6	3%	3	1%
84	control	180	78%	5	2%	46	20%
85	control	231	100%	0	0%	0	0%
86	control	194	84%	37	16%	0	0%
87	control	208	90%	23	10%	0	0%
88	control	206	89%	25	11%	0	0%
\bar{X}		160.3 (s=81.4)		69.5 (s=81.8)		3.9 (s=25.1)	

Table 5. Results of Kruskal-Wallis one-way analysis of variance between control, nest, and brood sites; and Mann-Whitney U paired comparisons, for microhabitat frequencies. Asterisks denote significant differences at the 0.05 level.

<u>Results of Kruskal-Wallis one-way analysis of variance:</u>			
Microhabitat type	<i>H</i>	<i>P</i>	<i>df</i>
*Unvegetated Flat	11.7	0.003	2
*Vegetation	11.2	0.004	2
Rock, Pebbles, and/or Debris	5.3	0.070	2
<u>Results of Mann-Whitney U paired comparisons:</u>			
Microhabitat type	<i>U</i>	<i>P</i>	<i>n</i>
Unvegetated Flat			
* brood-nest	206.5	<0.0005	15
* brood-control	341.5	0.003	15
nest-control	718.0	0.587	15
Vegetation			
* brood-nest	24.5	<0.0005	15
* brood-control	914.5	0.017	15
nest-control	470.5	0.075	15
Rock, Pebbles, and/or Debris			
brood-nest	127.0	0.497	15
brood-control	748.5	0.278	15
* nest-control	845.5	0.027	15

Table 6. Phenology of pair formation and nest-building from Page et al. (1995), *with Southern Texas findings included.*

Location	Latitude (North)	Pair formation	Nest initiation
Puerto Rico	18°	January	January
Coastal Florida	25-31°	February	March
<i>Coastal Texas</i>	<i>26°</i>	<i>February</i>	<i>March</i>
Coastal California	36-37°	February	March
Coastal Washington/Oregon	46-49°	March	—
Great Basin	40°	March-April	April
Great Plains	37°	March-April	April-June

VITA

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