FINAL REPORT

SNOWY PLOVER MOVEMENT, FIDELITY, AND DYNAMICS IN THE SOUTHERN HIGH PLAINS OF TEXAS

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By

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ABSTRACT

Snowy Plovers (*Charadrius alexandrinus*) have experienced declines throughout their range in the United States and are currently listed as threatened by the U.S. Fish and Wildlife Service along the Pacific Coast and as endangered, threatened, or of special concern in several states. The primary cause for the decline of western Snowy Plovers (*C. a. nivosus*) has been attributed to poor nest success and habitat destruction. Although populations west of the Rocky Mountains have been extensively studied, few studies have focused on interior populations. Unlike coastal regions where beaches comprise the majority of nesting habitat, within the Southern High Plains (SHP) of Texas, Snowy Plovers nest primarily on edges of saline lakes. However, habitat quality of saline lakes has declined (e.g., reduced spring production), making many of them unsuitable for nesting and migrating shorebirds. Due to the declining habitat conditions within the SHP of Texas, it is important to determine the current status of Snowy Plovers within this region, as well as examine potential causes of population declines. As such, the objectives for this research were to 1) estimate nest success and evaluate factors influencing nest success, 2) determine nest site selection patterns, 3) evaluate factors influencing incubation temperatures, 4) document offspring sex ratios and evaluate factors influencing sex ratio adjustment, 5) estimate apparent survival rates, and 6) document long-term changes in populations and evaluate factors influencing regional surveys counts of Snowy Plovers nesting on saline lakes within the SHP of Texas.

Overall, 215 nests were monitored from three saline lakes in 2008 – 2009, with Mayfield estimates of nest success ranging from 7 – 33% (mean = 22%) with leading causes of failure being predation (40%) and weather (36%). Nest success was influenced by location (i.e., saline lake), as well as negatively influenced by number of plants within 707-cm^2 plot, positively influenced by percent surface water availability, and negatively influenced by time during the nesting season. When compared to estimates 10 years prior (i.e., 1998 – 1999), mean nest success within this region declined by 31%, with greater percentage of failures due to predation. These results suggest that if nesting Snowy Plovers continue to experience increased predation rates, decreased hydrological integrity, and habitat alterations, populations will continue to decline throughout this region.

Habitat variables were collected at 180 nests in 2008 – 2009. Snowy Plover nests were best classified by pebble substrate, close to an object, and with more rocks, pebbles, and objects surrounding nests (i.e., 707-cm^2 plot) than random sites. Areas of high use within saline lakes generally were located in areas with pebble substrate and on manmade or natural islands, berms, and peninsulas. These results provide some guidance for habitat conservation and management strategies within this region. Specifically, decreasing irrigation and maintaining surrounding upland areas with native vegetation could result in decreased vegetation encroachment and sand deposition on saline lakes, ultimately, positively impacting nesting habitat for Snowy Plovers within the SHP of Texas.

Incubation temperatures from 104 Snowy Plover nests located on saline lakes within the SHP of Texas were examined in relation to 1) ambient substrate temperatures, 2) annual, temporal, and spatial variation, 3) nest site selection, 4) nest success, and 5) parental quality. Nest temperatures ranged from 12.7 – 47.2°C and varied between years and lakes. Within this region, Snowy Plovers may be able to alleviate some heat stress by performing adaptive behaviors, selecting pebble substrates, and initiating nests earlier in the season. Furthermore, Snowy Plovers appear to change incubation routines as nests approach hatching, potentially facilitating hatching synchronization during early morning hours.

Sex ratios and sex allocation theory were examined for 245 chicks from 118 clutches during 1999 – 2000 and 2008 – 2009. Offspring sex ratios did not differ from parity, although were slightly male biased in the majority of years. Male offspring were more costly to produce than females, with the probability of producing a male offspring having a bimodal distribution with more males produced earlier and later in the season as compared to the middle of the season. Seasonal changes in offspring sex ratios are likely the result of differential advantages in survival and reproduction between sexes born at specific times. However, mechanisms for seasonal variation in sex ratios remains unknown as well as the effects such changes in sex ratios may have on population growth and stability.

Return rates of adult Snowy Plovers were higher in 2000, with 77% of adults banded in 1999 observed in 2000, than 2009 – 2010, with only 58% of adults observed ≥ 1 year following capture. Juvenile return rates were lower than adult return rates and were lower in 2009 – 2010 (9% of juveniles observed at least one year following capture) than 2000 (i.e., 22% of juveniles banded in 1999 observed in 2000). In 2008 – 2010, yearly adult apparent survival was similar between sexes (65%); however, encounter rates were lower for females (70%) than males (100%). Yearly juvenile apparent survival (12%) and encounter rates (62%) were lower than adults, but similar between sexes. Long-term declines in apparent survival rates may be a factor of increased mortality or dispersal due to higher predation rates, lower nest success, and/or declining habitat conditions. Sex biased apparent survival rates are likely a factor of breeding and natal site fidelity, with males having greater fidelity than females due to the relative advantages of males being familiar with habitat for resource defense and acquisition. Along with lower survival rates, Snowy Plovers within this region tend to have high breeding site fidelity, suggesting the need for regional conservation efforts. Current estimates of adult and juvenile apparent survival rates indicate that 5.8 hatchlings per adult per year are needed to maintain the current population without immigration; however, this is not physiologically possible during the short nesting season. Therefore, conservation efforts must focus upon increasing adult and juvenile survival on both breeding and wintering grounds.

From 1998 – 2010, 184 surveys were conducted with mean counts of adult Snowy Plovers declining by 55% over the last decade. Nest success and apparent survival are likely important factors for these declines, as mean nest success has declined by 31% from 1999 – 2009, and adult and juvenile apparent survival have declined by 25% and 60%, respectively. Therefore, if nest success and apparent survival remain low or continue to decline, populations will continue to decline within this region. Regional populations may also fluctuate on an annual basis due to several factors including inadequate habitat conditions (e.g., low surface water availability) and catastrophic events that result in considerable adult mortality. Despite the current causes of population declines, recovery of Snowy Plover populations within the SHP of Texas may be restricted by low immigration rates from other populations. Therefore, population declines observed in this region likely can not be offset by immigration, making conservation of local populations within the SHP of Texas extremely important. In order to properly monitor local populations and assess apparent population declines, understanding factors influencing regional survey counts can be important. In the SHP of Texas, surface water availability and time during the nesting season were the most important factors influencing the number of Snowy Plovers observed during surveys. Therefore, population estimates may vary considerably if surveys are not standardized to account for changes in these factors.

The presence of predictable surface water regimes is one of the most important landscape features affecting nesting Snowy Plovers in inland areas. The presence of water during the nesting season is essential not only for foraging on aquatic insects, but may help facilitate cooling of nests and adults (e.g., belly soaking and standing in water) during extreme temperatures. Presence of water during the nesting season in several regions including the SHP of Texas is dependent upon unpredictable weather events as well as anthropogenic factors including presence of exotic invasive plants (e.g., salt cedar [*Tamarix* spp.]) and irrigation. Therefore, it remains important to conserve freshwater springs discharging into saline lakes as well as the Ogallala aquifer. However, because the Ogallala aquifer is recharged from playa wetlands, it also remains important to conserve the entire complex of wetlands within the SHP of Texas.

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CHAPTER I

NEST SUCCESS OF SNOWY PLOVERS IN THE SOUTHERN HIGH PLAINS OF TEXAS

INTRODUCTION

Snowy Plovers (*Charadrius alexandrinus*) have experienced declines throughout their range in the United States and are currently listed as threatened by the U.S. Fish and Wildlife Service along the Pacific Coast (U.S. Fish and Wildlife Service 1993) and as endangered, threatened, or of special concern in several states including Washington, Oregon, California, Mississippi, Florida, Puerto Rico, and Kansas (see Page et al. 2009). A primary cause for the decline of western Snowy Plovers (*C. a. nivosus*) is poor nest success (U.S. Fish and Wildlife Service 1993), with nest success showing considerable regional and annual variation (i.e., 5 – 77%; Wilson-Jacobs and Meslow 1984, Hill 1985, Lee 1989, Paton and Edwards 1990, Paton 1995, Winton et al. 2000, Powell 2001, Powell et al. 2002, Conway et al. 2005a, Page et al. 2009). Nest failures are often attributed to predation (including California Gull [*Larus californicus*], Ring-billed Gull [*L. delawarensis*], Common Raven [*Corvus corax*], American Crow [*C. brachyrhynchos*], coyote [*Canis latrans*], striped skunk [*Mephitis mephitis*], raccoon [*Procyon lotor*], red fox [*Vulpes vulpes*], domestic cat [*Felis catus*], and domestic dog [*C. lupus familiaris*]), weather (e.g., hail, wind, storm tides, and rain storms), trampling (by cattle, humans, and vehicles), and human disturbance (Page et al. 2009). Theoretically, Snowy Plovers have evolved with most of these pressures and should cope with losses attributed to these risks (Wilson-Jacobs and Meslow 1984). However, if population declines are a result of poor nest success, then current causes of nest failures may be more intense, more widespread, and/or Snowy Plovers may be less efficient in overcoming poor nest success than previously assumed (Wilson-Jacobs and Meslow 1984).

Numerous factors influence avian nest success including parental condition, clutch initiation dates, and nest site selection. Egg formation is costly (i.e., energetically and physiologically), especially for precocial species (Perrins 1996). Therefore, female condition can directly influence egg and clutch size, as larger, older individuals in better condition produce larger eggs and clutches (Coulson 1963, Davis 1975, Nisbet 1978, Thomas 1983, Ricklefs 1984, Meathrel and Ryder 1987, Lequette and Weimerskirch 1990, Croxall et al. 1992, Nol et al. 1997, Amat et al. 2001b). Along with egg formation, incubation can be physiologically costly for parents. Therefore, experienced parents and/or parents in good condition should positively influence nest success and brood survival by producing larger eggs, compensating for (or withstanding) high physiological costs of incubation, occupying nest sites of better quality (i.e., lower predation risks, lower risks of destruction from weather events, and/or closer to optimal foraging areas), and/or defending nests from predation risks (Blomqvist et al. 1997).

Although factors influencing laying date will vary (e.g., food abundance, competition, weather, etc.), earlier egg laying dates typically result in greater nest success (Perrins 1996). However, if females are unable to acquire necessary food and nutrients for egg formation, they may be unable to nest at the most opportune time (Perrins 1996). A relationship may exist between Snowy Plover nest success and laying date, but results have been inconsistent. For example, some studies have found a negative relationship between laying date and survival (Hood and Dinsmore 2007), others a positive relationship (Powell 2001, Conway et al. 2005a), and some have reported a bimodal effect with a clear decline in nest success in the middle of the breeding season (Page et al. 1983, Norte and Ramos 2004). However, inconsistencies among studies may be a factor of unpredictable causes of nest failures such as weather events (Norte and Ramos 2004, Conway et al. 2005a), as well as regional variability in predator communities and predation pressures.

Selection of nest sites is a key mechanism by which birds reduce risks to both nest contents and themselves during incubation. Because most Snowy Plover nest failures are a result of predation or weather events (Page et al. 2009), nest site characteristics and selection should mitigate risks associated with nest failures, and provide appropriate microclimate for incubation (Amat and Masero 2004b; see Chapter III). For example, amount and type of objects surrounding nests (Page et al. 1985, Norte and Ramos 2004, Hood and Dinsmore 2007), amount of cover surrounding nests (Amat and Masero 2004b, Norte and Ramos 2004, Hood and Dinsmore 2007), substrate type (Hill 1985, Page et al. 1985, Colwell et al. 2005), distance to upland areas (Koenen et al. 1996a), and degree of clustering with conspecific and nonconspecific nests (Hill 1985, Burger 1987, Powell 2001, Norte and Ramos 2004) should influence Snowy Plover nest success. However, nest site selection is often juxtaposed among potential benefits (e.g., predator avoidance, crypsis, safety from weather events, and temperature control). For example, selection of nest sites with greater vegetation cover may provide a less stressful thermal climate (i.e., due to shading), but increase predation risks due to reduced ability to detect approaching predators by incubating adults (Amat and Masero 2004b).

Along with poor nest success, habitat degradation is also a primary cause for the decline of western Snowy Plovers (U.S. Fish and Wildlife Service 1993). Unlike coastal regions where beaches comprise the majority of nesting habitat, within the Southern High Plains (SHP) of Texas, Snowy Plovers nest primarily on edges of saline lakes (Conway et al. 2005a). Saline lakes within the SHP of Texas are of continental importance to nesting Snowy Plovers, as a large proportion of the interior population nest within as well as migrate through this region (Conway 2001, Conway et al. 2005a). However, habitat quality of saline lakes has declined, making many of them unsuitable for migrating (Andrei et al. 2008) and nesting shorebirds. Because saline lakes within this semi-arid region are discharge wetlands containing springs fed by the Ogallala aquifer, historically many provided reliable freshwater during the breeding season (Brune 2002). However, declining spring flow due to decreasing water table levels of the aquifer has occurred since the 1950s (Brune 2002), resulting in shortened hydroperiods and increased salinity. Groundwater removal for irrigation during the breeding season can exacerbate these effects during crucial times when nesting Snowy Plovers rely on freshwater from saline lake springs (Conway et al. 2005a). Freshwater springs not only provide reliable surface water during the breeding season, a necessary landscape feature for nesting Snowy Plovers (Conway et al. 2005b), but also support salt intolerant invertebrate prey (Andrei et al. 2009). Due to these declining habitat conditions within the SHP of Texas, it is important to determine the current status of Snowy Plovers within this region, as well as examine potential causes of population declines. Therefore, the objectives of this study were to 1) estimate nest success, 2) determine timing and causes of nest failures, 3) evaluate potential factors (e.g., time during nesting season, year, lake, nest age, parental condition, distance to nearest active nest, surface water availability, and habitat variables) affecting nest success, and 4) determine associations between measures of Snowy Plover quality (i.e., egg volume, chick body mass, and parental body mass) and year, lake, nest initiation date, and surface water availability within the SHP of Texas.

METHODS

Study Area

The SHP is an approximately 80,000 km^2 region occurring from the panhandle of Texas, into New Mexico, and south to Midland, Texas (Osterkamp and Wood 1987). Within this region, approximately 40 saline lakes (i.e., primary regional nesting location for Snowy Plovers; Conway et al. 2005a) occur (Reeves and Temple 1986). Saline lakes are discharge wetlands containing freshwater springs fed by the Ogallala aquifer (Brune 2002), but having an overall saline water chemistry (often > 200g/L of dissolved solids; Osterkamp and Wood 1987). Three previously identified important (i.e., having consistent surface water throughout the nesting season and containing the majority of regional nesting Snowy Plovers) saline lakes (Conway et al. 2005a) ranging in size from ~ 270 – 600 ha were used as study sites in 2008 and 2009 (Figure 1.1). To maintain landowner anonymity, study site lakes will be referred to as lake A, lake B, and lake C. Each study site lake contained two – six fresh to slightly saline springs distributed along lake margins (Brune 2002). The primary landuse practice immediately surrounding study site lakes was pasture/rangeland with some held within the Conservation Reserve/Permanent Cover Program. Other landuse practices occurring within surrounding areas included row-crop agriculture production (i.e., mostly cotton

[*Gossypium* spp.]), mineral excavation (e.g., caliche), and development (i.e., mostly small home/ranch developments).

Nest Surveys

Surveys were conducted ≥ 1 time per week at each lake during the breeding season (i.e., early April – mid August; Conway et al. 2005a) in 2008 – 2009 to locate new nests and/or scrapes or monitor known nests until nest fate was determined. Nests were located by observing adult Snowy Plovers incubating nests, flushing from or returning to nest sites, and searching appropriate habitat (Conway et al. 2005a). If a nest was discovered with one egg, it was assumed that the nest was initiated the day of discovery; however if nests were discovered with two eggs, it was assumed that the nest was initiated the day prior to discovery. If nests were located after all three eggs (modal clutch size) were laid, eggs were floated to determine incubation stage (Hays and LeCroy 1971). Once located, 120 GPS positions were obtained per nest using a Trimble GeoXH GPS unit (Trimble Navigation Ltd, Sunnyvale, CA) and length (mm) and breadth (mm) of all eggs were measured with calipers (Coulson 1963). Egg volume (V_e; a measure of parental quality) was calculated similar to Amat et al. (2001a) using the equation $V_e = K_vLW^2$, where K_v corrects for variation in egg shape and is calculated by $K_v = 0.5236 - [0.5236*2(L/W)/100]$, with L = egg length (cm) and W = egg width (cm).

Nests were checked ≥ 1 time per week until nest fate was determined. A successful nest was defined as a nest in which ≥ 1 egg hatched (Mayfield 1975). Evidence of hatching included visually locating chicks in/near nest, breeding pair displaying distraction displays, and/or presence of egg shell fragments indicative of hatching (i.e., < 1 mm shell fragments found in scrape and/or top or bottom of egg shell located < 10 m from nest with membrane detached; Mabee 1997). Nests were considered failed when 1) eggs were absent prior to estimated hatching date, 2) presence of signs of predation or trampling, 3) evidence suggested nests were destroyed by weather (i.e., hail, wind, flooding, etc.), or 4) evidence suggested abandonment (i.e., eggs were present one week after estimated hatching date or when one egg was moved such that the smaller end pointed up and remained for > 24 hrs). If nest fate did not match these definitions, fate was classified as unknown (Manolis et al. 2000).

During weekly surveys, ocular estimates of percent dry ground, wet mud (areas wet from spring flow rather than rainwater), shallow water (1 – 5 cm deep; shallow enough for wading Snowy Plover), medium water (5 – 15 cm deep; too deep for wading Snowy Plover, but shallow enough for wading American Avocet [*Recurvirostra americana*]), and deep water (> 15 cm deep; too deep for wading American Avocet) were recorded to determine availability of surface water for nesting plovers throughout the breeding season. Specifically, during weekly surveys, locations of above categories were drawn on 2004 NAIP digital orthophoto quarter-quadrangle (DOQQ) aerial photographs (Texas Natural Resources Information System 2004) to estimate percent composition. To obtain total surface water availability, percent wet mud, shallow water, medium water, and deep water were summed for each survey. Mean percent surface water availability was then determined for each nest during the time the nest was active (i.e., from time first egg was laid until hatching or failure).

Capture and Handling

Adult Snowy Plovers were captured on nests using nest traps (Conway and Smith 2000) from early April – early August, 2008 and 2009. Adults were sexed in the field based upon plumage characteristics, where males generally have larger and darker breast and forehead patches as compared to females. All adults were banded with a uniquely numbered U.S. Fish and Wildlife Service aluminum band on the upper part (i.e., tibiotarsus) of their left leg, a dark green color band on the upper part of their right leg, and a unique combination of two color bands on both right and left lower legs. Upon capture, body mass (g) and the following morphological characteristics were measured for each adult (see Pyle et al. 1987 for descriptions): wing chord (mm), flattened wing chord (mm), tarsus (mm), tail (mm), culmen (mm), bill depth (mm), bill width (mm), and head length (mm). Mass was measured to the nearest 0.1 g with a digital scale (Ohaus® Scout Pro Balance, Pine Brook, NJ). Wing chord and flattened wing chord length were measured with a wing rule from the carpal joint to the tip of the longest primary, with wings pressed flat against a ruler for flattened wing chord measurement. Tarsus length was measured with calipers from the intertarsal joint to the distal end of the last leg scale. Tail length was measured with a ruler parallel to the tail from the point of insertion to the tip of tail. Culmen, bill length, bill width, and head length were measured with calipers. Culmen was measured from the anterior end of the nostril to the tip of bill, bill depth from the anterior end of the nostrils to the lower mandible perpendicular to the bill length measurement, bill width perpendicular to the bill length measurement at the anterior end of the nostrils, and head length from the back to the front of the head.

Snowy Plover chicks were captured by hand in nests at hatching. The same handling techniques as adults were used for chicks, where each bird was banded with a U.S. Fish and Wildlife Service aluminum band on the left upper leg, a dark green color band on right upper leg, and a unique combination of color bands on the lower legs. The same morphological characteristics as adults were also measured.

Nest Habitat Measurements

After nest fate was determined, the following habitat characteristics were recorded at nest sites: primary nest substrate (i.e., sand or pebble), height of (cm) and distance to (cm) nearby (i.e., generally < 12.5 cm) objects (e.g., rocks, pebbles, woody debris, plants, etc.), and distance to and average height of surrounding objects. In some instances, no object was located near nests. In these instances, 0 cm was used as the average height of surrounding objects and 50 cm (i.e., slightly longer than longest distance measured to nearest object [40.5 cm]) was used as the distance to nearest object. A 30-cm diameter hoop (707 cm^2) was also centered on each nest and two photographs of each nest were taken with a Canon Digital Rebel XT SLR equipped with a Canon EF 50 mm compact macro standard auto focusing lens, mounted on a tripod, kept at the same height (i.e., 126 cm from ground to top of camera), focal length, and aperture. From pictures, all rocks (i.e., > 8 cm), pebbles (i.e., < 8 cm; includes gypsum), plant stems, woody debris, and other objects (i.e., cow feces, feathers and bones, clumps of dirt, and manmade objects) were counted within the 707-cm^2 plot. Because parents often bring additional objects (e.g., pebbles) into the nest scrape (Page et al. 2009), objects located within the nest scrape were not counted.

All GPS positions were differentially corrected using GPS Pathfinder Office software (Trimble Navigation Ltd, Sunnyvale, CA) from six base stations and averaged to obtain one position for each nest. The differentially corrected positions were imported into ArcGIS 9.2 (ESRI, Redlands, CA) and mapped. Distance (m) to nearest upland was calculated using Euclidian distance to nearest upland edge, where upland boundaries were digitized using 2004 NAIP digital orthophoto quarter-quadrangle (DOQQ) aerial photographs (Texas Natural Resources Information System 2004). Distance (m) to nearest active (i.e., day first egg was laid to day hatched or failed) nest was determined using Hawth's Analysis Tools (Beyer 2004).

DATA ANALYSIS

Condition Indices

To calculate an index of parental body condition, a measure of body size was first derived using principal component analysis (PCA) to determine the first principal component corresponding to measurements explaining the majority of the variability in size (PROC PRINCOMP; SAS Institute 2002). To derive an index of body condition, the residuals of a regression of body mass on the first principal component scores were used (similar to Amat et al. 2001a). Due to low sample sizes within a specific sex and little variability between sexes, when more than one putative parent was captured from a given nest, the mean body mass and body condition index for both parents was used for analyses.

To determine if measures of quality (i.e., egg volume, parental body mass, parental body condition index, and chick body mass) varied among lakes and between years, a repeated measures analysis of variance (ANOVA; repeated among nests) with a compound symmetric covariance structure (PROC MIXED; SAS Institute 2002) was used for egg volume and chick body mass. An ANOVA (PROC GLM; SAS Institute 2002) was used for parental body mass, as only one measurement for parental body mass was obtained per nest. A Pearson correlation analysis (PROC CORR; SAS Institute

2002) was used to examine potential associations between mean egg volume for clutch and 1) Julian date of first egg laid, 2) percent surface water available the week eggs were laid for a given clutch, and 3) percent surface water available the week before eggs were laid for a given clutch. A Pearson correlation analysis was also used to examine potential associations between mean parental body mass and 1) mean egg volume for clutch and 2) Julian date of first egg laid.

Nest Success

Apparent nest success was determined for each year and lake separately using a standard proportion (i.e., number of successful nests divided by total number of nests). Differences in apparent nest success between years for each lake were examined using Chi-square analysis (PROC FREQ; SAS Institute 2002). The Mayfield Method (Mayfield 1975) in Program MARK (Dinsmore et al. 2002) was used to estimate nest success for each year and lake separately. A 30-day incubation period (mean incubation period of nests [i.e., from first egg laid until first egg hatched] with known egg laying date = 29.54 days) was used when calculating Mayfield estimates of nest success from daily survival rates. The delta method was used (Seber 1982) to estimate variances of nest success (from standard errors for daily survival rates given in Program MARK), as the Mayfield estimate is a transformed variable (i.e., daily nest survival extrapolated to a 30-day incubation period). In some instances, nests were found the day of hatching, or after nest failure (e.g., nest scrape found with crushed egg shells). Because the number of exposure days in both instances was zero, these nests were not included in Mayfield estimates of nest success. However, these nests were included in estimates of apparent nest success.

Nest Survival Analysis

The Mayfield Method (Mayfield 1975) in Program MARK (Dinsmore et al. 2002) was used to examine the influence of temporal (e.g., year, time during nesting season, and age of nest), spatial (e.g., lake and distance to nearest active nest), condition (e.g., egg volume), and habitat variables on nest success. Daily nest survival was modeled with a set of 85 *a priori* candidate models including a linear time trend (i.e., linear relationship between daily nest survival and day during the nesting season; Cooch and White 2002, Dinsmore et al. 2002), nest age (i.e., number of days since first egg laid; Cooch and White 2002, Dinsmore et al. 2002), year, lake, mean egg volume per nest, distance to nearest active nest, mean surface water available during time nest was active (i.e., date first egg laid to hatching or failure), distance to upland, average height of surrounding objects, distance to nearest object, substrate type (i.e., sand or pebble), and total number of objects as well as number of pebbles/rocks, plants, woody debris, feathers/bones and other objects (i.e., manmade objects, cow feces, and clumps of dirt) within 707-cm^2 plot. Correlated variables ($P \leq 0.05$) were not permitted to enter the same model. In instances where there were missing covariate data for a given nest, population means were used (Cooch and White 2002). Akaike's Information Criterion corrected for small sample size (AIC_c) was used to rank models (a model was considered plausible when $\Delta AIC_c < 2$; Burnham and Anderson 2002) and calculate AIC_c weights. Parameter likelihoods were determined using model averaging (i.e., sum of model weights for models that included a given parameter; Burnham and Anderson 2004). However, parameter estimates, standard errors, and 95% confidence intervals were presented from the top-ranked models.

RESULTS

Condition Indices

There was low variability among individuals in body size measurements and the first principle component score had poor predictive power of body mass ($R^2 = 0.065$). Therefore, parental body condition was not used in the following analyses, but parental body mass was used as a surrogate for parental condition. Egg volume and chick body mass were similar among lakes ($P > 0.05$); however, parental body mass at lake C was lower than lake A ($P = 0.017$; Table 1.1). Chick body mass and parental body mass were similar between 2008 and 2009 ($P > 0.05$); however, egg volume was lower in 2008 than 2009 ($P = 0.017$; Table 1.2).

Julian date was negatively correlated ($r = -0.25$; $P = 0.038$) with parental body mass, but not correlated ($P > 0.05$) with egg volume. Percent surface water available the week eggs were laid and the week before eggs were laid were not correlated ($P > 0.05$) with mean egg volume. Mean parental body mass was not correlated ($P > 0.05$) with mean egg volume of clutch.

Nest Success

In this study, 215 Snowy Plover nests were located, of which 44 were located at lake A (15 in 2008 and 29 in 2009), 125 at lake B (47 in 2008 and 78 in 2009), and 46 at lake C (24 in 2008 and 22 in 2009). A 112-day nesting season was estimated from 16 April – 5 August (i.e., day first nest discovered to day last nest hatched or failed). The most common cause of nest failure was predation by mammalian and avian predators (40.4%), followed by weather events that hailed, flooded, blew out, cracked, and/or silted in eggs (36.3%; Table 1.3). Although relatively minor, other causes of nest failure included unknown causes, abandonment, trampling by cattle, vehicles, and humans, and unviable eggs (23.3%; Table 1.3). Fate could not be determined for < 4% (*n* = 8) of all nests. Removing unknown fates can result in extreme bias of nest success estimates; therefore, nests with unknown fates were treated as failures in nest success estimates (Manolis et al. 2000). Two nests failed at lake B due to capture myopathy of parent; therefore, 213 nests were used for apparent nest success analyses. Apparent nest success ranged from 8 – 41% (Table 1.3), but never varied between 2008 and 2009 at lake A (χ^2 = 0.92; df = 1; *P* = 0.336), lake B (χ^2 = 0.1.65; df = 1; *P* = 0.199), or lake C (χ^2 = 0.98; df = 1; *P* = 0.322; Table 1.3). Of these 213 nests, one was found the day of hatching and seven were found after nest failure. Therefore, 205 nests (44 at lake A, 116 at lake B, and 45 at lake C) were used for Mayfield estimates (Table 1.3) and nest survival analysis.

Mayfield estimates of nest success ranged from 7 – 33% among lakes, with mean nest success being 22.1% for all lakes and years (Table 1.3).

Nest Survival Analysis

Among 85 candidate models (see Table 1.4 for means and standard errors of variables entered into models by nest fate), the first four models were considered plausible (i.e., $\Delta AIC_c < 2$; Table 1.5). These models indicate that daily survival rates of Snowy Plover nests varied among lakes and with number of plants within 707-cm^2 plot, percent surface water available during incubation, time during the nesting season (i.e., linear time trend), and distance to nearest object (Table 1.6). Parameter likelihoods also indicated that percent surface water available during incubation (likelihood = 0.81), number of plants within 707-cm^2 plot (likelihood = 0.54), the interaction between linear time trend and lake (likelihood = 0.38), the interaction between number plants within 707-cm^2 plot and lake (likelihood = 0.21), and the interaction between distance to nearest object and lake (likelihood = 0.15) were the most important variables included in the top-ranked models. For all four top-ranked models (Table 1.6), a negative relationship existed between nest daily survival rate and number of plants within 707-cm^2 plot (Figure 1.2), but daily survival rate was positively related to percent surface water available during incubation (Figure 1.3). Within the top-ranked model, nest daily survival rates were positively influenced by time during the season (i.e., linear time trend) at lake A, but negatively influenced at lakes B and C, although the 95% confidence intervals about the beta coefficient overlapped zero for lakes A and B (Figure 1.4, Table 1.6). Within the second ranked model, nest daily survival rates were negatively influenced by number of plants within 707-cm^2 plots at all lakes; however, the 95% confidence intervals included zero at lakes A and C (Figure 1.5, Table 1.6). Within the third-ranked model, nest daily survival rates were positively influenced by distance to nearest object at lakes B and C, but negatively influenced at lake A; however, the 95% confidence intervals included zero at all lakes (Figure 1.6, Table 1.6).

DISCUSSION

Mayfield estimates of nest success for Snowy Plovers in the SHP of Texas ranged from 7 – 33% depending upon lake, of which the majority of failures were attributed to predation by both mammalian and avian predators (i.e., 33 – 56% of total failures) and weather events (i.e., 19 – 46% of total failures). These estimates were generally within the range of nest success estimates from previous studies in the SHP of Texas (i.e., 30 – 34%; Conway et al. 2005a), Great Salt Lake, Utah (26 – 37%: Paton and Edwards 1990, 5 – 49%: Paton 1995), Salt Plains National Wildlife Refuge, Oklahoma (17 – 60%: Hill 1985), and Oregon (13%: Wilson-Jacobs and Meslow 1984), but lower than studies from California (50%: Powell 2001, 36 – 77%: Powell et al. 2002), Salt Plains National Wildlife Refuge, Oklahoma (37 – 58%: Winton et al. 2000), and Puerto Rico (61 – 73%: Lee 1989). Across all lakes and both years, the mean Mayfield estimate of nest success was 22.1%. Although the range of current nest success estimates were similar to estimates obtained 10 years prior on the SHP of Texas (Conway et al. 2005a), mean nest success has declined by 31%.

Yearly variation in nest success is not unexpected, as nest success within this region is influenced by unpredictable weather events, variation in hydroperiod, and/or climatic conditions (Conway et al. 2005a). For example, during both years of this study, drought conditions existed, with cumulative rainfall in the city of Tahoka (Lynn County, Texas) from January – July 2008 and 2009 estimated at 10.5 cm and 19.9 cm below the long-term average, respectively (National Climate Data Center; http://cdo.ncdc.noaa.gov). However, drought conditions were also present in a year of the previous study (i.e., cumulative rainfall was 11.8 cm below average and 7.1 cm above average in 1998 and 1999, respectively) and did not affect yearly nest success estimates (data obtained from the National Climate Data Center; http://cdo.ncdc.noaa.gov). Similarly, little variation in nest success estimates occurred between years in this study, suggesting that dramatic yearly variation may not exist in this population. Therefore, the decline in nest success as compared to 10 years prior likely is not the result of annual variation, but may be indicative of long-term regional nest success declines.

The higher rate of nest failure in this study as compared to 10 years prior may be attributed to greater predation rates, which increased from 27% to 40% between studies. Greater predation rates can be the result of numerous factors including changes in habitat characteristics, decreased densities of alternate prey species, increased predator densities, increased predation pressure, and/or presence of new predator species. The main predators observed in this study were coyote, feral dog, raven (*Corvus* spp.), and Black-crowned Night Heron (*Nycticorax nycticorax*). In the previous study, however, no avian predators (Conway et al. 2005a) or feral dogs (W. Conway per. com.) were documented on saline lakes during the breeding season. Although Chihuahuan Ravens (*C. cryptoleucus*) have historically wintered throughout the SHP of Texas (Bednarz and Raitt

2002), few individuals were documented breeding within this region (Sauer 2008). However, both Common and Chihuahuan Ravens have experienced population increases and range expansions (Boarman and Heinrich 1999, Bednarz and Raitt 2002), and currently, more individuals have been documented in the breeding season within the SHP of Texas (Sauer 2008). Although causes of raven breeding range expansion in the SHP of Texas during the last 10 years are difficult to determine, potential factors may include reduction in West Nile virus (resulting in higher survival and population increases) and anthropogenic factors (e.g., increased nesting habitat due to woody vegetation encroachment as well as additional anthropogenic food sources). In other regions (i.e., California, Oklahoma, Oregon, Utah), avian predators, including ravens, American Crows, and gulls (*Larus* spp.) are important Snowy Plover egg and chick predators (Page et al. 1983, Wilson-Jacobs and Meslow 1984, Paton 1995, Koenen et al. 1996b, Winton et al. 2000, Powell et al. 2002) and can have dramatic impacts on nest success. For example, in Oregon, 30% of all nest failures were caused by corvid predation (Wilson-Jacobs and Meslow 1984). Therefore, if raven and other predator (e.g., feral dog) populations continue to increase, nest success will continue to decline.

The second major cause of nest failures (36.3%) was due to weather events (i.e., wind, flooding, and hail). While these events tend to be unpredictable during the nesting season, similar weather-related failure rates were observed in the previous study (i.e., 44.5%; Conway et al. 2005a). However, the importance of weather events as a source of nest failures varies regionally and has been identified as important in Oklahoma (Grover and Knopf 1982, Winton et al. 2000) and Texas (45%: Conway et al. 2005a), but not important in California (4%: Warriner et al. 1986, < 10%: Powell et al. 2002), Oregon (16%: Wilson-Jacobs and Meslow 1984), or Utah (14%: Paton 1995). Regional differences in nest failures due to weather are likely a factor of severity of weather events, where probability of occurrence of severe hail storms is much greater within the mid-continental U.S. than elsewhere (Schaefer et al. 2004). Such violent precipitation events can result not only in nest failures, but also mortality of incubating adults (W. Conway per. com.), potentially exacerbating population growth rate declines (see Chapter VI). Despite the negative effects, precipitation during the nesting season is required to provide surface water, a necessary landscape feature for nesting Snowy Plovers (Conway et al. 2005b). Furthermore, Snowy Plovers likely evolved with unpredictable weather patterns; therefore, current declines are likely not the result of nest failures due to weather events, but may exacerbate poor nesting success or failure rates of a numerically smaller population (see Chapter VI). Current climate change models for the SHP of Texas suggest drier summers and more severe and frequent extreme weather events as the result of global warming (Matthews 2008). With such changes, nest failures due to severe weather events could increase within this region, exacerbating current declines of Snowy Plovers.

Several other causes of nest failures were documented including trampling (by cattle, humans, and vehicles), abandonment, and unviability. Although only contributing to a small percentage of nest failures, any additional causes of nest failure beyond predation and weather will negatively impact population stability (see Chapter VI). In this study, fewer nest failures were due to abandonment and unviability (8.2%) as compared to the previous study (19.2%; Conway et al. 2005a). Abandonment would be expected in instances when parents must focus upon self sustainment rather than incubation behaviors (Amat and Masero 2004a). Therefore, abandonment would be expected during times of low food availability, high thermal stress, or low surface water availability. For example, Kentish Plovers (*Charadrius alexandrinus*) are more likely to abandon nests during heat waves (i.e., maximum daily air temperature > 45°C) when nests are located further from water (Amat and Masero 2004a). Because drought conditions were present in both studies, this is not likely a driving factor in abandonment rates; therefore, causes of decreased frequency of abandonment remains unknown.

Nest success was variable among lakes, with lower estimates obtained from lake C (i.e., 7 – 18%). Therefore, it may be particularly important to estimate saline lake-specific nest success, as assuming all lakes have similar nest success is apparently misguided and inaccurate. Within lake, nest success was consistent between years, indicating lake-specific mechanisms influencing nest success. Several factors could affect nest success within each lake; however, the most likely cause was increased predation rates at lake C. For example, at lake C, 43% of nests were predated, as compared to only 23 – 25% at lakes A and B. Although causes of increased predation rates at this lake are unknown, increased predator densities, increased predation pressure, and presence of more predator species likely contribute to poor nest success. For example, at lake C, more mammalian predators (i.e., coyotes and feral dogs) were using lake bottoms, as tracks were observed more frequently than at other lakes (S. Saalfeld per. obs.). Ravens were also observed more frequently at lake C than other lakes, and were nesting in upland areas bordering this lake as well (S. Saalfeld per. obs.). Therefore, the presence of additional predator species and increased predation pressure could dramatically increase predation rates within this lake.

Individual saline lake structure and/or location within the landscape may also influence predation rates at lake C as compared to other lakes, resulting in greater efficiency of predators to locate and approach nests undetected. For example, at lake C, the majority of nesting habitat was located within a narrow strip between the average high water mark and upland areas (see Chapter II for map). By nesting closer to upland areas, predation rates may increase (Koenen et al. 1996a), as predators are able to find and approach nests more easily than areas located further from upland areas or in areas with natural barriers (e.g., islands). Also, most nests located at lake C were placed on sand substrate (see Chapter II), which tend to have higher predation rates than those placed on heterogeneous substrates (i.e., pebble) that are more camouflaged (Bowman and Harris 1980, Colwell et al. 2005). Therefore, increased predation rates, nesting habitat in close proximity to upland areas, and predominance of sand substrate likely resulted in lower nest success at lake C as compared to other lakes.

In many avian species, earlier nesting results in increased nest success (Perrins 1996); however, inconsistent relationships (e.g., positive and bimodal) have been observed in Snowy Plovers (Page et al. 1983, Powell 2001, Norte and Ramos 2004, Conway et al. 2005a, Hood and Dinsmore 2007). Time during the season had variable effects on nest survival depending upon individual saline lake, where time during the nesting season had little effect on daily survival rates of nests at two lakes, but at lake C, daily survival rates dramatically declined over time. The mechanisms controlling these fluctuations likely vary and are difficult to isolate. However, in regions where weather is an important cause of nest failures, timing of weather events can impact timing of nest failures. For example, Norte and Ramos (2004) detected greater Kentish Plover nest success rates in early and late periods of the nesting season than the middle period and attributed those differences to flooding events that destroyed nests in the middle period. Similarly, within the SHP of Texas, Conway et al. (2005a) found greater nest success later in the breeding season, as devastating weather events occurred earlier in the season (W. Conway per. com.). However, such localized weather events are unpredictable and provide inconsistent pressure on nest success from year to year. For example, in this study, devastating weather events (i.e., flooding and hail) occurred later in the season at lake C, causing daily survival rates to decline as the season progressed.

Snowy Plover nest success was negatively influenced by the presence of plants near nests, as few nests (i.e., 21; 10.7%) were placed near plants (mostly near inland salt grass [*Distichlis spicata*]), and only three successfully hatched. Previous studies examining relationships between nest success and vegetative cover in ground nesting shorebirds have shown mixed results (Prindiville Gaines and Ryan 1988, Colwell 1992, Koenen et al. 1996a, Mabee and Estelle 2000, Hood and Dinsmore 2007), perhaps due to regional differences in predator communities and behavioral responses to predators among prey species (Mabee and Estelle 2000). Most Snowy Plover nest sites are located adjacent to objects (e.g., rocks, woody debris, etc.; see Chapter II) potentially due to the advantages of disruptive effects (Page et al. 1985, Flemming et al. 1992), temperature control, and safety from weather events. Snowy Plovers may select nest sites adjacent to plants for similar reasons as well as benefits due to shading (e.g., smaller temperature fluctuations; Amat and Masero 2004b). However, incubating adults may be more susceptible to predation while incubating nests near plants because of poorer detectability of approaching predators (Amat and Masero 2004b). In regions where predation occurs primarily from mammals (locating nests by scent or happenstance), Snowy Plover nests with greater vegetation cover are likely more susceptible to predation (Page et al. 1983). As plovers have both cryptic plumage (Graul 1973) and eggs (Nguyen et al. 2007), nests may be placed in more open areas with greater visibility (Götmark et al. 1995), where adults rely upon cryptic concealment to avoid detection and predation (Graul 1973). Nests placed in the open, further from upland areas were typically more successful, as incubating adults likely detected approaching predators earlier, retreated from nests earlier, and performed distraction displays (Amat and Masero 2004b). Therefore, incubating adults may be better able to protect nests in open areas by relying on crypsis of eggs for predation avoidance while simultaneously distracting predators from nest locations.

Beyond behavioral adaptations to avoid predation, saline lake surface water availability is the most important landscape feature affecting nesting Snowy Plovers in inland areas. In Oregon and Nevada, Herman et al. (1988) concluded that the most serious threats to nesting habitat were diversion of water for irrigation, high water conditions, and potentially lowered water levels from geothermal development. Similarly, in this study, daily survival rates of Snowy Plover nests increased as percent surface water available increased during incubation. Therefore, Snowy Plovers likely use the presence, or amount, of surface water to cue nest initiation and begin egg laying (Figures 1.7, 1.8). Surface water during the nesting season is essential not only for foraging on aquatic insects, but may help facilitate cooling of nests and adults (e.g., belly soaking and standing in water) during extreme temperatures (Maclean 1975, Kainady and Al-Dabbagh 1976, Purdue 1976, Amat and Masero 2009; see Chapter III). Therefore, if surface water is absent or is far from nesting locations, incubating adults may be more likely to abandon nests during times of extreme heat (Amat and Masero 2004a).

Presence of surface water on saline lakes during the nesting season in the SHP of Texas is dependent upon faltering spring flow, unpredictable weather events, presence of exotic invasive plants (e.g., salt cedar [*Tamarix* spp.]), and irrigation for row-crop agriculture. Presence of salt cedar in and on the margins of regional saline lakes can have dramatic impacts on surface water presence; especially during the nesting season when ambient temperatures are high (see Chapter III). Mature stands of salt cedar use large volumes of water (e.g., annual water consumption estimated 4 – 32 million L/ha; U.S.

Bureau of Reclamation 1992), especially during summer (Sala et al. 1996), reducing both surface and groundwater levels. Therefore, salt cedar encroachment in saline lakes, especially near freshwater springs is dramatically impacting nesting habitat for Snowy Plovers by reducing surface water availability during the nesting season. Along with water availability, salt cedar may also provide nesting and roosting habitat for avian predators (e.g., ravens). Therefore, to conserve subsurface and surface water in saline lakes as well as reduce habitat for avian predators, salt cedar should be removed from areas surrounding lakes, and especially near freshwater springs.

Irrigation can also impact surface water availability. It was suggested that crop irrigation in the upstream reaches of the Platte River has contributed to declines in annual flow, ultimately negatively affecting (e.g., increased vegetation encroachment) Piping Plover (*Charadrius melodus*) and Least Tern (*Sternula antillarum*) nest sites in Nebraska (Faanes 1983). Similarly, irrigation has affected Snowy Plovers nesting on saline lakes in the SHP of Texas. Because these lakes have a direct input from springs connected to the Ogallala Aquifer (Brune 2002), crop irrigation relying on the same aquifer during the nesting season has decreased the amount of freshwater input from functioning springs into saline lakes and resulted in permanent drying of most springs in saline lakes within this region (Conway et al. 2005a). Therefore, it remains important to conserve freshwater springs discharging into saline lakes as well as the Ogallala aquifer. However, because the Ogallala aquifer is recharged from playa wetlands (Osterkamp and Wood 1987, Bolen et al. 1989), it also remains important to conserve the entire complex of wetlands within the SHP of Texas (Andrei et al. 2008, Andrei et al. 2009).

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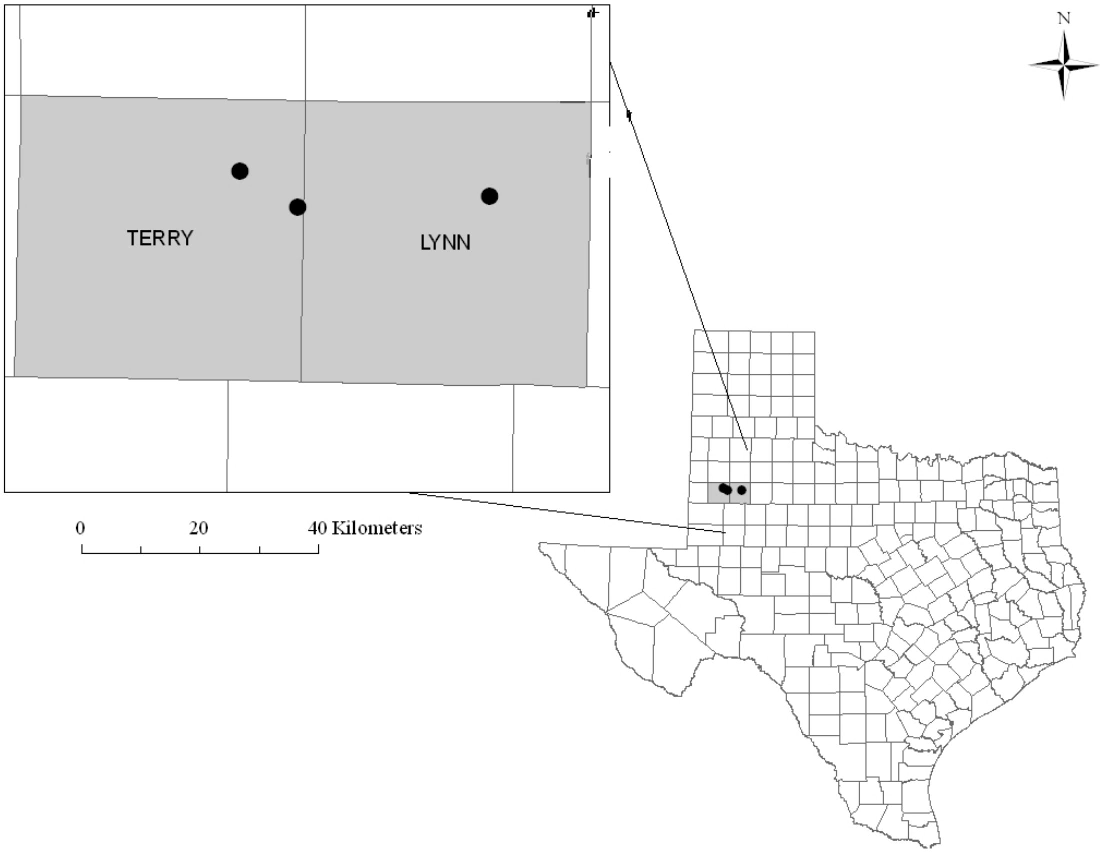

Figure 1.1. Location of saline lake study sites used to examine Snowy Plover breeding ecology within the Southern High Plains of Texas, USA, 2008 – 2009.

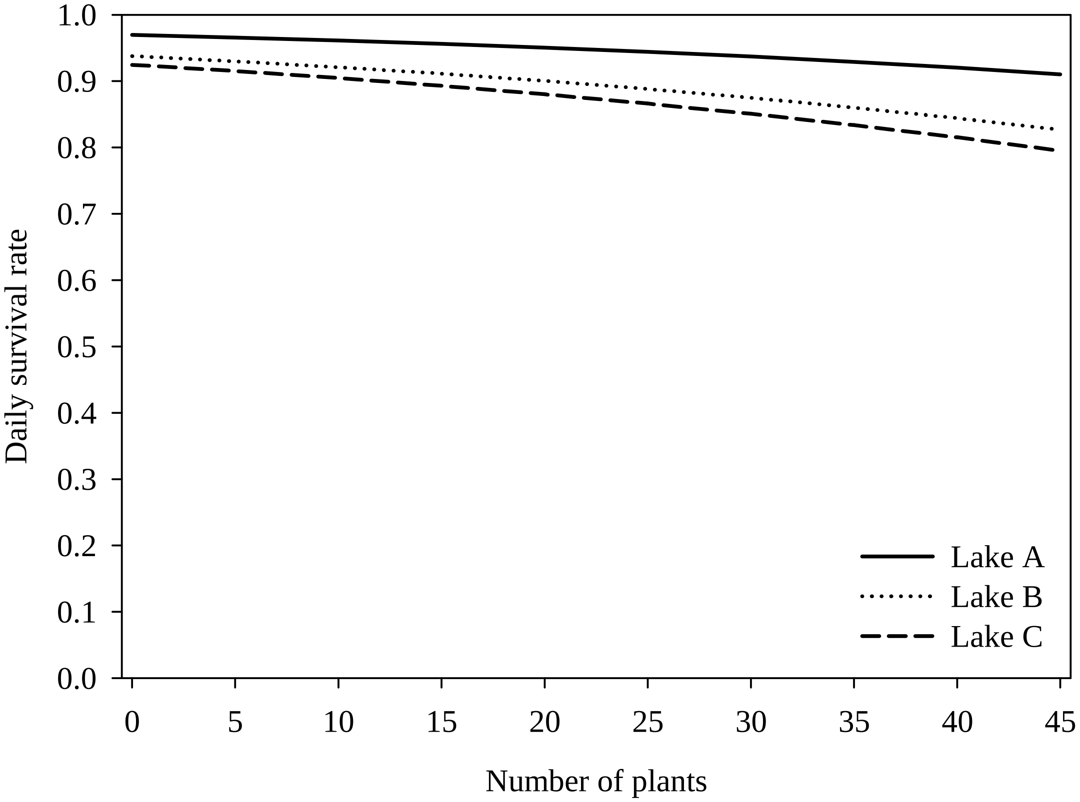

Figure 1.2. The effects of lake and number of plants within 707-cm^2 plot from model = S (linear time trend*lake + percent surface water + no. plants) on daily survival rates of Snowy Plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. To illustrate the relationship between nest daily survival rates and number of plants, time during the nesting season (i.e., linear time trend) and percent surface water were held constant at their mean values (i.e., 56 [10 June] and 50%, respectively).

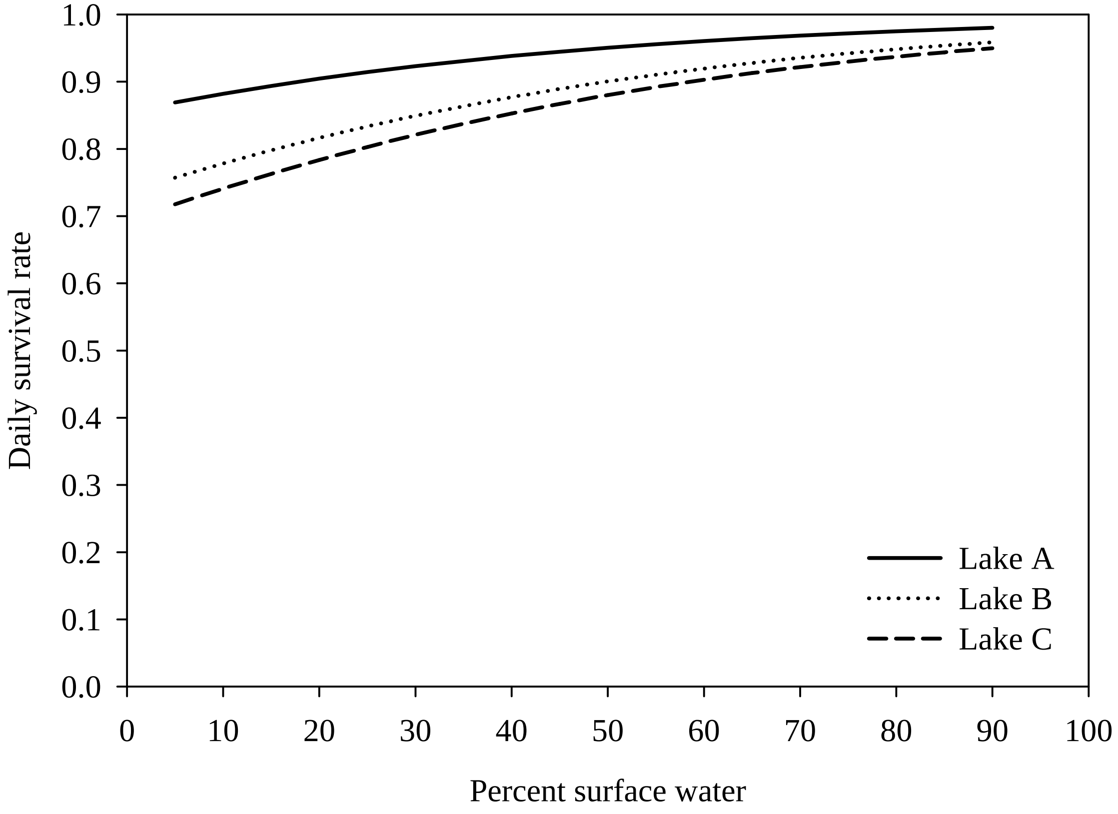

Figure 1.3. The effects of lake and percent surface water from model = S (linear time trend*lake + percent surface water + no. plants) on daily survival rates of Snowy Plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. To illustrate the relationship between nest daily survival rates and percent surface water availability, time during the nesting season (i.e., linear time trend) and number of plants within 707-cm^2 plot were held constant at their mean values (i.e., 56 [10 June] and 20, respectively).

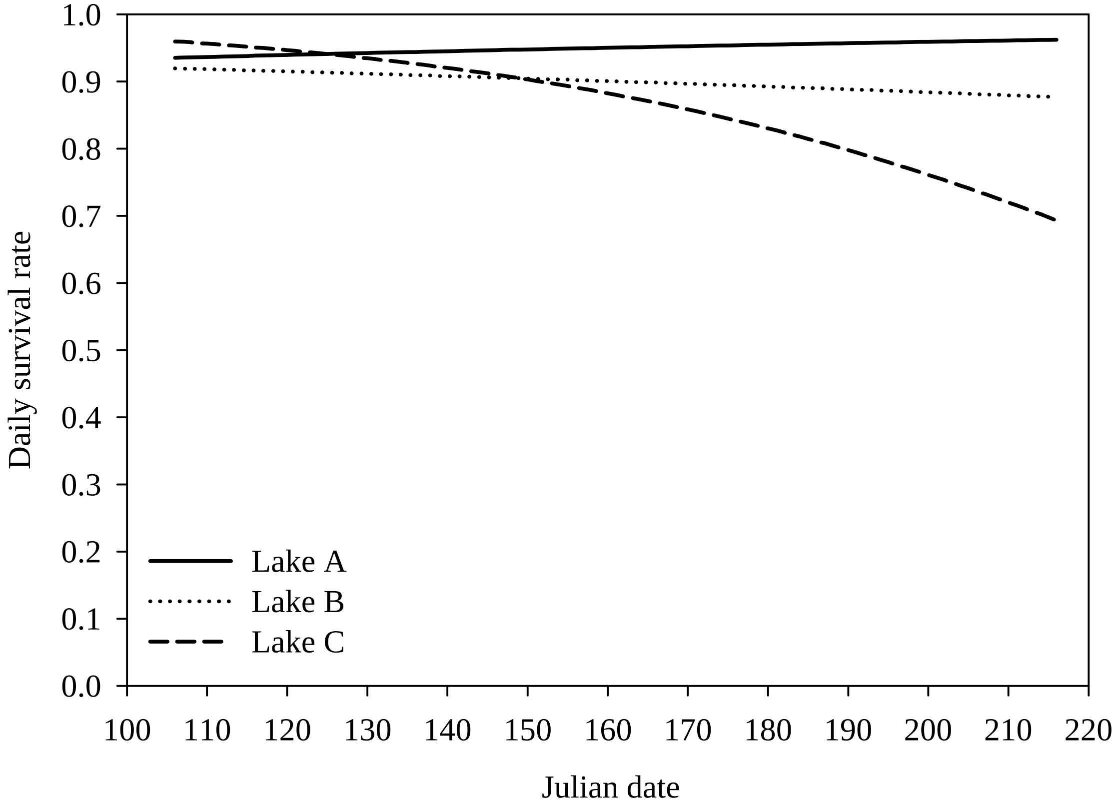

Figure 1.4. The effects of lake, time during nesting season (i.e., linear time trend), and interaction between them from model = S (linear time trend*lake + percent surface water + no. plants) on daily survival rates of Snowy Plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. To illustrate the relationship between nest daily survival rates and time during the nesting season among lakes, number of plants within 707-cm^2 plot and percent surface water were held constant at their mean values (i.e., 20 and 50%, respectively).

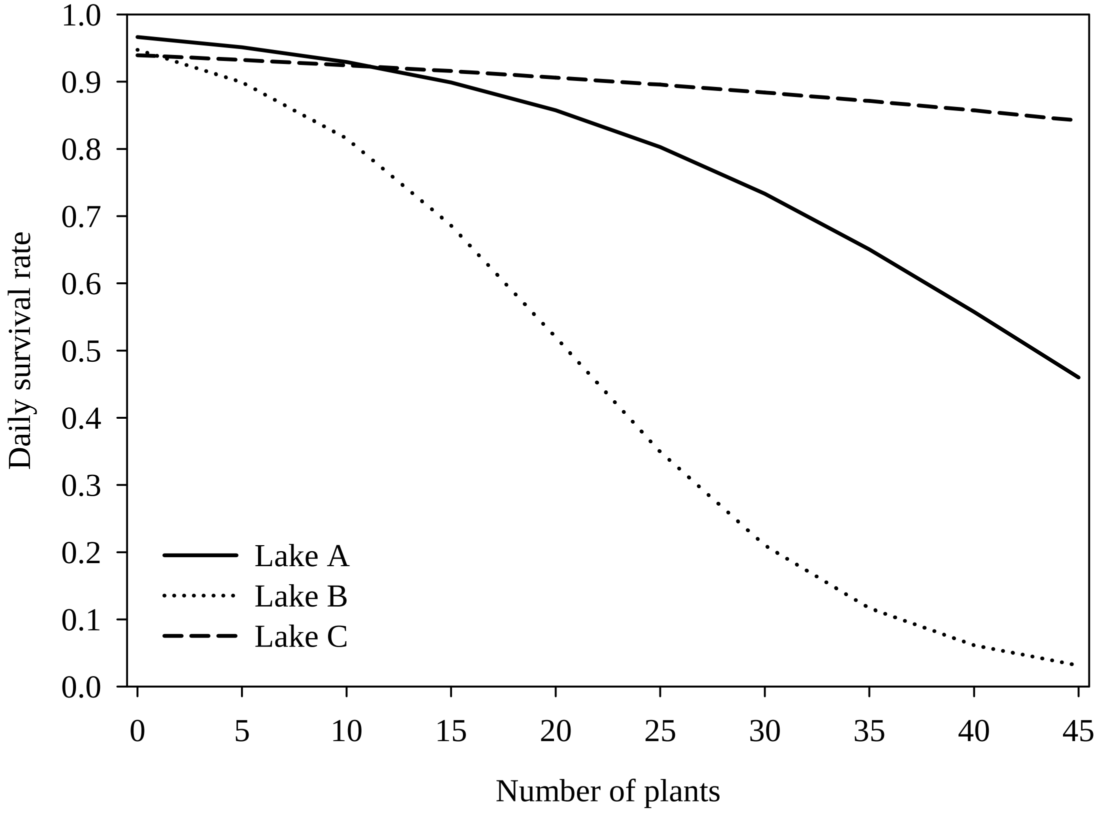

Figure 1.5. The effects of lake, number of plants within 707-cm^2 plot, and interaction between them from model = S (no. plants*lake + percent surface water) on daily survival rates of Snowy Plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. To illustrate the relationship between nest daily survival rates and number of plants, percent surface water was held constant at its mean value (i.e., 50%).

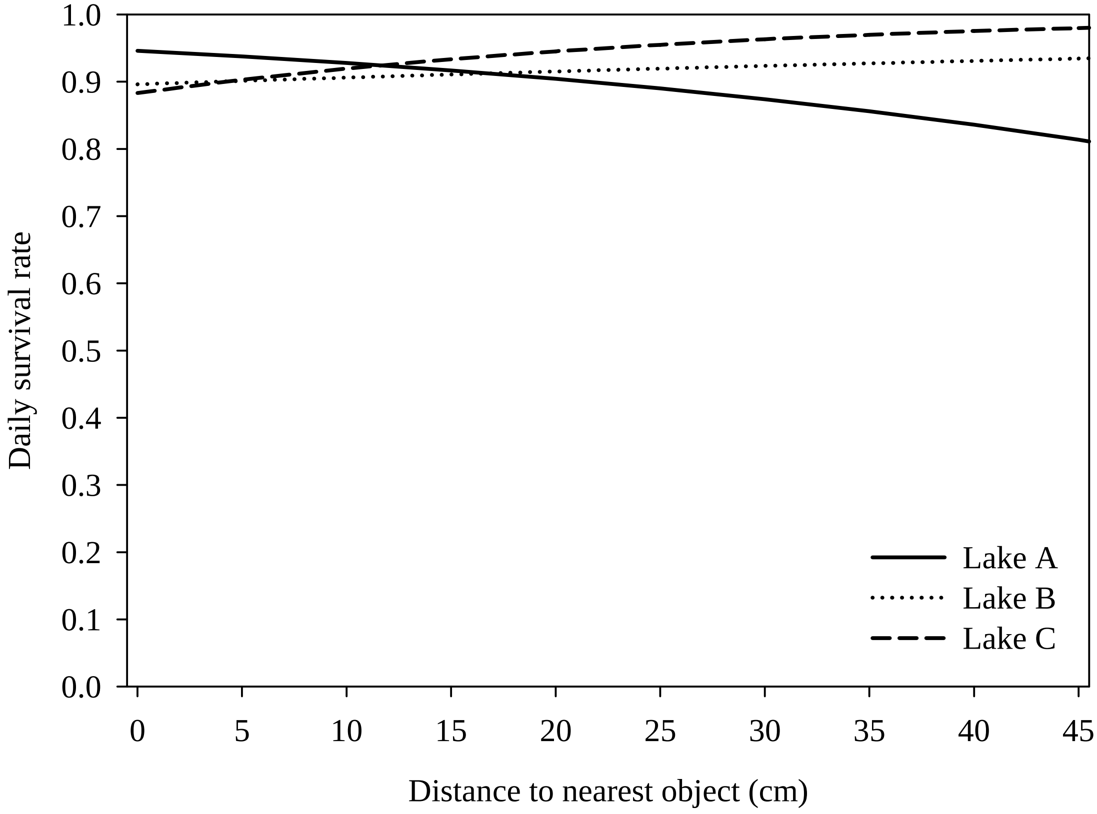

Figure 1.6. The effects of lake, distance to nearest object (cm), and interaction between them from model = S (dis. object*lake + percent surface water + no. plants) on daily survival rates of Snowy Plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. To illustrate the relationship between nest daily survival rates and distance to nearest object, number of plants within 707-cm^2 plot and percent surface water were held constant at their mean values (i.e., 20 and 50%, respectively).

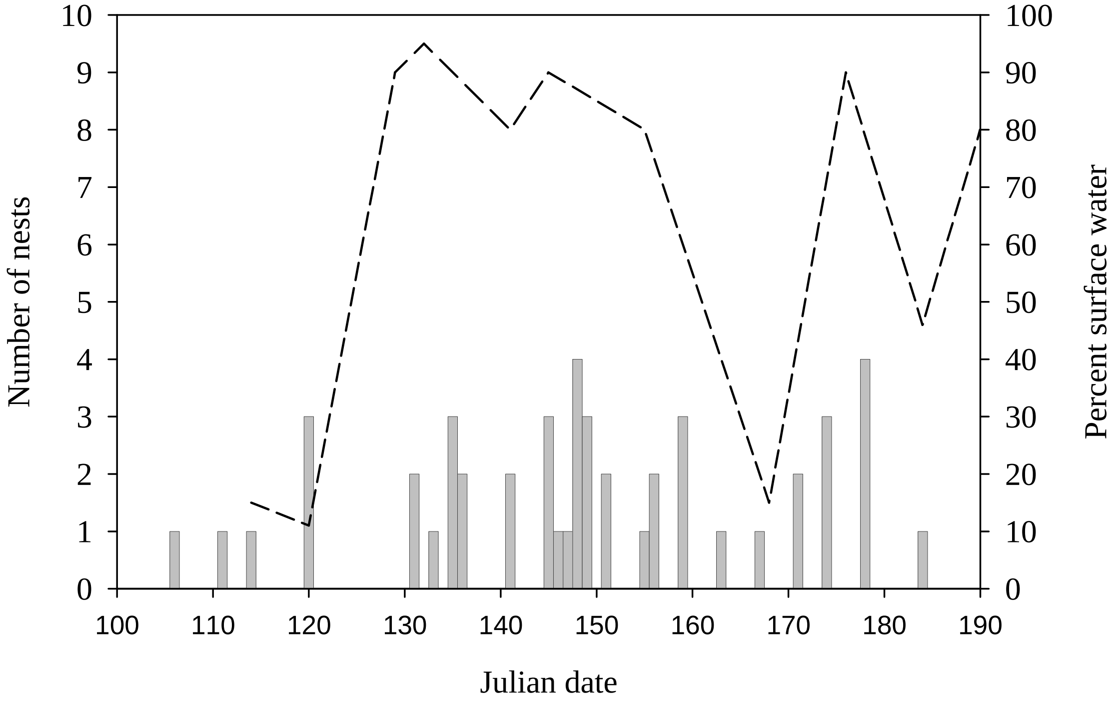

Figure 1.7. Chronology of Snowy Plover nest initiation dates (i.e., dates first egg was laid; bar graph) in relation to percent surface water availability (line plot) on lake B within the Southern High Plains of Texas, USA, 2008.

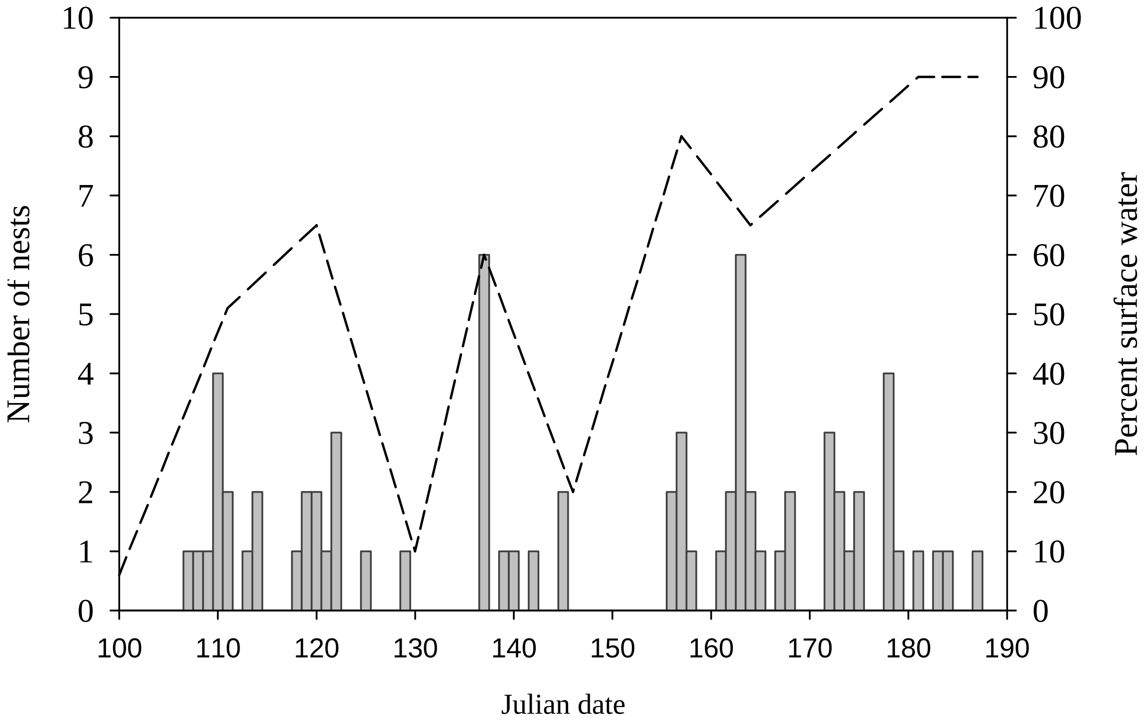

Figure 1.8. Chronology of Snowy Plover nest initiation dates (i.e., dates first egg was laid; bar graph) in relation to percent surface water availability (line plot) on lake B within the Southern High Plains of Texas, USA, 2009.

Table 1.1. Means ($\bar{x}$), standard errors (SE), and F and P-values resulting from analyses of variance (ANOVA) of parental body mass and repeated measures ANOVA of egg volume and chick body mass among lakes for Snowy Plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Lake A			Lake B			Lake C				
	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	*F*	*P*
Parental body mass (g)	43.66 a[a]	0.83	26	41.79 ab	0.56	39	39.86 b	1.22	13	4.31	0.017*
Egg volume (cm^3)	8.52 a	0.04	108	8.47 a	0.03	314	8.32 a	0.08	87	1.71	0.184
Chick body mass (g)	5.95 a	0.10	28	6.03 a	0.06	74	5.75 a	0.19	11	1.99	0.146

[a] Means followed by same letter within a row are not different ($P > 0.05$; least squares cross validation).

* Significant P-value ($P < 0.05$).

Table 1.2. Means ($\bar{x}$), standard errors (SE), and *F* and *P*-values resulting from analyses of variance (ANOVA) of parental body mass and repeated measures ANOVA of egg volume and chick body mass between years for Snowy Plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	2008			2009				
	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	*F*	*P*
Parental body mass (g)	41.41	0.69	41	42.85	0.60	37	2.46	0.121
Egg volume (cm^3)	8.34	0.04	186	8.53	0.03	323	5.82	0.017*
Chick body mass (g)	5.98	0.09	38	5.98	0.06	75	0.01	0.910

* Significant *P*-value ($P < 0.05$).

Table 1.3. Number of nests, nest fates, and nest success estimates for Snowy Plovers nesting on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Lake A		Lake B		Lake C	
	2008	2009	2008	2009	2008	2009
Total number of nests (*n*)	15	29	46	77	24	22
Successful (*n*)	4	12	17	20	2	4
Unsuccessful (*n*)	10	15	25	57	21	18
Predated (*n*, %)	5 (50.0)	6 (40.0)	9 (36.0)	19 (33.3)	10 (47.6)	10 (55.6)
Weather (*n*, %)	2 (20.0)	4 (26.7)	10 (40.0)	26 (45.6)	4 (19.0)	7 (38.9)
Trampled (*n*, %)	1 (10.0)	0 (0.0)	0 (0.0)	6 (10.5)	0 (0.0)	0 (0.0)
Abandoned (*n*, %)	0 (0.0)	3 (20.0)	1 (4.0)	6 (10.5)	0 (0.0)	0 (0.0)
Unviable (*n*, %)	0 (0.0)	1 (6.7)	0 (0.0)	0 (0.0)	0 (0.0)	1 (5.6)
Unknown (*n*, %)	2 (20.0)	1 (6.7)	5 (20.0)	0 (0.0)	7 (33.3)	0 (0.0)
Unknown[a] (*n*)	1	2	4	0	1	0
Apparent nest success (%)	26.7	41.4	37.0	26.0	8.3	18.2
Mayfield (%, 95% CI)	22.4 (3-42)	32.6 (15-50)	31.1 (18-44)	21.6 (13-31)	7.1 (0-15)	18.1 (3-33)

[a] Unknown clutches may have been successful or failed, but were classified as failed for success estimates.

Table 1.4. Means ($\bar{x}$) and standard errors (SE) of variables potentially influencing Snowy Plover nest success on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Successful (n = 58)			Unsuccessful (n = 147)		
	n	$\bar{x}$	SE	n	$\bar{x}$	SE
Mean egg volume (cm^3)	58	8.50	0.06	123	8.44	0.05
Distance to nearest active nest (m)	58	104.97	18.48	147	158.57	19.52
Mean percent surface water (%)	58	59.41	2.35	147	55.14	1.58
Distance to upland (m)	58	177.79	21.88	147	144.92	13.10
Average height of surrounding objects (cm)	54	2.40	0.23	126	2.79	0.26
Distance to nearest object (cm)	54	5.80	1.69	126	3.77	0.86
Total number of objects within 707 cm^2	58	576.31	63.16	139	532.82	48.47
Number of pebbles and rocks within 707 cm^2	58	276.14	32.19	139	247.03	25.04
Number of plants within 707 cm^2	58	0.14	0.09	139	2.82	0.75
Number of woody debris within 707 cm^2	58	8.98	2.51	139	10.27	1.73
Number of feathers and bones within 707 cm^2	58	2.76	1.21	139	7.31	2.10
Number of other objects within 707 cm^2	58	1.76	0.85	139	1.72	0.54

Table 1.5. Model results from Program MARK nest survival analysis of daily survival rates of Snowy Plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
S (linear time trend*lake + percent surface water + no. plants) [c]	8	0.00	0.24
S (no. plants*lake + percent surface water)	7	0.69	0.17
S (distance to object*lake + percent surface water + no. plants)	8	1.78	0.10
S (lake + percent surface water + no. plants)	5	1.96	0.09
S (linear time trend*lake + percent surface water)	7	2.47	0.07
S (percent surface water + no. plants)	3	3.03	0.05
S (no. plants*lake)	6	3.60	0.04
S (linear time trend*lake + percent surface water + avg. height objects)	8	3.89	0.03
S (percent surface water*lake + no. plants)	7	5.33	0.02
S (no. plants)	2	5.52	0.02
S (linear time trend*lake + no. plants)	7	5.82	0.01
S (no. plants*year + lake + percent surface water)	7	5.90	0.01
S (dist. object*lake + dist. nest)	7	6.12	0.01
S (dist. object*lake + percent surface water)	7	6.45	0.01
S (dist. object*lake + no. plants)	7	6.57	0.01

Table 1.5. Continued.

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
S (dist. object*lake + dist. nest + avg. height objects)	8	6.63	0.01
S (linear time trend*lake + dist. nest)	7	6.66	0.01
S (dist. object*lake + percent surface water + avg. height objects)	8	6.85	0.01
S (no. plants*year + percent surface water)	5	6.97	0.01
S (woody debris*lake + percent surface water)	7	7.25	0.01
S (lake + no. plants)	4	7.26	0.01
S (lake + percent surface water)	4	7.41	0.01
S (linear time trend*lake)	6	7.49	0.01
S (lake + percent surface water + avg. height objects)	5	7.73	0.01
S (woody debris*lake + percent surface water + avg. height objects)	8	7.77	0.00
S (linear time trend*lake + substrate)	7	7.79	0.00
S (linear time trend*lake + dist. nest + avg. height objects)	8	7.82	0.00
S (no. pebbles/rocks*lake + percent surface water + avg. height objects)	8	8.56	0.00
S (no. pebbles/rocks*lake + percent surface water)	7	8.58	0.00
S (linear time trend*lake + avg. height objects)	7	8.60	0.00
S (lake + dist. nest)	4	8.94	0.00

Table 1.5. Continued.

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
S (lake + dist. nest + avg. height objects)	5	9.07	0.00
S (dist. nest)	2	9.14	0.00
S (linear time trend*lake + substrate + avg. height objects)	8	9.15	0.00
S (dist. nest + avg. height objects)	3	9.17	0.00
S (no. plants*year)	4	9.40	0.00
S (percent surface water*lake + avg. height objects)	7	9.44	0.00
S (dist. object*lake + avg. height objects)	7	10.21	0.00
S (dist. object*lake)	6	10.23	0.00
S (percent surface water*lake)	6	10.30	0.00
S (percent surface water)	2	10.81	0.00
S (no. pebbles/rocks*lake + dist. nest + avg. height objects)	8	11.01	0.00
S (percent surface water + avg. height objects)	3	11.04	0.00
S (no. plants*year + lake)	6	11.17	0.00
S (no. pebbles/rocks*lake + dist. nest)	7	11.39	0.00
S (lake + avg. height objects)	4	11.55	0.00
S (lake)	3	11.68	0.00

Table 1.5. Continued.

Model	No. parameters	ΔAIC$_c$[a]	AIC$_w$[b]
S (no. pebbles/rocks*lake + avg. height objects)	7	11.71	0.00
S (woody debris*lake)	6	11.77	0.00
S (woody debris*lake + avg. height objects)	7	11.89	0.00
S (dist. nest*lake)	6	12.19	0.00
S (no. pebbles/rocks*lake)	6	12.26	0.00
S (dist. nest*lake + avg. height objects)	7	12.39	0.00
S (dist. nest*year + lake)	6	12.67	0.00
S (dist. nest*year + lake + avg. height objects)	7	12.77	0.00
S (lake + substrate)	4	12.93	0.00
S (lake + substrate + avg. height objects)	5	12.98	0.00
S (dist. nest*year + avg. height objects)	5	13.02	0.00
S (dist. nest*year)	4	13.06	0.00
S (avg. height objects)	2	13.28	0.00
S (substrate + avg. height objects)	3	13.49	0.00
S (substrate)	2	13.50	0.00
S (.) [d]	1	13.61	0.00

Table 1.5. Continued.

Model	No. parameters	$\Delta\mathrm{AIC}_c$[a]	AIC_w[b]
S (woody debris)	2	13.74	0.00
S (nest age)	2	13.82	0.00
S (lake*year)	6	13.92	0.00
S (dist. upland)	2	14.17	0.00
S (total no. objects*lake)	6	14.56	0.00
S (percent surface water*year)	4	14.59	0.00
S (dist. object)	2	14.67	0.00
S (linear time trend)	2	14.67	0.00
S (no. feathers/bones)	2	14.80	0.00
S (no. other objects)	2	14.88	0.00
S (no. pebbles/rocks)	2	15.41	0.00
S (avg. height objects*lake)	6	15.53	0.00
S (year)	2	15.54	0.00
S (egg volume)	2	15.54	0.00
S (total no. objects)	2	15.54	0.00
S (substrate*year)	4	15.71	0.00

Table 1.5. Continued.

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
S (substrate*lake)	6	16.28	0.00
S (no. feathers/bones*lake)	6	16.61	0.00
S (dist. upland*lake)	6	16.85	0.00
S (linear time trend*year)	4	17.48	0.00
S (egg volume*year)	4	17.54	0.00
S (nest age*year)	4	17.65	0.00

[a] Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[b] AIC_c relative weight attributed to model.

[c] Model of additive effects of linear time trend, lake, percent surface water, and no. plants and the interaction between linear time trend and lake.

[d] Model of no effects on nest survival.

Table 1.6. Maximum likelihood (logit-link) estimates from Program MARK for plausible models (i.e., $\Delta AIC_c < 2$) of daily survival rates of Snowy Plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

			95% CI	
Parameter	Estimate	SE	Lower	Upper
Top-ranked model				
Lake A	1.997	0.519	0.979	3.015
Lake B	1.771	0.422	0.943	2.599
Lake C	2.524	0.512	1.521	3.527
Linear time trend (lake A)	0.005	0.008	-0.011	0.021
Linear time trend (lake B)	-0.004	0.006	-0.016	0.008
Linear time trend (lake C)	-0.021	0.008	-0.036	-0.006
Percent surface water	0.024	0.009	0.007	0.040
No. plants	-0.026	0.012	-0.048	-0.003
Second-ranked model				
Lake A	2.643	0.325	2.006	3.279
Lake B	2.174	0.433	1.326	3.022
Lake C	2.024	0.356	1.326	2.721
No. plants (lake A)	-0.078	0.086	-0.246	0.090
No. plants (lake B)	-0.140	0.056	-0.249	-0.031
No. plants (lake C)	-0.024	0.013	-0.049	0.001
Percent surface water	0.014	0.006	0.002	0.027

Table 1.6. Continued.

			95% CI	
Parameter	Estimate	SE	Lower	Upper
Third-ranked model				
Lake A	2.676	0.322	2.044	3.307
Lake B	1.966	0.411	1.160	2.773
Lake C	1.835	0.358	1.134	2.537
Dist. object (lake A)	-0.031	0.017	-0.065	0.003
Dist. object (lake B)	0.011	0.013	-0.013	0.036
Dist. object (lake C)	0.041	0.031	-0.020	0.103
Percent surface water	0.016	0.006	0.004	0.028
No. plants	-0.031	0.011	-0.053	-0.009
Forth-ranked model				
Lake A	2.521	0.306	1.922	3.120
Lake B	1.977	0.409	1.175	2.779
Lake C	1.972	0.350	1.286	2.659
Percent surface water	0.017	0.006	0.005	0.029
No. plants	-0.033	0.011	-0.055	-0.011

CHAPTER II

NEST SITE SELECTION BY SNOWY PLOVERS IN THE SOUTHERN HIGH PLAINS OF TEXAS

INTRODUCTION

Nest site selection is an important means by which birds reduce risks to nest contents and themselves during incubation and brood rearing. Therefore, natural selection should favor individuals that select nest sites that minimize these risks (Amat and Masero 2004). Snowy Plover (*Charadrius alexandrinus*) is a ground nesting shorebird that nests in sparsely vegetated habitats including coastal beaches, salt pans, river gravel and sand bars, salt flats, dredge spoil deposits, salt evaporation ponds, and alkaline or saline lakes, reservoirs, and ponds (Page et al. 2009). Because most Snowy Plover nest failures are a result of predation (Page et al. 2009; see Chapter I), nest site characteristics should mitigate risks associated with these pressures. For example, Snowy Plovers can reduce risks of predation to themselves and nests by adjusting spacing patterns (Page et al. 1983), distance to upland areas (Koenen et al. 1996), adjacency to objects (Page et al. 1985), substrate type (Page et al. 1985, Colwell et al. 2005), and adjacency to vegetation cover (Amat and Masero 2004).

Predation avoidance can elicit variable responses in nest spacing patterns depending upon behaviors of incubating parents and associated predator species. For example, for species that cannot defend themselves or their nests, the most evolutionarily favorable strategies would be to rely on camouflage to prevent nest detection and space nests further apart to reduce density dependent predation (Tinbergen et al. 1967, Andersson and Wiklund 1978, McCrimmon 1980, Page et al. 1983, Rippin Armstrong and Nol 1993). Conversely, species that use defense or alarm calls may benefit by nesting communally, working together to detect and defend against predators (Göransson et al. 1975, Andersson and Wiklund 1978, Wiklund and Andersson 1980, Götmark and Andersson 1984). Specific threat(s) a predator imposes on a colony depends upon predatory type, predator size, method of approach by predators and their response to antipredator behaviors, and physical nest site characteristics (Kruuk 1964, Brunton 1990, Brunton 1997). Most avian nest predators have greater success when nests are clustered and colony size is large, due to ease of finding clustered nests from the air, reliability of prey for an extended time, and aggregating of avian predators at prey sites (Tinbergen et al. 1967, Page et al. 1983). Conversely, mammalian predators may have greater success preying upon solitary nests, because such nests rely on camouflage defense and mammalian predators often locate nests by scent or happenstance (Page et al. 1983). Because mammalian predators enter colonies from edges, colonial nests may be better protected against mammalian than avian predators due to early detection and group defense (Brunton 1997).

Along with social factors influencing nest site selection, nest site habitat may also reduce nest predation. In areas where most nests are predated by mammals, nesting close to upland areas may reduce nest success due to greater rates of detection and predation (Burger 1987, Koenen et al. 1996). Because upland areas provide cover for ground-approaching nest predators such as coyotes (*Canis latrans*), nests placed closer to these areas may be more susceptible to predation as predators are easily concealed as they approach nests. Regardless of distance to upland, nesting adjacent to objects (e.g., driftwood, vegetation, rocks, etc.), can provide concealment from predators due to disruptive effects (Page et al. 1985, Flemming et al. 1992). However, many studies on Snowy and Kentish Plovers (*Charadrius alexandrinus*) have not reported a positive effect of nesting near objects (Hill 1985, Paton 1994, Powell 2001, Norte and Ramos 2004). In fact, several studies have documented a negative relationship between nesting near objects and nest success (Page et al. 1985, Winton et al. 2000), where predation rates increased when nests were placed near objects, as predators were thought to be using objects or debris lines as search images for nests (Grover and Knopf 1982, Page et al. 1985, Winton et al. 2000).

Beyond providing protection from predation and weather events, nest sites should also provide appropriate microclimate for incubation (Amat and Masero 2004). Nesting Snowy Plovers in the Southern High Plains (SHP) of Texas are exposed to high ambient temperatures, creating a thermally stressful nesting environment (see Chapter III). Thermally favorable nest sites should be selected to alleviate heat stress, but selection of such sites may simultaneously improve nest detection by predators and reduce predator detection by incubating adults (Götmark et al. 1995, Amat and Masero 2004, Mayer et al. 2009). For example, nests in areas with greater vegetation experience smaller temperature fluctuations, but incubating adults are more susceptible to predation due to reduced detectability of approaching predators (Amat and Masero 2004). However, for species with cryptic plumage (Graul 1973) and/or eggs (Nguyen et al. 2007) like plovers, nests may be placed in more open areas, rely on crypsis for predator avoidance, and forego advantages offered in more thermally favorable environments (Götmark et al. 1995). Substrate type may be important for camouflage, as nests on heterogeneous (i.e., lack of uniformity in color and shape) substrates are more camouflaged and experience lower predation rates than nests located on either more homogeneous substrates or in more vegetated areas (Bowman and Harris 1980, Page et al. 1985, Colwell et al. 2005). Furthermore, different substrate types have different thermal conductance (Ackerman and Seagrave 1987), with pebble substrates generally having lower temperatures than sand substrates (see Chapter III). As such, selection of substrate type by Snowy Plovers is likely a compromise to simultaneously improve crypsis and alleviate heat stress to incubating adults and eggs (Page et al. 1985, Mayer et al. 2009).

Because a primary cause for the decline of western Snowy Plovers (*C. a. nivosus*) has been attributed to habitat degradation (U.S. Fish and Wildlife Service 1993, Page et al. 2009), conservation guidelines typically focus upon nesting habitat management including creation and restoration of nesting habitat, substrate modification, and vegetation control (Mabee and Estelle 2000). However, unlike coastal regions where beaches comprise the majority of nesting habitat, within the SHP of Texas, Snowy Plovers nest primarily on edges of saline lakes (Conway et al. 2005a) for which nesting management guidelines are more coarsely defined. Because habitat likely varies among nesting locations, determining regionally specific selection and spatial patterns remains important in developing habitat conservation and management guidelines for nesting Snowy Plovers within the SHP of Texas. Therefore, the objectives of this study were to 1) determine habitat characteristics influencing probability of Snowy Plover nest sites and 2) examine spatial patterns of Snowy Plover nests in relation to habitat characteristics in the SHP of Texas during 2008 and 2009.

METHODS

Study Area

The SHP is an approximately 80,000 km^2 region occurring from the panhandle of Texas, into New Mexico, and south to Midland, Texas (Osterkamp and Wood 1987). Within this region, approximately 40 saline lakes (i.e., primary regional nesting location for Snowy Plovers; Conway et al. 2005a) occur (Reeves and Temple 1986). Saline lakes are discharge wetlands containing freshwater springs fed by the Ogallala aquifer (Brune 2002), but having an overall saline water chemistry (often > 200g/L of dissolved solids; Osterkamp and Wood 1987). Three previously identified important (i.e., having consistent surface water throughout the nesting season and containing the majority of regional nesting Snowy Plovers) saline lakes (Conway et al. 2005a) ranging in size from ~ 270 – 600 ha were used as study sites in 2008 and 2009 (Figure 1.1). To maintain landowner anonymity, study site lakes will be referred to as lake A, lake B, and lake C. Each study site lake contained two – six fresh to slightly saline springs distributed along lake margins (Brune 2002). The primary landuse practice immediately surrounding study site lakes was pasture/rangeland with some held within the Conservation Reserve/Permanent Cover Program. Other landuse practices occurring within surrounding areas included row-crop agriculture production (i.e., mostly cotton

[*Gossypium* spp.]), mineral excavation (e.g., caliche), and development (i.e., mostly small home/ranch developments).

Nest Surveys

Surveys were conducted ≥ 1 time per week at each lake during the breeding season (i.e., early April – mid August; Conway et al. 2005a; see Chapter I) in 2008 – 2009 to locate new nests. Nests were located by observing adult Snowy Plovers incubating nests, flushing from or returning to nest sites, and searching appropriate habitat (Conway et al. 2005a). Once located, 120 GPS positions were obtained per nest using a Trimble GeoXH GPS unit (Trimble Navigation Ltd, Sunnyvale, CA). To compare nest sites with habitat available, an equal number of random sites per year and study site were located using Hawth's Analysis Tools in ArcGIS 9.2 (Beyer 2004). Random sites were restricted to unvegetated areas between upland and the average high water mark, digitized from 2004 National Agriculture Imagery Program (NAIP) digital orthophoto quarter-quadrangle aerial photographs (Texas Natural Resources Information System 2004).

Nest Habitat Measurements

After nest fate (i.e., hatching or failure; see Chapter I) was determined, the following habitat characteristics were recorded at nest sites: primary nest substrate (i.e., sand or pebble), height of (cm) and distance to (cm) nearby (i.e., generally < 12.5 cm) objects (e.g., rocks, pebbles, woody debris, plants, etc.), and distance to nearest object and average height of surrounding objects. In some instances, no object was located near nests or random points. In these instances, 0 cm was used as the average height of surrounding objects and 50 cm (i.e., slightly longer than longest distance measured to nearest object [40.5 cm]) was used as the distance to nearest object. A 30-cm diameter hoop (707 cm^2) was also centered on each nest and random site, and two photographs were taken with a Canon Digital Rebel XT SLR equipped with a Canon EF 50 mm compact macro standard auto focusing lens, mounted on a tripod, kept at the same height (i.e., 126 cm from ground to top of camera), focal length, and aperture. From pictures, all rocks (i.e., > 8 cm), pebbles (i.e., < 8 cm; includes gypsum), plant stems, woody debris, and other objects (i.e., cow feces, feather and bone, clumps of dirt, and manmade objects) were counted within the 707-cm^2 plot. Because parents often bring additional objects (e.g., pebbles) into the nest scrape (Page et al. 2009), objects located within the nest scrape were not counted. For random plots, to remain consistent with nest sites, a circle the same size as an average nest scrape (i.e., 10.4-cm diameter) was placed in the center of the hoop and objects within were excluded from counts.

All GPS positions were differentially corrected using GPS Pathfinder Office software (Trimble Navigation Ltd, Sunnyvale, CA) from six base stations and averaged to obtain one position for each nest. The differentially corrected positions were imported into ArcGIS 9.2 (ESRI, Redlands, CA) and mapped. Distance (m) to nearest upland was calculated using Euclidian distance to nearest upland edge, where upland boundaries were digitized using 2004 NAIP digital orthophoto quarter-quadrangle (DOQQ) aerial photographs (Texas Natural Resources Information System 2004).

DATA ANALYSIS

Logistic regression was used to determine habitat variable(s) best predicting Snowy Plover nest sites for all lakes combined and within lakes (PROC LOGISTIC; SAS Institute 2002). A set of 15 – 36 (depending upon lake) candidate models was developed, *a priori*, consisting of biologically relevant combinations of habitat variables (i.e., distance to upland, substrate type [coded: pebble = 1, sand = 0], distance to nearest object, average height of surrounding objects, and total number of objects as well as number of pebbles/rocks, plants, woody debris, feathers/bones, and other objects [i.e., manmade objects, cow feces, and clumps of dirt] within 707-cm^2 plot). Correlated ($P \leq 0.05$) variables were not permitted to enter the same model. Akaike's Information Criterion corrected for small sample size (AIC_c) was used to rank models (a model was considered plausible when $\Delta AIC_c < 2$; Burnham and Anderson 2002). Parameter estimates, standard errors, confidence intervals, and *P*-values from the top-ranked model(s) were presented. Parameter likelihoods were determined using model averaging (i.e., sum of model weights for models that included a given parameter; Burnham and Anderson 2004). To test the goodness-of-fit of the top-ranked model, the Hosmer and Lemeshow goodness-of-fit statistic was used (PROC LOGISTIC: SAS Institute 2002). Accuracy of plausible models was estimated by determining the number of correctly classified observations, where an observation was considered correct for nests when the predicted probability was > 0.5 and for random sites when predicted probability was < 0.5.

To examine nest spatial patterning, distance to nearest active (i.e., day first egg was laid to day hatched or failed) nest was determined for each nest using Hawth's Analysis Tools (Beyer 2004). To locate areas of high use, kernel density estimates were obtained in ArcGIS 9.2 using consistent output cell size (i.e., 6.0 m) and search radius (i.e., 50.0 m) for each lake and year separately.

RESULTS

Overall, 215 Snowy Plover nests and associated random sites were located, of which, 44 were located at lake A (15 in 2008 and 29 in 2009), 125 at lake B (47 in 2008 and 78 in 2009), and 46 at lake C (24 in 2008 and 22 in 2009). However, complete habitat data were only obtained from 180 nests (34 from lake A, 105 from lake B, and 41 from lake C). Habitat data could not be obtained from 35 nests due to rain events altering habitat conditions prior to measurements being collected. Therefore, all nest site selection analyses and results are based upon these 180 nests. Most nests were placed in open areas, with little cover or shade; however, four nests were placed in areas with some vegetative cover or shade (i.e., nests placed below or adjacent to vegetation tall enough to provide shade for majority of nest). However, nearly all nests (97% at lake A, 95% at lake B, and 98% at lake C) were located < 15 cm to an object (i.e., pebble, rock, plant, woody debris, bone, feather, cow feces, coyote feces, clump of dirt, and manmade object). Additionally, more nests had pebble substrate and objects (e.g., rocks, pebbles, woody debris, etc.) present than random sites (Figures 2.1 – 2.6, Tables 2.1 – 2.8). Most (57%) Snowy Plover nests were located < 100 m to the nearest active nest ($\bar{x}$ = 144.1 m; range = 5.6 – 1810.9 m; *n* = 215; Figure 2.7). Kernel density estimates for all lakes and years showed areas of high use corresponded with areas of pebble substrate and natural or manmade islands, berms, and peninsulas (Figures 2.8 – 2.13).

Nest Site Selection

Lakes Combined

Among 16 candidate models examining nest site selection among all lakes simultaneously, the first two models should be considered plausible (i.e., $\Delta AIC_c < 2$; Table 2.9). In these models, distance to nearest object had a negative model coefficient, and average height of surrounding objects and substrate type had positive model coefficients (Table 2.10). Therefore, probability of a nest increased with shorter distances to nearest object (Figure 2.14), greater height of objects (Figure 2.15), and pebble substrate (Figure 2.15) as compared to random sites. Parameter likelihoods also indicated that distance to nearest object (likelihood = 0.52), substrate type (likelihood = 0.48), and average height of surrounding objects (likelihood = 0.45) were the most important variables included in the top-ranked models. The logistic regression model correctly predicted nest and random sites based upon distance to nearest object with 71.4% accuracy, while the model containing substrate type and average height of surrounding objects had an accuracy of 74.7%. The Hosmer-Lemeshow goodness-of-fit statistic indicated that the top-ranked model fit the data well ($P = 0.356$).

Lake A

Among 36 candidate models, the model best predicting a Snowy Plover nest site was the additive model of substrate type and average height of surrounding objects (Table 2.11), with both parameters having positive model coefficients (Table 2.12).

Therefore, probability of a nest increased with pebble substrate and greater height of objects as compared to random sites (Figure 2.16). Parameter likelihoods indicated that average height of surrounding objects (likelihood = 0.99) and substrate type (likelihood = 0.75) were the most important variables included in the top-ranked models. The logistic regression model correctly predicted nest and random sites based upon average height of surrounding objects and substrate type with 87.2% accuracy. Because the top-ranked model contained a categorical variable (i.e., substrate type), the Hosmer-Lemeshow goodness-of-fit statistic was not determined.

Lake B

Among 15 candidate models, the first two models should be considered plausible (i.e., $\Delta AIC_c < 2$; Table 2.13). In these models, substrate type and average height of surrounding objects had positive model coefficients (Table 2.14), although average height of surrounding objects was not a significant parameter. Parameter likelihoods also indicated that substrate type (likelihood = 1.00) and average height of surrounding objects (likelihood = 0.36) were the most important variables included in the top-ranked models. The logistic regression model correctly predicted nest and random sites using only substrate type with 82.2% accuracy. Adding average height of surrounding objects did not increase model prediction accuracy (i.e., 82.2% accuracy). Therefore, the most parsimonious model was the single variable model containing substrate type (Figure 2.17). Because the top-ranked model contained a categorical variable (i.e., substrate type), the Hosmer-Lemeshow goodness-of-fit statistic was not determined.

Lake C

Among 16 candidate models, the first two models should be considered plausible (i.e., $\Delta AIC_c < 2$; Table 2.15). In these models, average height of surrounding objects and total number of objects within 707-cm^2 plot had positive model coefficients (Table 2.16), although average height of surrounding objects was not a significant parameter. Parameter likelihoods also indicated that total number of objects within 707-cm^2 plot (likelihood = 0.94) and average height of surrounding objects (likelihood = 0.31) were the most important variables included in the top-ranked models. The logistic regression model correctly predicted nest and random sites using only total number of objects with 80.5% accuracy. Adding average height of surrounding objects did not increase model prediction accuracy (i.e., 80.5% accuracy). Therefore, the most parsimonious model was the single variable model containing total number of objects within 707-cm^2 plot (Figure 2.18). The Hosmer-Lemeshow goodness-of-fit statistic indicated that the top-ranked model fit the data well ($P = 0.433$).

DISCUSSION

Similar to previous studies (Boyd 1972, Grover and Grover 1982, Grover and Knopf 1982, Wilson-Jacobs and Meslow 1984, Hill 1985, Paton and Edwards 1990, Powell and Collier 2000, Winton et al. 2000, Conway 2001, Powell 2001, Norte and Ramos 2004), almost all (i.e., 96%) Snowy Plover nests were placed adjacent to ≥ 1 object. Distance to nearest object, average height of surrounding objects (mean average height of surrounding objects was < 3 cm), total number of objects within 707-cm^2 plot, and substrate type were the key habitat variables that Snowy Plovers used to select nest sites on saline lakes within the SHP of Texas. By nesting adjacent, or in close proximity, to specific objects, Snowy Plovers gain protection against extreme weather (e.g., wind, hail, and rain; Flemming et al. 1992, Norte and Ramos 2004), concealment from predators due to disruptive effects (Page et al. 1985, Flemming et al. 1992), and/or perhaps enhanced visual cues to incubating adults for nest relocation (Grover and Grover 1982, see Page et al. 1985). However, like many previous studies on Snowy and Kentish Plovers, (Hill 1985, Paton 1994, Conway 2001, Powell 2001, Norte and Ramos 2004), nesting near objects did not affect nest success (see Chapter I). Advantages gained by nesting near objects may only be beneficial in environments that are saturated with objects, so that systematically searching objects would not be cost effective for predators searching for nests (Page et al. 1985). In this region, nesting habitat is not saturated with objects and predators often search appropriate habitat (i.e., debris lines) for nests (S. Saalfeld per. obs.). Therefore, placing nests near objects may be an artifact from species-wide evolutionary selection and predation pressures or geographical selection and predation pressures (Paton 1994), and therefore, have little effect on present nest success (see Chapter I) for Snowy Plovers nesting within the SHP of Texas.

In conjunction with presence of objects, Snowy Plovers also selected nest sites based upon substrate type, where areas of high use were dominated by pebble substrate (Figures 2.8 – 2.13). Although heterogeneous substrates (e.g., pebble) should increase camouflage and reduce predation rates as compared to nests located on more homogeneous substrates like sand (Bowman and Harris 1980, Page et al. 1985, Prindiville Gaines and Ryan 1988, Lauro and Nol 1995, Colwell et al. 2005), substrate type did not influence nest success (see Chapter I). However, substrate type is likely important to allow Snowy Plovers to alleviate heat stress during incubation. For example, selection of light colored pebbles with greater heat reflectance provided thermal benefits for Piping Plover (*Charadrius melodus*) nests, with nests remaining 2 – 6ºC cooler than surrounding substrate (Mayer et al. 2009). Similarly, in the SHP of Texas, pebble substrates were up to 2.5ºC cooler than sand substrates during the day (see Chapter III). Although substrate type did not influence nest success, Snowy Plovers cluster nests on pebble substrate and gain thermoregulatory (but not safety) benefits during incubation.

Previous studies have shown that most Snowy Plovers nests are placed in areas with some nearby cover (Wilson 1980, Paton and Edwards 1990, Powell and Collier 2000, Powell 2001, Norte and Ramos 2004, Conway et al. 2005b). However, amount of vegetation within 707-cm^2 plot was not an important factor in predicting nest locations, as only 21 nests had plants within 707-cm^2 plot and only four plots had vegetation tall enough to provide shade to nests. Although Snowy Plovers do not use plants to place nests, avoidance of plants was not apparent despite the trend of decreasing daily survival rates as the number of plants surrounding nests increased (see Chapter I). In areas with greater vegetation cover, nests may be more camouflaged and have lower temperature fluctuations (due to the benefits of shading by vegetation) than nests with little cover. However, incubating adults and eggs may be susceptible to predation while incubating nests with more cover because of their decreased visibility and/or ability to detect approaching predators (Amat and Masero 2004). Therefore, selection of nest sites with little or no cover is likely an adaptive behavior that facilitates early detection of predators by incubating parents (Burger 1987, Götmark et al. 1995, Lauro and Nol 1995, Amat and Masero 2004) and placement of nests in open areas may increase daily survival rates and nest success (see Chapter I).

Similar to previous studies on Snowy (Powell 2001) and Kentish Plovers (Norte and Ramos 2004), the majority (57%) of Snowy Plover nests were located < 100 m from the nearest active nest. However, isolated nests (i.e., > 100 m from the nearest active nest) were also frequently (43%) documented. Although nest success of Snowy and

Kentish Plovers generally improves when nests are placed close to conspecifics (Powell 2001, Norte and Ramos 2004), in some areas, the opposite has occurred (Page et al. 1983), and distance to nearest nest was unrelated to success in this study (see Chapter I). Spatially separated populations of the same species may experience different predation risks when nesting communally, due to local predator community and/or predation pressures (Rippin Armstrong and Nol 1993). Within the SHP of Texas, Snowy Plovers may invoke a mixed-strategy for nest clustering, with some nests placed close to conspecifics, while others are placed in isolation. Clustering of nests may result in decreased predation by mammalian predators. However, predation by avian predators (i.e., ravens [*Corvus* spp.], Black-crowned Night Herons [*Nycticorax nycticorax*]) seems to have increased in recent years (see Chapter I). Because most avian predators have greater success when nests are clustered and colony size is large, clustering of nests may be ineffective at reducing predation from avian predators (Tinbergen et al. 1967, Page et al. 1983) and would favor a more spaced-out distribution.

Nest clustering may be an artifact of population density if nest site availability becomes limited as population size and/or density increases (Page et al. 1983). Although regional populations of Snowy Plovers nest on saline lakes, which are numerically limiting, no evidence exists to suggest that these lakes are saturated, where clustering occurs because of limited physical space. In fact, regional Snowy Plover populations seem to experience fluctuations in numbers and density (see Chapter VI), where nest clustering may be a social decision, rather than density related. However, within each saline lake, the amount, extent, and distribution of pebble substrates (i.e., microhabitat) may be limiting. Because pebble substrates may provide advantages to incubating adults, eggs, and/or chicks (e.g., decreased predation risks and temperature control); areas of high use correspond to areas with pebble substrate. Because pebble substrate is generally limited within saline lakes (S. Saalfeld per. obs.), nests become clustered within individual saline lakes. Additionally, selection of manmade or natural islands, berms, and peninsulas that are further from lake edges or upland areas may reduce nest predation rates because these areas tend to be further from upland areas and may be inaccessible to land-based predators during times of high water. Because these areas also are generally limited, clustering within these areas was also apparent.

Snowy Plovers tended to select areas with more objects, intermediate amounts of vegetation, and pebble substrate, as well as manmade or natural islands, berms, and peninsulas. These selection patterns clearly provide some guidance for habitat conservation and management strategies within this region. For example, vegetation encroachment may have serious impacts to nesting Snowy Plovers. Flooding events may decrease vegetation growth on saline lakes (Faanes 1983); however, these events are dependent upon unpredictable weather events as well as surface flow and groundwater seepage. Therefore, the amount of water saline lakes receive from local rain events depends upon land use practices. Because these saline lakes have a direct input from springs connected to the Ogallala Aquifer (Brune 2002), crop irrigation relying on the same aquifer during the nesting season could decrease the amount of freshwater input into saline lakes (Conway et al. 2005a). Additionally, land use practices surrounding saline lakes can impact erosion rates and ultimately the amount of sediments reaching saline lakes during local rain events. If erosion and the amount of sediments reaching these lakes is high, sand deposition may dramatically impact the geomorphology of these lakes, potentially negatively influencing nesting habitat by increasing amount of sand substrate while decreasing amount of pebble substrate. Therefore, decreasing groundwater withdraws and maintaining surrounding upland areas with native vegetation could positively impact nesting habitat for Snowy Plovers within the SHP of Texas.

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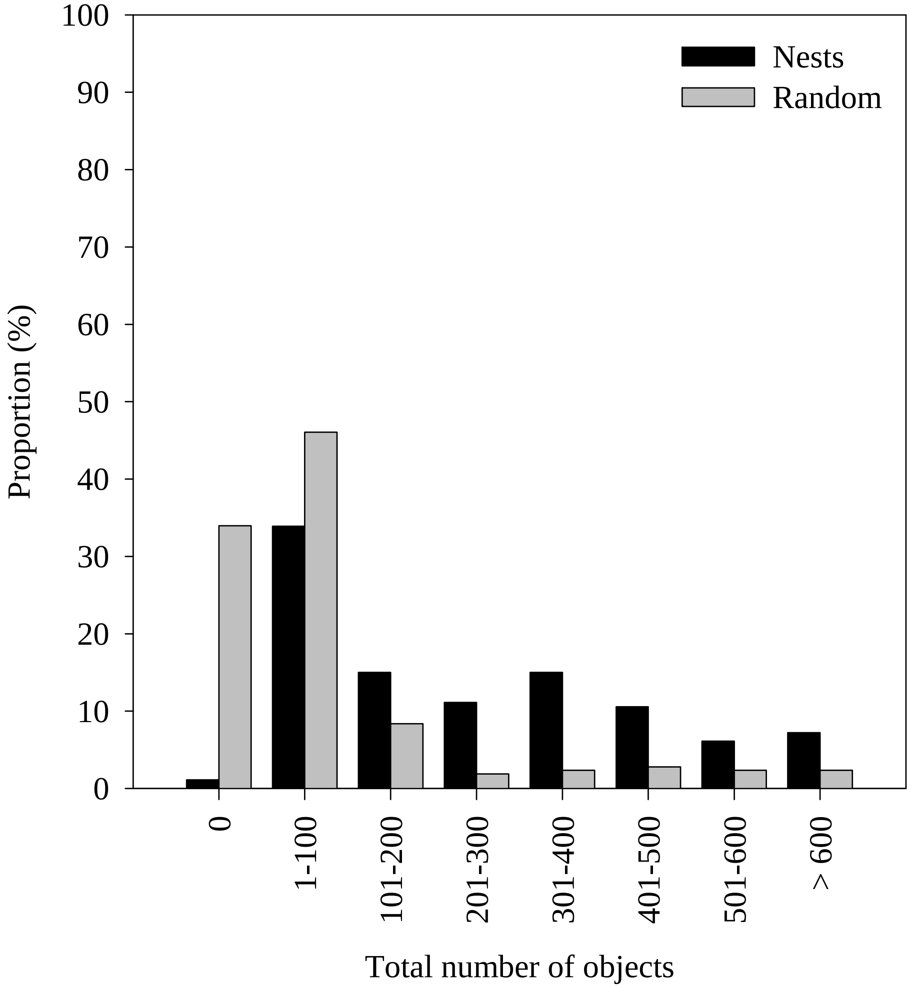

Figure 2.1. Proportion of Snowy Plover nests or random sites that contained any object (e.g., pebble, rock, plant, woody debris, feather, bone, manmade, etc.) within 707-cm^2 plot on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

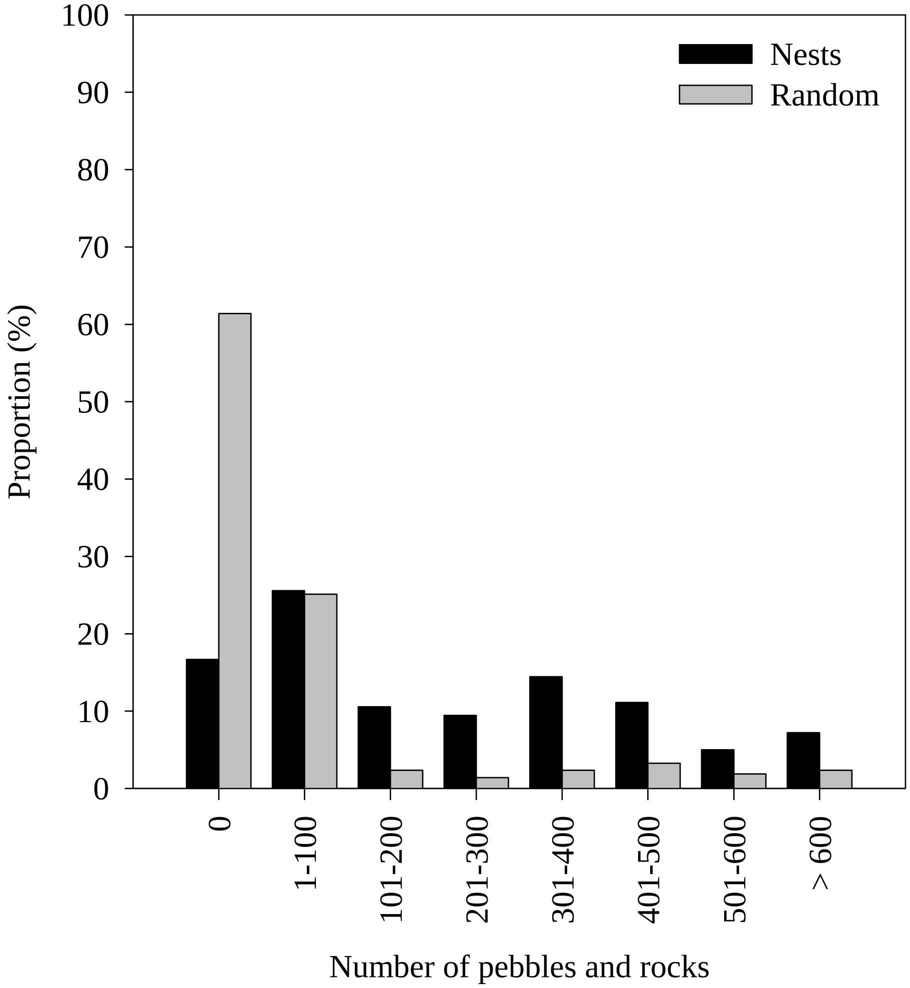

Figure 2.2. Proportion of Snowy Plover nests or random sites that contained pebbles and rocks within 707-cm^2 plot on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

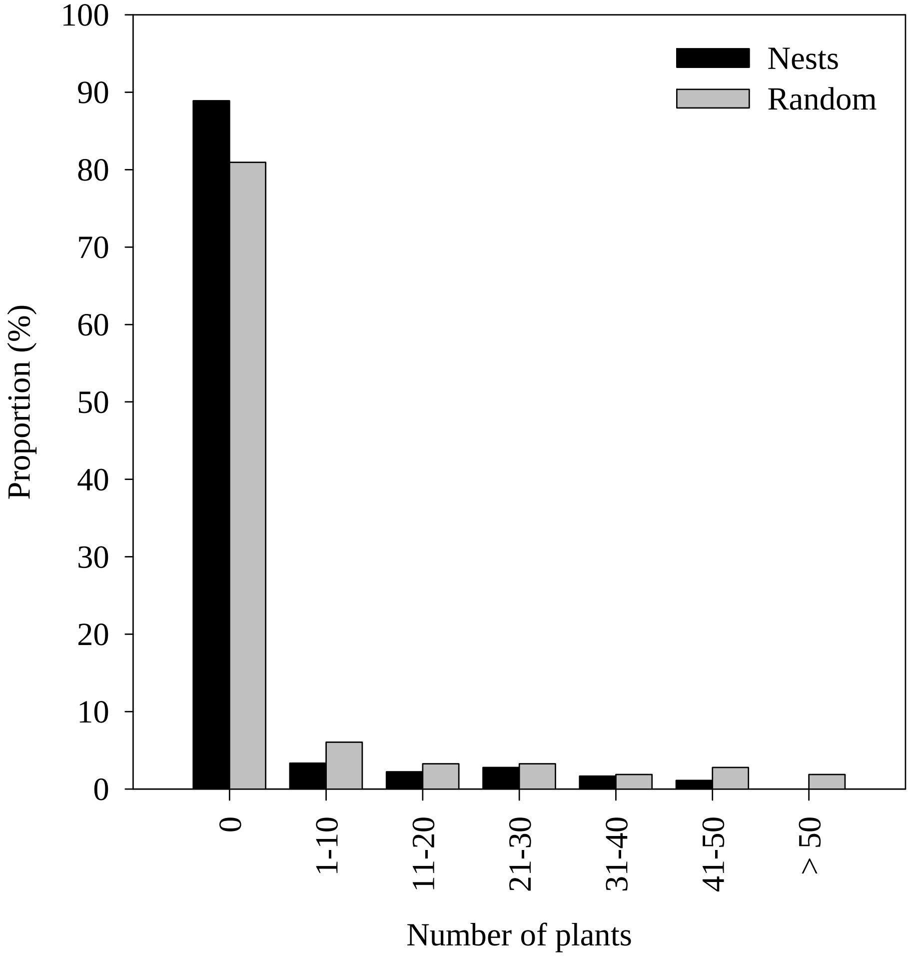

Figure 2.3. Proportion of Snowy Plover nests or random sites that contained plants within 707-cm^2 plot on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

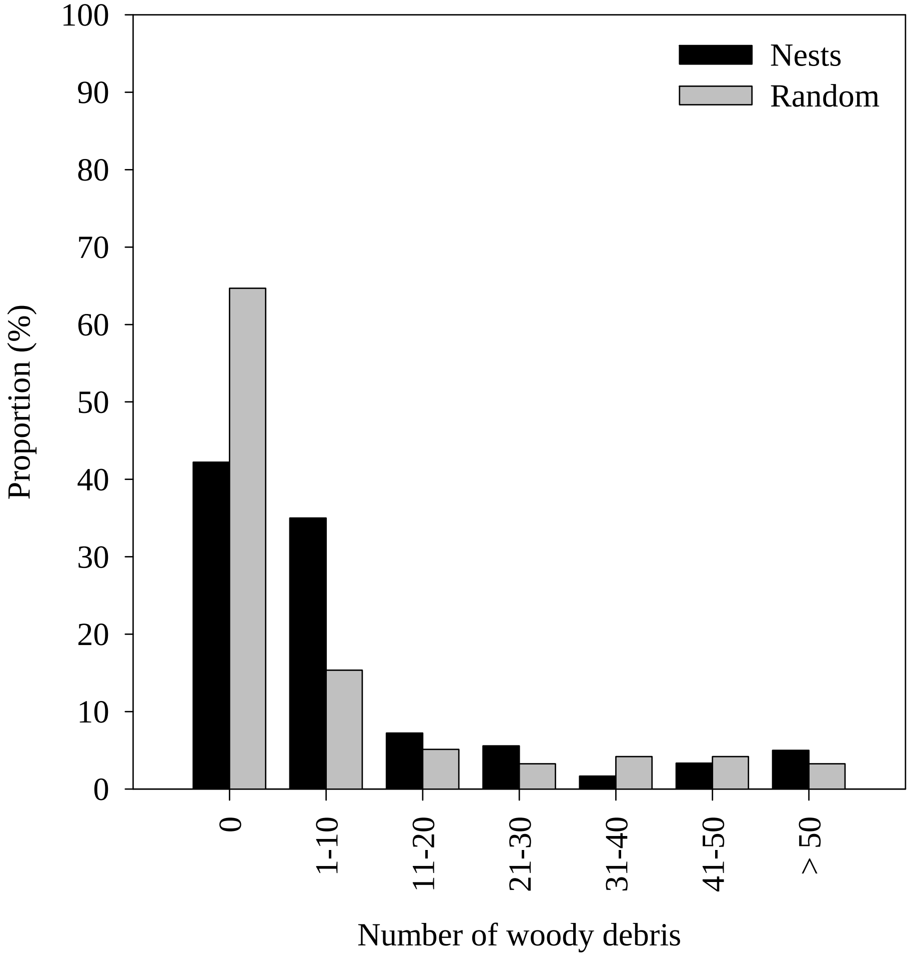

Figure 2.4. Proportion of Snowy Plover nests or random sites that contained woody debris within 707-cm^2 plot on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

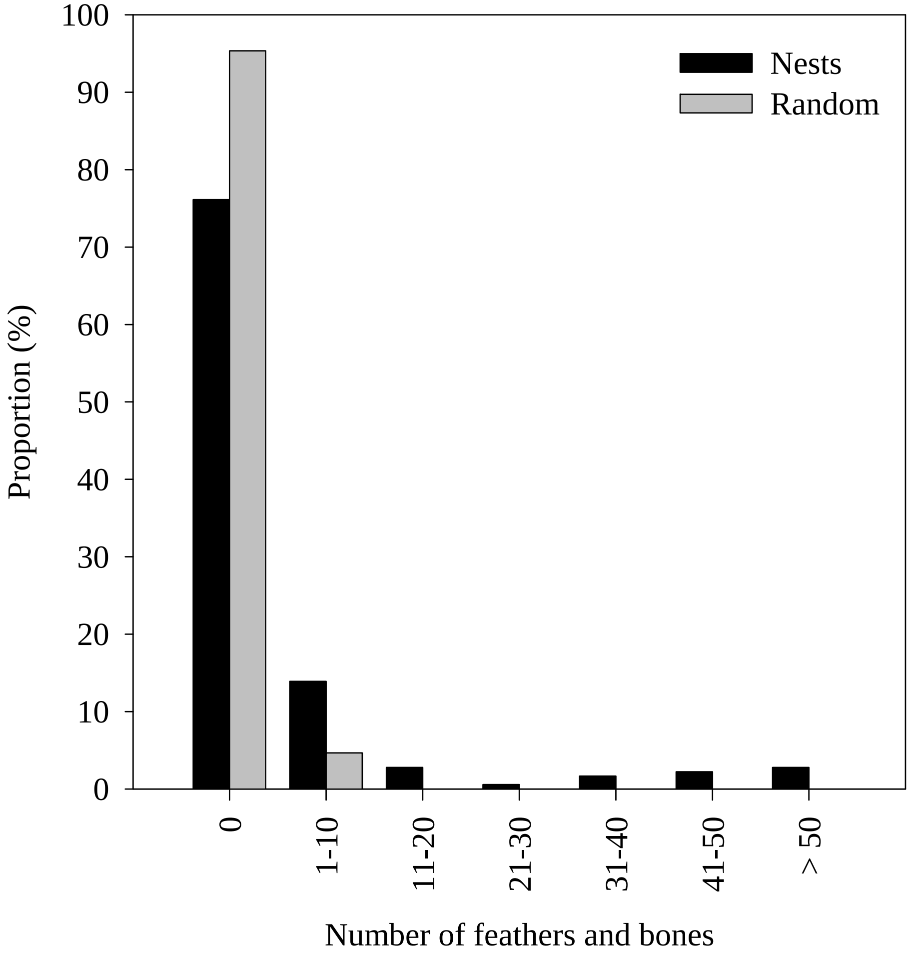

Figure 2.5. Proportion of Snowy Plover nests or random sites that contained feathers and bones within 707-cm^2 plot on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

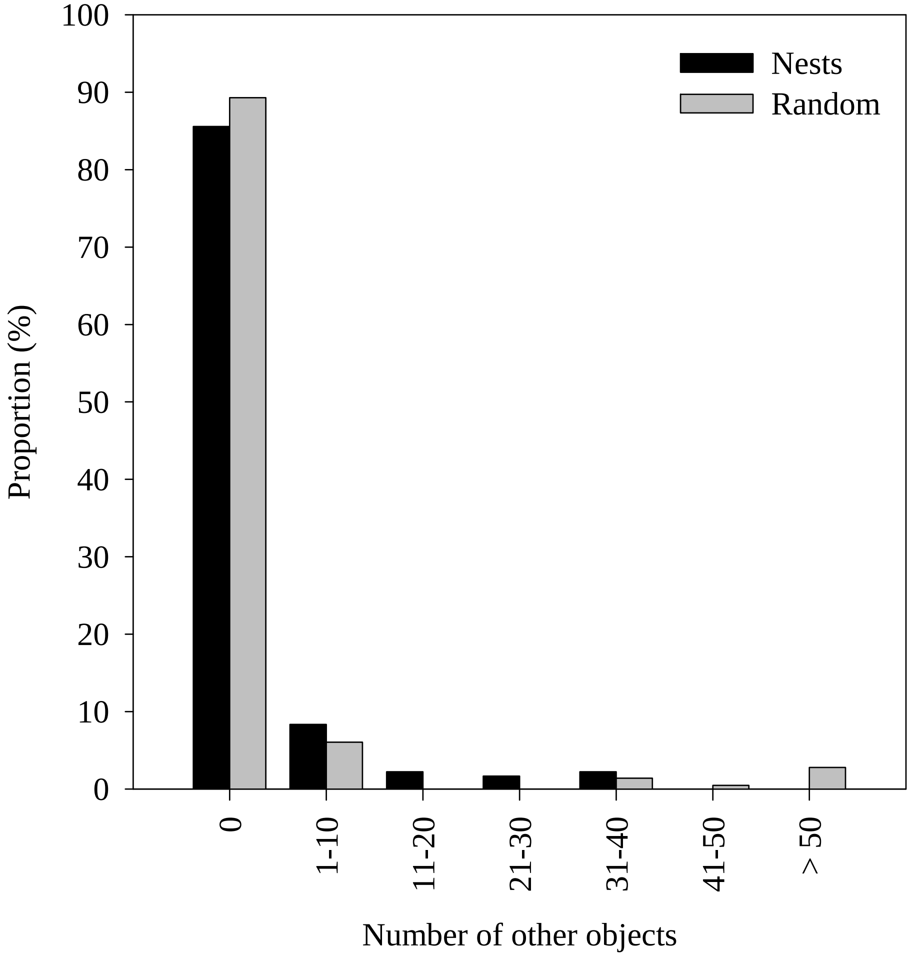

Figure 2.6. Proportion of Snowy Plover nests or random sites that contained other objects (i.e., manmade objects, cow feces, and clumps of dirt) within 707-cm^2 plot on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

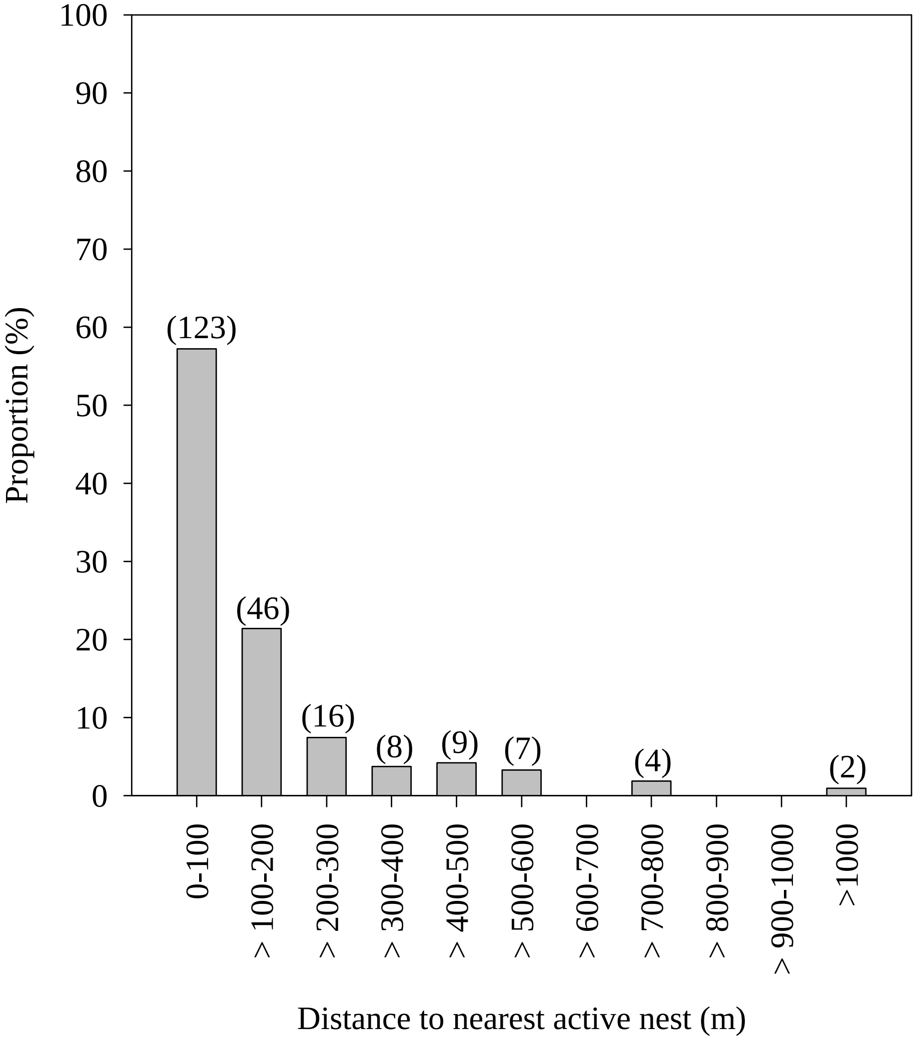

Figure 2.7. Proportion of Snowy Plover nests in relation to distance to nearest active nest on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. Numbers correspond to sample sizes of nests within distance categories.

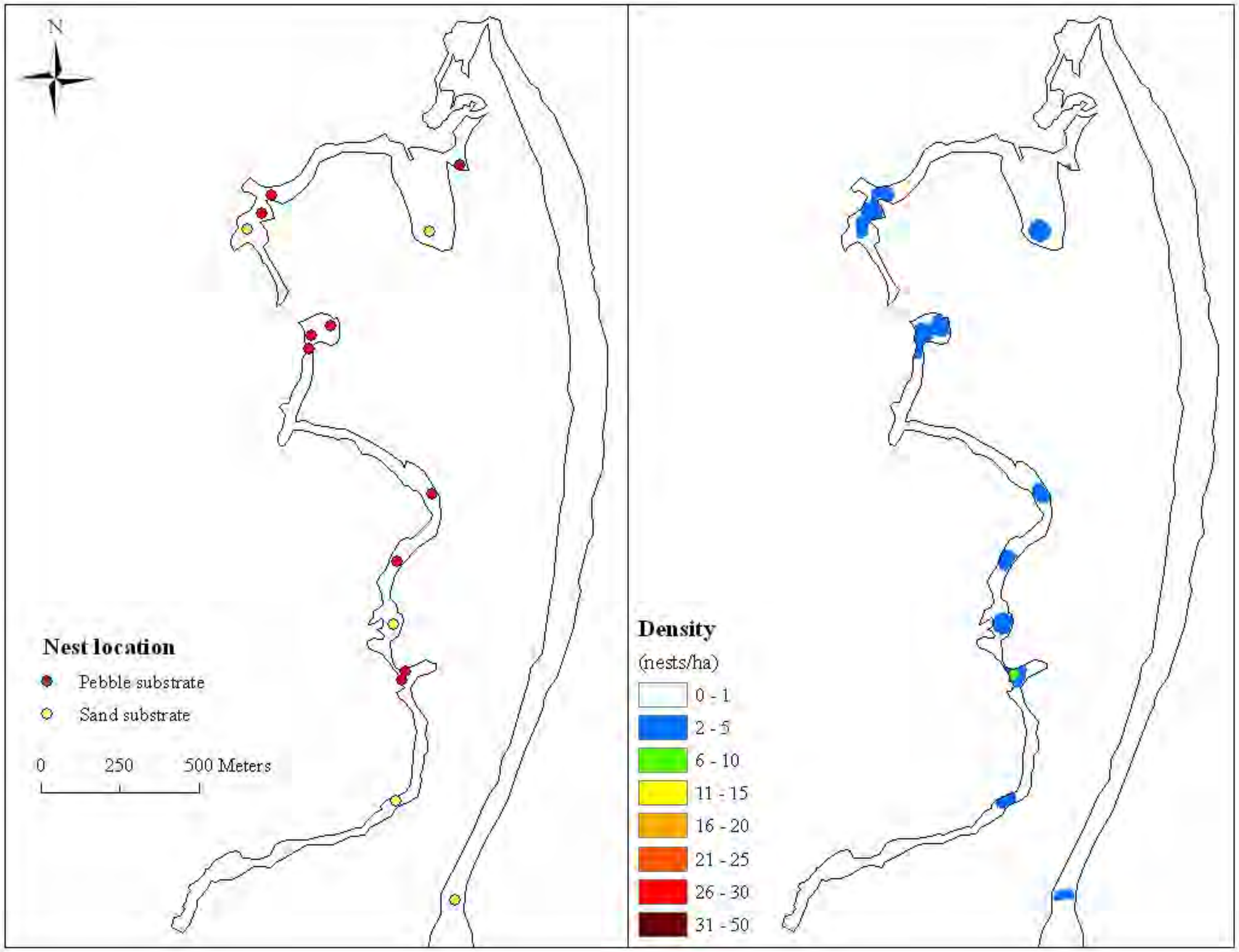

Figure 2.8. Kernel density estimates of Snowy Plover nests on lake A within the Southern High Plains of Texas, USA, 2008.

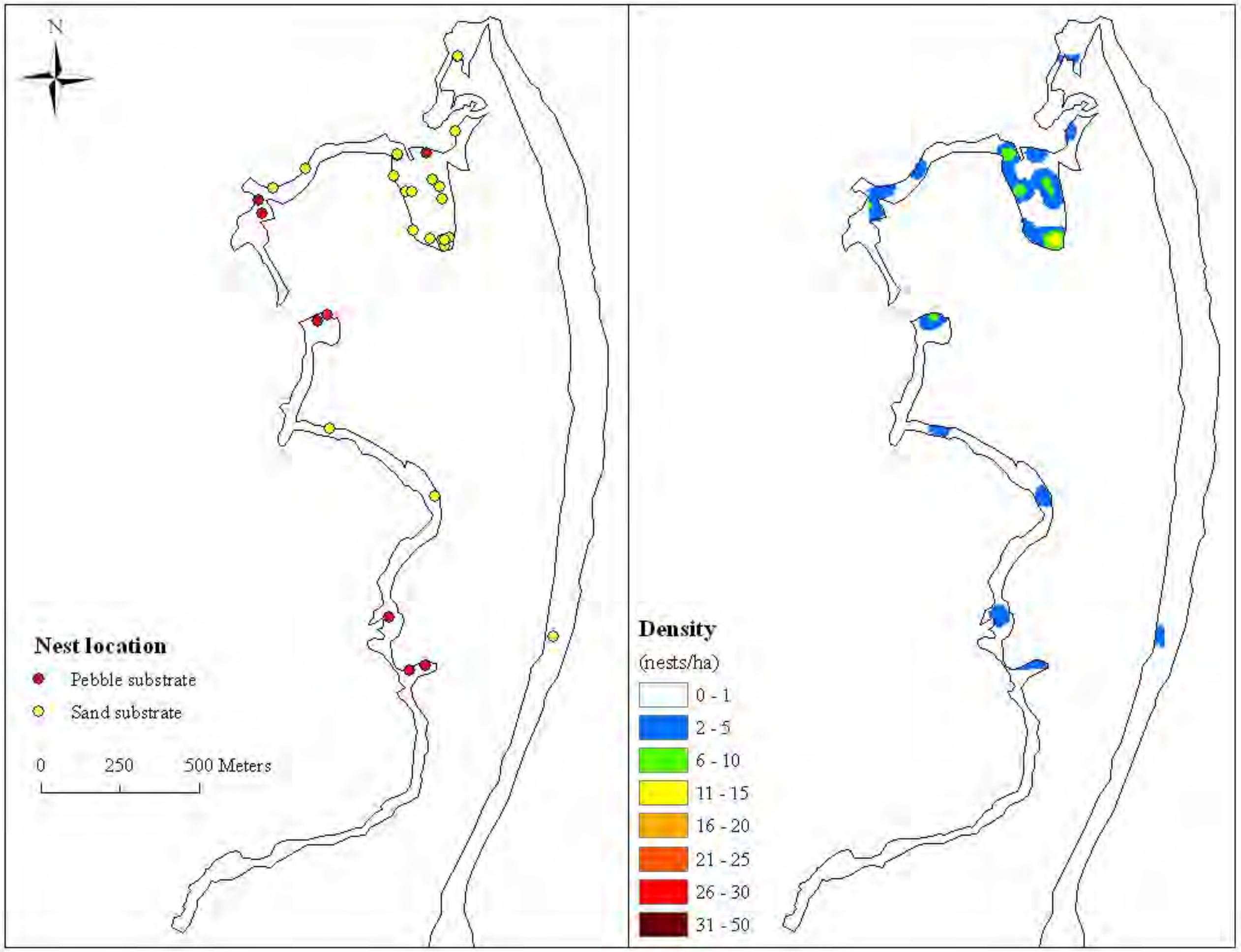

Figure 2.9. Kernel density estimates of Snowy Plover nests on lake A within the Southern High Plains of Texas, USA, 2009.

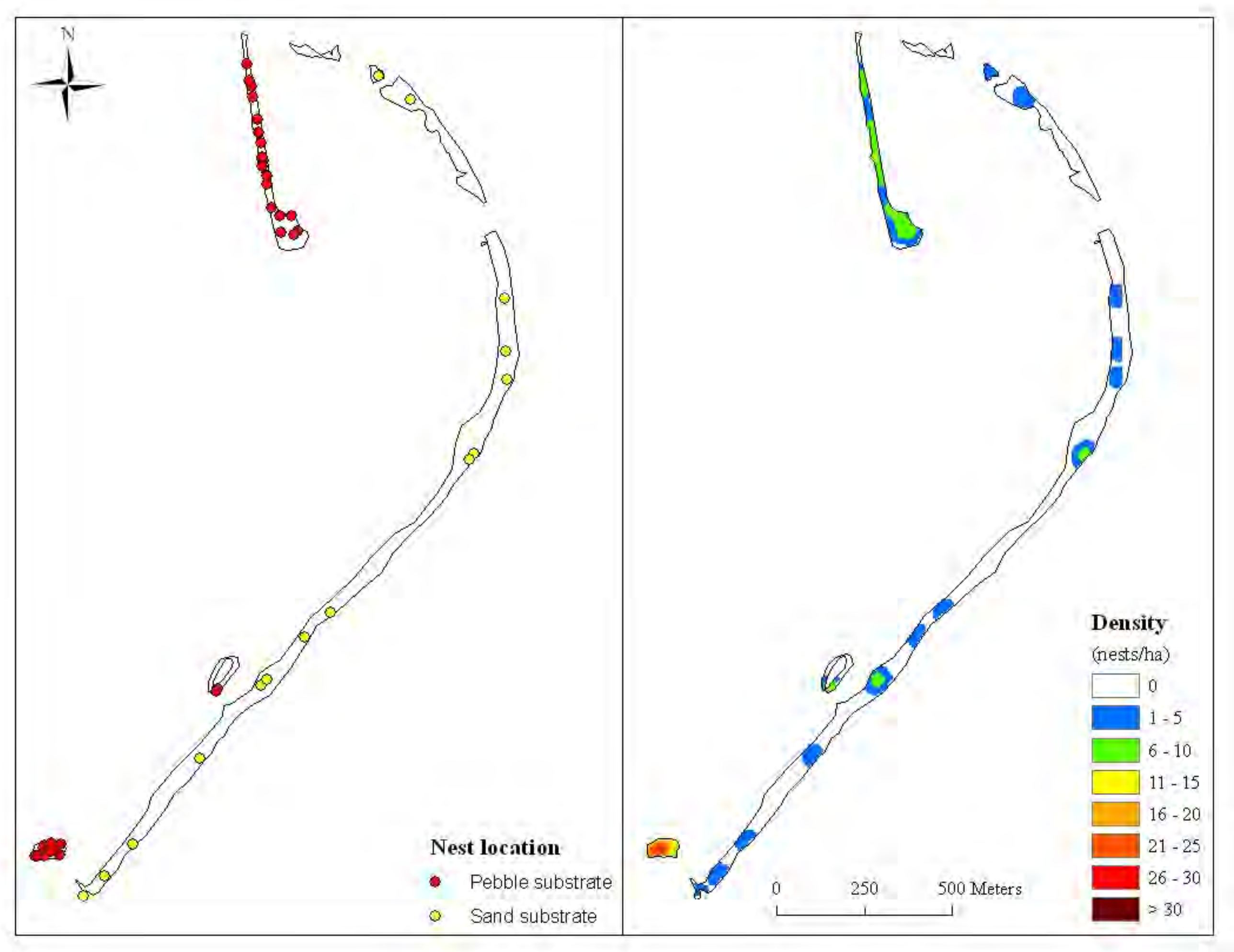

Figure 2.10. Kernel density estimates of Snowy Plover nests on lake B within the Southern High Plains of Texas, USA, 2008.

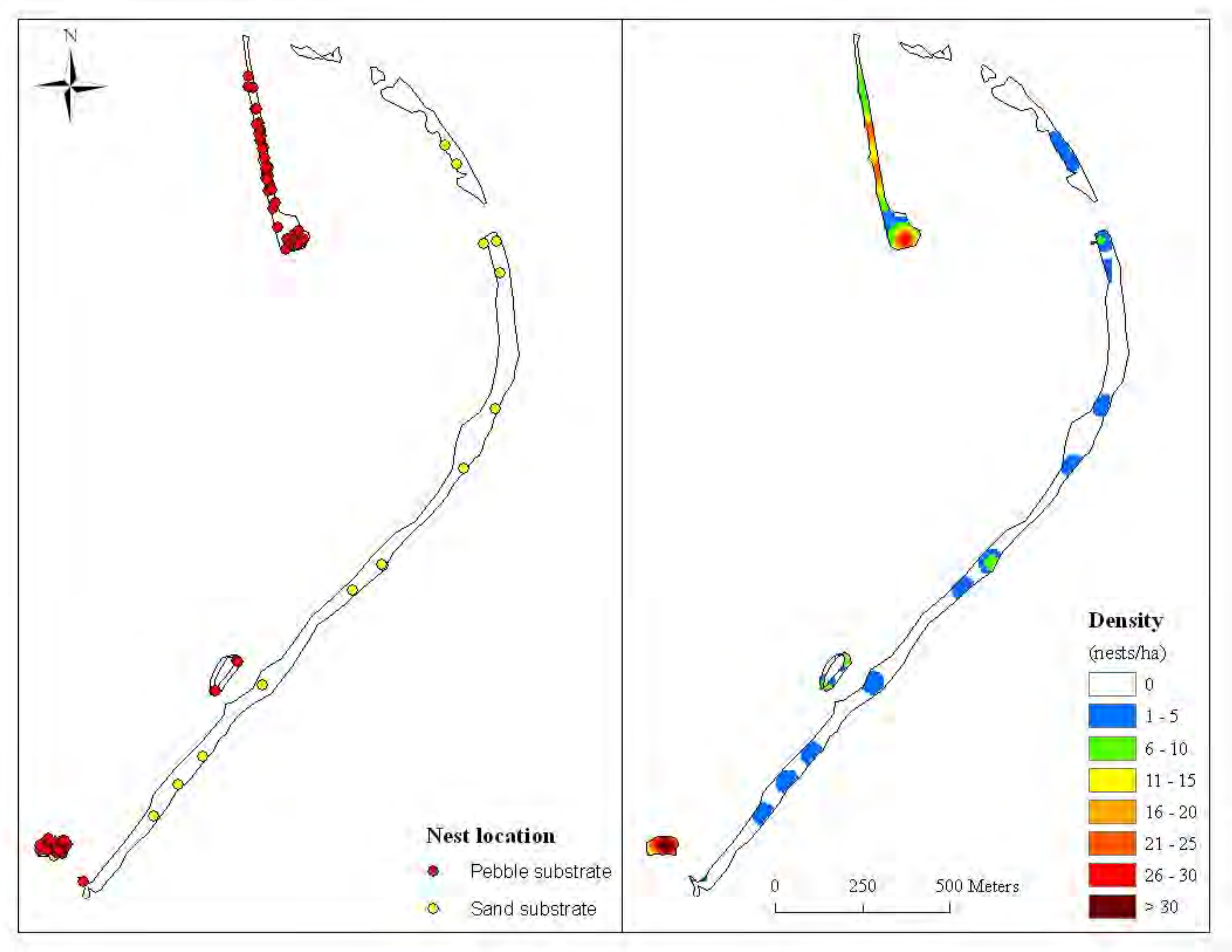

Figure 2.11. Kernel density estimates of Snowy Plover nests on lake B within the Southern High Plains of Texas, USA, 2009.

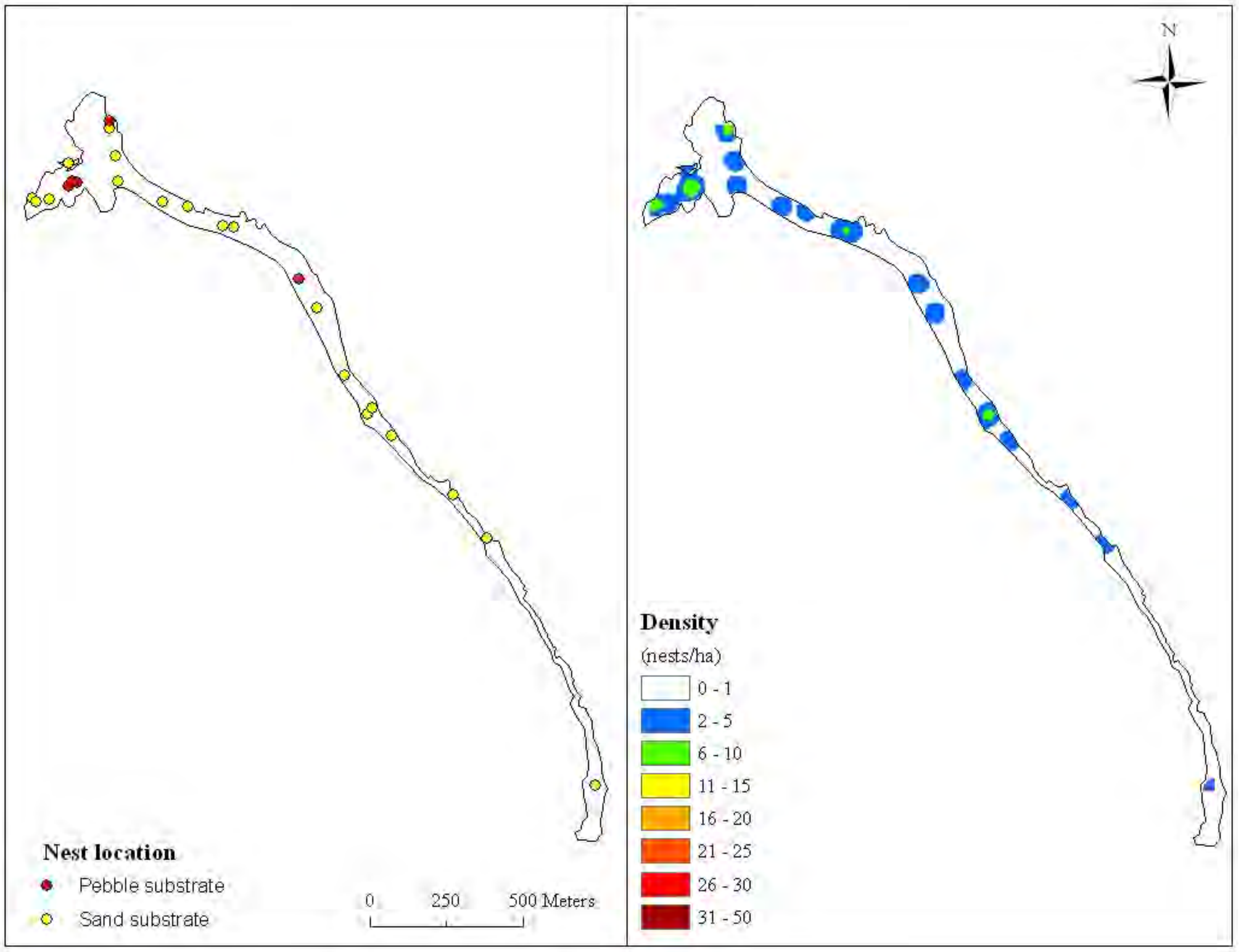

Figure 2.12. Kernel density estimates of Snowy Plover nests on lake C within the Southern High Plains of Texas, USA, 2008.

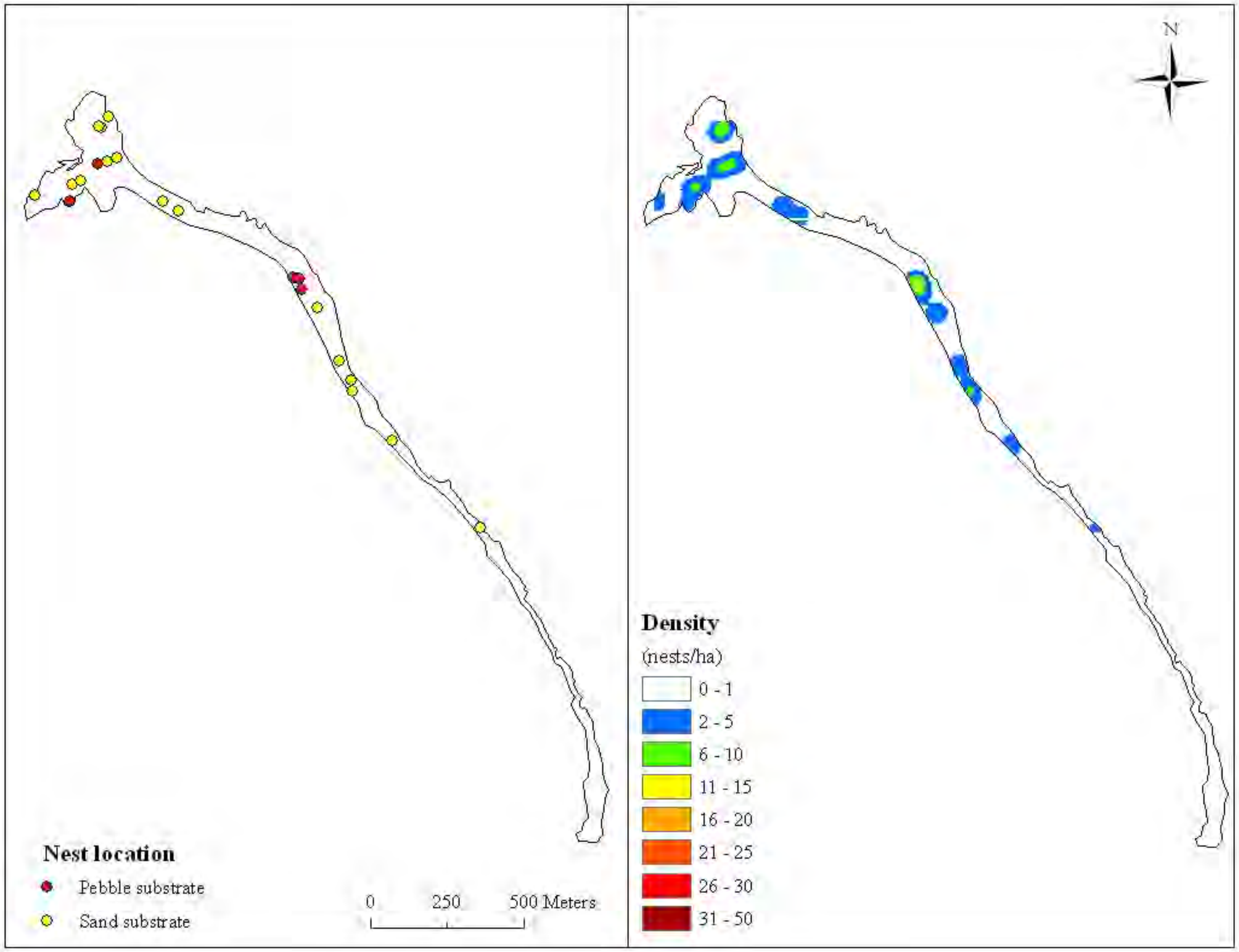

Figure 2.13. Kernel density estimates of Snowy Plover nests on lake C within the Southern High Plains of Texas, USA, 2009.

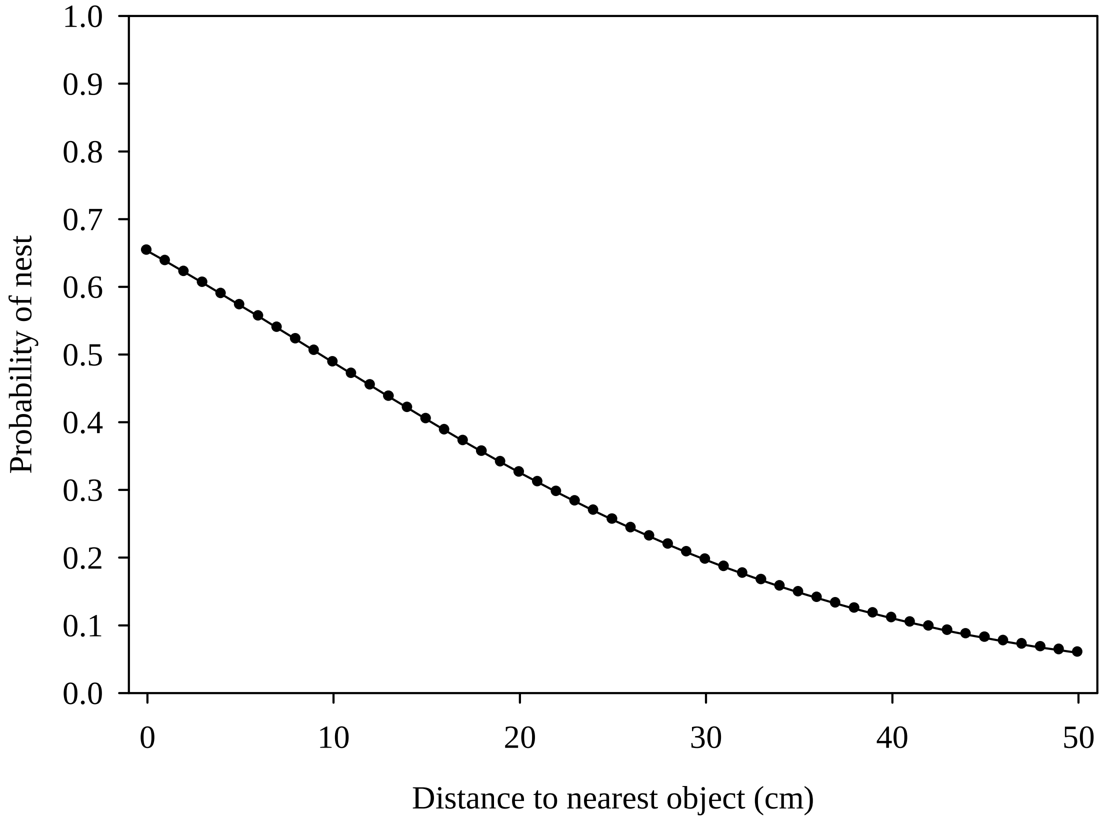

Figure 2.14. Probability of Snowy Plover nest occurrence estimated from top-ranked logistic regression model (dist. object) on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

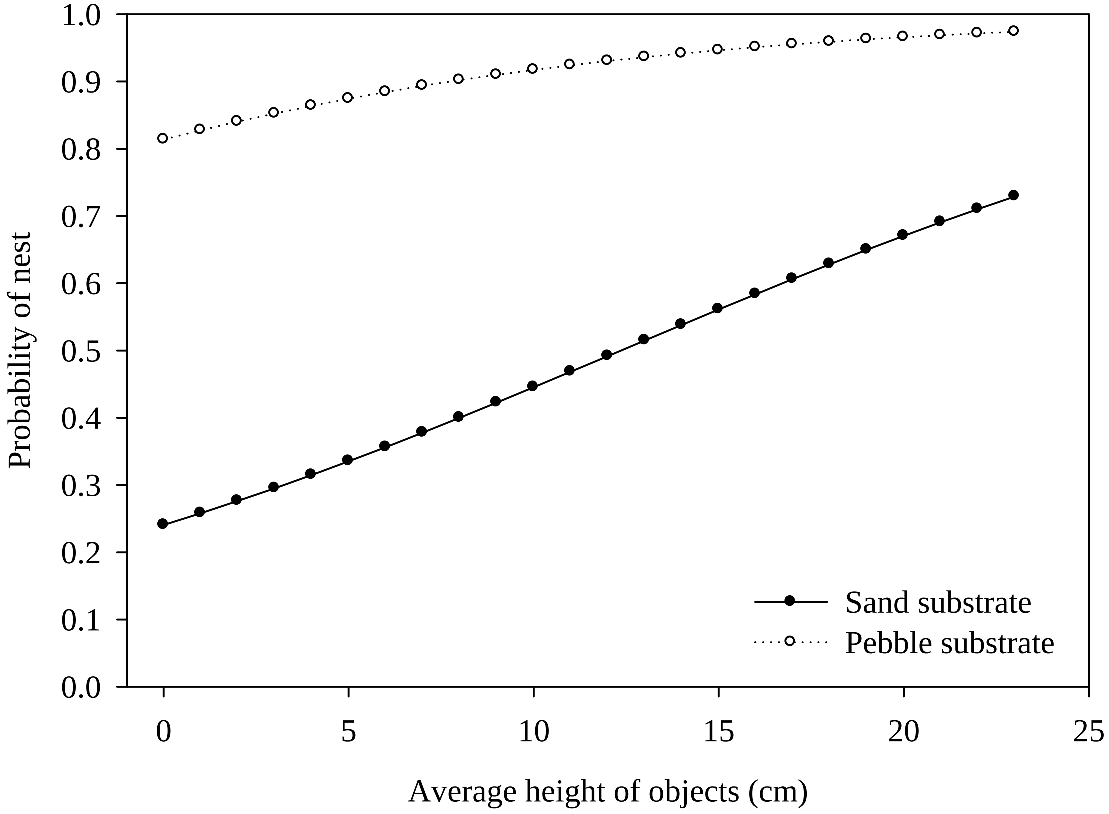

Figure 2.15. Probability of Snowy Plover nest occurrence estimated from second-ranked logistic regression model (substrate + avg. height objects) on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

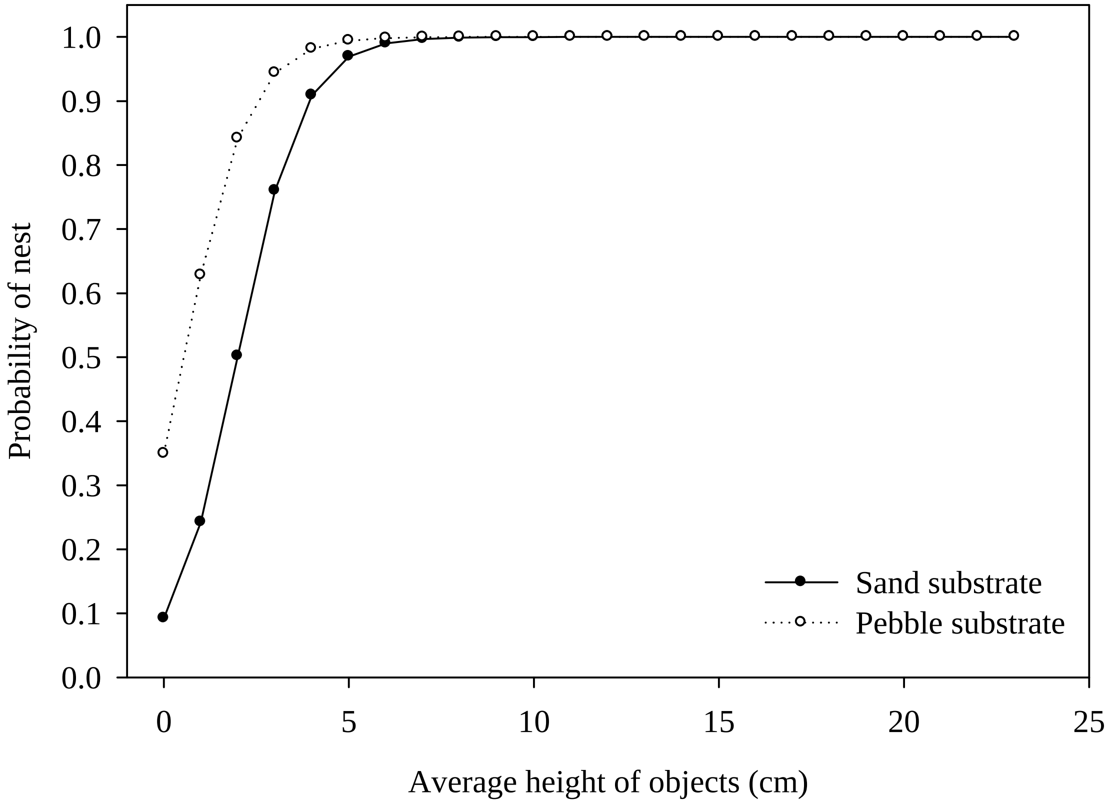

Figure 2.16. Probability of Snowy Plover nest occurrence estimated from top-ranked logistic regression model on lake A (substrate + avg. height objects) within the Southern High Plains of Texas, USA, 2008 – 2009.

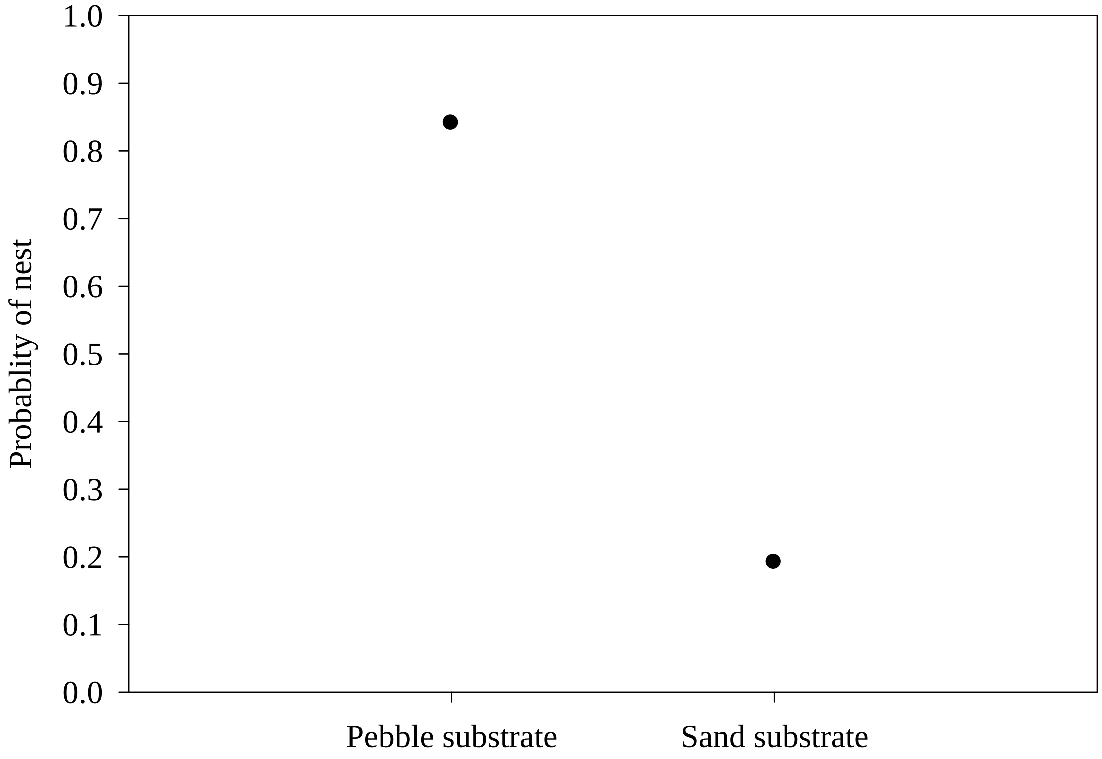

Figure 2.17. Probability of Snowy Plover nest occurrence estimated from top-ranked logistic regression model (substrate) on lake B within the Southern High Plains of Texas, USA, 2008 – 2009.

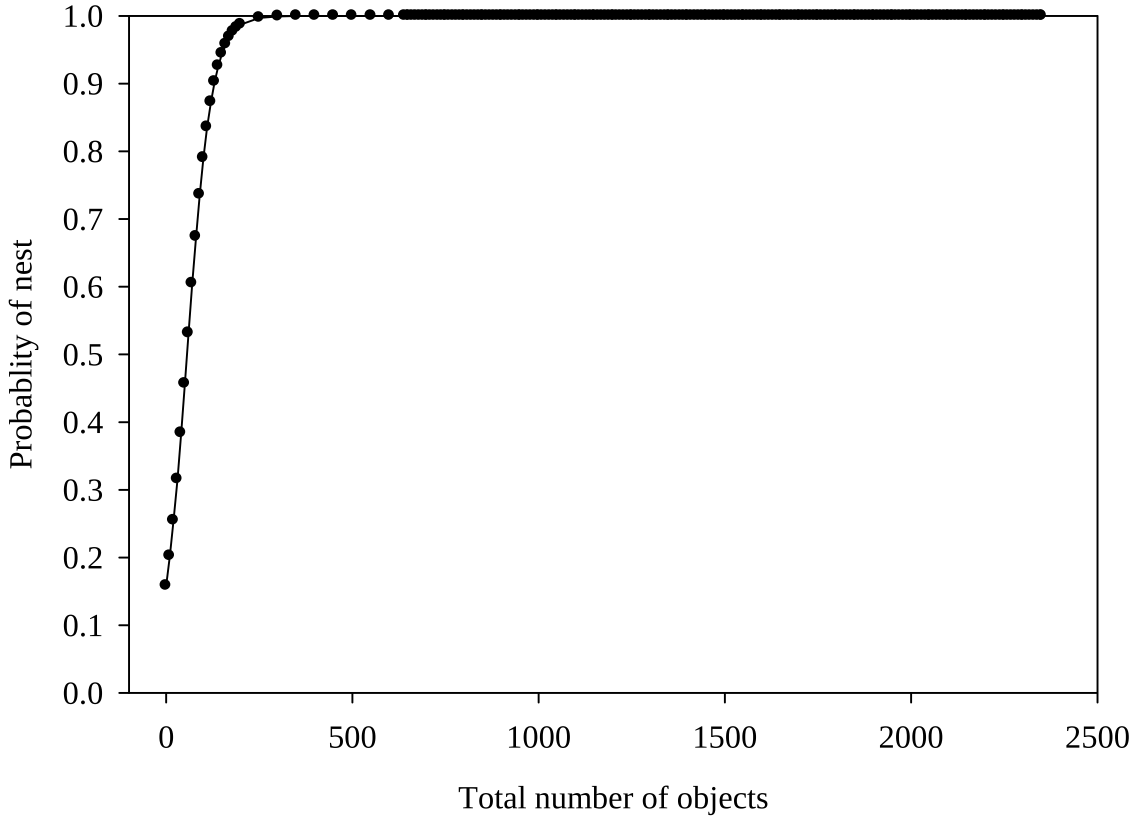

Figure 2.18. Probability of Snowy Plover nest occurrence estimated from top-ranked logistic regression model (total no. objects) on lake C within the Southern High Plains of Texas, USA, 2008 – 2009.

Table 2.1. Proportion (%) of Snowy Plover nests or random sites that contained substrate type and objects within 707-cm^2 plot on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Proportion (%)	
	Nest (*n* = 180)	Random (*n* = 215)
Sand substrate	43.3	91.2
Pebble substrate	56.7	8.8
Pebble and rock	83.3	38.6
Pebble	83.3	38.6
Rock	41.7	1.9
Plant	11.1	19.1
Woody debris	57.8	35.4
Feather and bone	23.9	4.7
Other	14.4	10.7
Cow feces	4.4	0.0
Clump of dirt	6.1	10.2
Manmade object	3.9	0.5
Any object	98.9	66.1

Table 2.2. Proportion (%) of Snowy Plover nests or random sites that contained substrate type and objects within 707-cm^2 plot on lake A within the Southern High Plains of Texas, USA, 2008 – 2009.

	Proportion (%)	
	Nest (*n* = 34)	Random (*n* = 44)
Sand substrate	61.8	90.9
Pebble substrate	38.2	9.1
Pebble and rock	94.1	65.9
Pebble	94.1	65.9
Rock	41.2	2.3
Plant	8.8	4.6
Woody debris	52.9	34.1
Feather and bone	38.2	4.6
Other	8.8	4.6
Cow feces	5.9	0.0
Clump of dirt	2.9	4.6
Manmade object	0.0	0.0
Any object	97.1	75.0

Table 2.3. Proportion (%) of Snowy Plover nests or random sites that contained substrate type and objects within 707-cm^2 plot on lake B within the Southern High Plains of Texas, USA, 2008 – 2009.

	Proportion (%)	
	Nest (*n* = 105)	Random (*n* = 125)
Sand substrate	24.8	88.0
Pebble substrate	75.2	12.0
Pebble and rock	83.8	28.0
Pebble	83.8	28.0
Rock	55.2	2.4
Plant	8.6	26.4
Woody debris	55.2	39.2
Feather and bone	13.3	4.0
Other	16.2	13.6
Cow feces	1.9	0.0
Clump of dirt	7.6	12.8
Manmade object	6.7	0.8
Any object	99.1	64.8

Table 2.4. Proportion (%) of Snowy Plover nests or random sites that contained substrate type and objects within 707-cm^2 plot on lake C within the Southern High Plains of Texas, USA, 2008 – 2009.

	Proportion (%)	
	Nest (*n* = 41)	Random (*n* = 46)
Sand substrate	75.6	100.0
Pebble substrate	24.4	0.0
Pebble and rock	73.2	41.3
Pebble	73.2	41.3
Rock	7.3	0.0
Plant	19.5	13.0
Woody debris	68.3	26.1
Feather and bone	39.0	6.5
Other	14.6	8.7
Cow feces	9.8	0.0
Clump of dirt	4.9	8.7
Manmade object	0.0	0.0
Any object	100.0	60.9

Table 2.5. Means ($\bar{x}$) and standard errors (SE) of habitat variables potentially influencing nest site selection by Snowy Plovers on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Nest (*n* = 180)		Random (*n* = 215)	
	$\bar{x}$	SE	$\bar{x}$	SE
Distance to upland (m)	161.00	12.40	73.00	8.35
Average height of surrounding objects (cm)	2.73	0.21	1.87	0.24
Distance to nearest object (cm)	4.09	0.75	25.87	1.60
Total number of objects within 707 cm^2	253.37	16.23	85.71	13.63
Number of pebbles and rocks within 707 cm^2	233.39	17.03	69.53	13.71
Number of plants within 707 cm^2	2.18	0.58	4.75	0.90
Number of woody debris within 707 cm^2	10.19	1.56	8.07	1.21
Number of feathers and bones within 707 cm^2	5.58	1.50	0.09	0.04
Number of other objects within 707 cm^2	2.02	0.51	3.25	1.07

Table 2.6. Means ($\bar{x}$) and standard errors (SE) of habitat variables potentially influencing nest site selection by Snowy Plovers on lake A within the Southern High Plains of Texas, USA, 2008 – 2009.

	Nest (n = 34)		Random (n = 44)	
	$\bar{x}$	SE	$\bar{x}$	SE
Distance to upland (m)	116.07	20.34	79.90	13.77
Average height of surrounding objects (cm)	2.88	0.55	0.72	0.20
Distance to nearest object (cm)	3.90	1.49	23.51	3.54
Total number of objects within 707 cm^2	205.79	36.82	121.80	47.23
Number of pebbles and rocks within 707 cm^2	184.94	36.89	113.75	47.46
Number of plants within 707 cm^2	0.56	0.38	0.64	0.55
Number of woody debris within 707 cm^2	14.38	4.14	7.27	2.98
Number of feathers and bones within 707 cm^2	5.47	2.02	0.07	0.05
Number of other objects within 707 cm^2	0.44	0.26	0.07	0.05

Table 2.7. Means ($\bar{x}$) and standard errors (SE) of habitat variables potentially influencing nest site selection by Snowy Plovers on lake B within the Southern High Plains of Texas, USA, 2008 – 2009.

	Nest (*n* = 105)		Random (*n* = 125)	
	$\bar{x}$	SE	$\bar{x}$	SE
Distance to upland (m)	224.74	17.44	85.99	13.19
Average height of surrounding objects (cm)	2.66	0.20	2.52	0.37
Distance to nearest object (cm)	4.24	1.08	25.03	2.13
Total number of objects within 707 cm^2	310.37	22.03	97.54	16.06
Number of pebbles and rocks within 707 cm^2	298.39	22.87	76.48	16.27
Number of plants within 707 cm^2	1.37	0.63	7.03	1.42
Number of woody debris within 707 cm^2	6.88	1.32	9.59	1.59
Number of feathers and bones within 707 cm^2	1.14	0.56	0.09	0.05
Number of other objects within 707 cm^2	2.58	0.75	4.35	1.57

Table 2.8. Means ($\bar{x}$) and standard errors (SE) of habitat variables potentially influencing nest site selection by Snowy Plovers on lake C within the Southern High Plains of Texas, USA, 2008 – 2009.

	Nest (*n* = 41)		Random (*n* = 46)	
	$\bar{x}$	SE	$\bar{x}$	SE
Distance to upland (m)	35.01	3.69	31.13	4.81
Average height of surrounding objects (cm)	2.78	0.61	1.21	0.43
Distance to nearest object (cm)	3.89	1.30	30.43	3.27
Total number of objects within 707 cm^2	146.85	21.84	19.02	4.67
Number of pebbles and rocks within 707 cm^2	107.12	23.78	8.37	2.64
Number of plants within 707 cm^2	5.59	1.88	2.50	1.28
Number of woody debris within 707 cm^2	15.20	4.75	4.72	2.32
Number of feathers and bones within 707 cm^2	17.05	5.91	0.13	0.08
Number of other objects within 707 cm^2	1.90	1.11	3.30	2.55

Table 2.9. Logistic regression models for habitat variables predicting Snowy Plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
Dist. object	2	0.00	0.52
Substrate + avg. height objects[c]	3	0.28	0.45
Substrate	2	6.07	0.03
Avg. height objects + total no. objects	3	50.04	0.00
Total no. objects + no. plants	3	52.43	0.00
Total no. objects	2	53.28	0.00
Avg. height objects + no. pebbles/rocks	3	57.12	0.00
No. pebbles/rocks	2	64.10	0.00
No. feathers/bones	2	75.30	0.00
Dist. upland + avg. height objects	3	77.22	0.00
Dist. upland	2	83.01	0.00
Avg. height objects	2	111.10	0.00
No. plants	2	112.37	0.00
Intercept[d]	1	116.00	0.00
No. woody debris	2	116.84	0.00
No. other objects	2	117.02	0.00

[a] Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[b] AICc relative weight attributed to model.

[c] Model of additive effects of substrate type and average height of surrounding objects.

[b] Model of no effects.

Table 2.10. Characteristics of plausible (i.e., $\Delta AIC_c < 2$) top-ranked logistic regression models for habitat variables predicting Snowy Plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

Parameter	Estimate	SE	χ^2	*P*
Top-ranked model				
Intercept	0.631	0.131	23.31	<0.001
Dist. object	-0.068	0.009	62.43	<0.001
Second-ranked model				
Intercept	-1.150	0.161	50.83	<0.001
Substrate	2.626	0.285	84.91	<0.001
Avg. height objects	0.093	0.033	7.71	0.006

Table 2.11. Logistic regression models for habitat variables predicting Snowy Plover nests on lake A within the Southern High Plains of Texas, USA, 2008 – 2009.

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
Substrate + avg. height objects[c]	3	0.00	0.74
Avg. height objects	2	3.65	0.12
Avg. height objects + total no. objects	3	4.89	0.06
Avg. height objects + no. pebbles/rocks	3	4.98	0.06
Substrate + dist. object	3	10.13	0.00
Substrate + dist. object + no. plants	4	12.20	0.00
Dist. object + total no. objects	3	14.17	0.00
Dist. object	2	14.33	0.00
Dist. object + no. pebbles/rocks	3	14.52	0.00
Dist upland + dist. object + total no. objects	4	14.81	0.00
No. feathers/bones	2	15.00	0.00
Dist. object + total no. objects + no. pebbles/rocks	4	15.11	0.00
Dist. upland + dist. object + no. pebbles/rocks	4	15.16	0.00
Dist. upland + dist. object	3	15.76	0.00
Dist. object + total no. objects + no. plants	4	16.11	0.00
Dist. object + no. plants	3	16.11	0.00
Dist. object + no. pebbles/rocks + no. plants	4	16.45	0.00
Dist. upland + dist. object + total no. objects + no. plants	5	16.60	0.00
Dist. upland + dist. object + no. pebbles/rocks + no. plants	5	16.95	0.00
Dist. upland + dist. object + no. plants	4	17.41	0.00
Substrate	2	25.23	0.00
Substrate + no. plants	3	27.38	0.00

Table 2.11. Continued.

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
Dist. upland + total no. objects	3	31.73	0.00
No. other objects	2	32.16	0.00
Dist. upland + no. pebbles/rocks	3	32.42	0.00
Dist. upland	2	32.68	0.00
Intercept[d]	1	32.87	0.00
No. woody debris	2	32.93	0.00
Total no. objects	2	33.10	0.00
No. pebbles/rocks	2	33.66	0.00
Dist. upland + total no. objects + no. plants	4	33.86	0.00
Dist. upland + no. pebbles/rocks + no. plants	4	34.56	0.00
Dist upland + no. plants	3	34.73	0.00
No. plants	2	34.97	0.00
Total no. objects + no. plants	3	35.27	0.00
No. pebbles/rocks + no. plants	3	35.82	0.00

[a] Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[b] AICc relative weight attributed to model.

[c] Model of additive effects of substrate type and average height of surrounding objects.

[b] Model of no effects.

Table 2.12. Characteristics of plausible (i.e., $\Delta AIC_c < 2$) logistic regression model for habitat variables predicting Snowy Plover nests on lake A within the Southern High Plains of Texas, USA, 2008 – 2009.

Parameter	Estimate	SE	χ^2	*P*
Top-ranked model				
Intercept	-2.286	0.531	18.54	<0.001
Substrate	1.664	0.724	5.29	0.022
Avg. height objects	1.146	0.286	16.08	<0.001

Table 2.13. Logistic regression models for habitat variables predicting Snowy Plover nests on lake B within the Southern High Plains of Texas, USA, 2008 – 2009.

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
Substrate	2	0.00	0.64
Substrate + avg. height objects[c]	3	1.18	0.35
Dist. object	2	41.53	0.00
No. pebbles/rocks	2	45.15	0.00
Avg. height objects + no. pebbles/rocks	3	45.91	0.00
Total no. objects	2	46.30	0.00
Avg. height objects + total no. objects	3	48.26	0.00
Dist. upland	2	64.30	0.00
Dist. upland + avg. height objects	3	65.54	0.00
No. plants	2	88.30	0.00
No. feathers/bones	2	94.17	0.00
Intercept[d]	1	99.83	0.00
No. woody debris	2	100.19	0.00
No. other objects	2	100.89	0.00
Avg. height objects	2	101.77	0.00

[a] Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[b] AICc relative weight attributed to model.

[c] Model of additive effects of substrate type and average height of surrounding objects.

[b] Model of no effects.

Table 2.14. Characteristics of plausible (i.e., $\Delta AIC_c < 2$) logistic regression models for habitat variables predicting Snowy Plover nests on lake B within the Southern High Plains of Texas, USA, 2008 – 2009.

Parameter	Estimate	SE	χ^2	*P*
Top-ranked model				
Intercept	-1.442	0.218	43.75	<0.001
Substrate	3.104	0.356	75.92	<0.001
Second-ranked model				
Intercept	-1.576	0.266	35.01	<0.001
Substrate	3.130	0.359	76.02	<0.001
Avg. height objects	0.045	0.048	0.91	0.341

Table 2.15. Logistic regression models for habitat variables predicting Snowy Plover nests on lake C within the Southern High Plains of Texas, USA, 2008 – 2009.

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
Total no. objects	2	0.00	0.47
Avg. height objects + total no. objects[c]	3	0.83	0.31
Total no. objects + no. plants	3	2.14	0.16
Dist. object	2	4.15	0.06
Avg. height objects + no. pebbles/rocks	3	16.92	0.00
No. pebbles/rocks + no. plants	3	19.55	0.00
No. pebbles/rocks	2	20.05	0.00
No. feathers/bones	2	25.84	0.00
Avg. height objects	2	39.48	0.00
No. woody debris	2	39.72	0.00
Dist. upland + avg. height objects	3	40.37	0.00
Intercept[d]	1	42.60	0.00
No. plants	2	42.74	0.00
Dist. upland + no. plants	3	44.01	0.00
Dist upland	2	44.29	0.00
No. other objects	2	44.45	0.00

[a] Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[b] AICc relative weight attributed to model.

[c] Model of additive effects of average height of objects and total number of objects.

[b] Model of no effects.

Table 2.16. Characteristics of plausible (i.e., $\Delta AIC_c < 2$) logistic regression models for habitat variables predicting Snowy Plover nests on lake C within the Southern High Plains of Texas, USA, 2008 – 2009.

Parameter	Estimate	SE	χ^2	*P*
Top-ranked model				
Intercept	-1.675	0.392	18.28	<0.001
Total no. objects	0.030	0.007	18.07	<0.001
Second-ranked model				
Intercept	-1.803	0.416	18.83	<0.001
Avg. height objects	0.081	0.075	1.19	0.276
Total no. objects	0.029	0.007	16.66	<0.001

CHAPTER III

SNOWY PLOVER NEST TEMPERATURES IN THE SOUTHERN HIGH PLAINS OF TEXAS

INTRODUCTION

Avian incubation is generally defined as regulating egg temperatures so that developing embryos are maintained within thermally neutral zones (i.e., range of temperatures required for successful development; White and Kinney 1974, Carey 1980). For most birds, incubation results in adults transferring body heat to eggs to maintain egg temperatures greater than surrounding ambient temperatures (White and Kinney 1974). However, some species, including Snowy Plovers (*Charadrius alexandrinus*), nest in areas with little to no cover and high ambient air temperatures (> 40°C), creating a hot, thermally stressful nesting environment (Purdue 1976a, Purdue 1976b, Page et al. 1985, Warriner et al. 1986). Therefore, these species must cool eggs during incubation in order for them to remain viable.

Maintaining eggs within the thermal neutral zone must be achieved through incubation strategies that allow adults to acquire sufficient nutrients (White and Kinney 1974), avoid predation of themselves and nests, and cope with heat stress and energy demands (Hinsley and Ferns 1994). Within Charadriidae, several adaptive behaviors have developed to allow incubating parents, eggs, and chicks to cope with extremely high temperatures. For example, in Snowy and Kentish Plovers (*Charadrius alexandrinus*), biparental incubation, shading nests, belly soaking, standing in water, panting, and gular fluttering may singularly or synergistically alleviate heat stress (Maclean 1975, Kainady and Al-Dabbagh 1976, Purdue 1976a, Purdue 1976b, Amat and Masero 2004a).

Biparental incubation allows caregiving adults to constantly attend and/or incubate eggs, while intermittently acquiring food, resting, and/or alleviating heat stress (White and Kinney 1974, Carey 1980, Hinsley and Ferns 1994, Kosztolányi et al. 2009, AlRashidi et al. 2010). Female Kentish and Snowy Plovers dominate diurnal incubation, while males are thought to incubate nocturnally (Kosztolányi and Székely 2002, Amat and Masero 2004a). However, during periods of high ambient temperatures and/or when incubating nests in exposed sites, the probability of diurnal male incubation increases as females are unable to incubate continuously during thermally stressful times (Purdue 1976b, Ward 1990, Amat and Masero 2004a). At nests, adult Kentish and Snowy Plovers can aid thermoregulation of themselves and their eggs by panting (Kainady and Al-Dabbagh 1976, Grant 1982, Ward 1990, Amat and Masero 2004a), gular fluttering (Kainady and Al-Dabbagh 1976, Ward 1990, Amat and Masero 2004a), utilizing postures that lower body temperatures (e.g., shading posture: Downs and Ward 1997, standing: Amat and Masero 2004a), and shading from direct sunlight (Purdue 1976b, Grant 1982, Bergstrom 1989, Ward 1990). However, when temperatures become too high, adults leave nests to thermoregulate by belly soaking (i.e., wetting of the ventral plumage in order to aid in heat dissipation of adults and/or eggs; Maclean 1975, Kainady and Al-Dabbagh 1976, Grant 1982, Bergstrom 1989, Amat and Masero 2004a, Amat and Masero 2007, Amat and Masero 2009) or standing in water (Purdue 1976a) or shade (Maclean

1967). Therefore, by sharing parental duties, adults keep eggs within the thermal neutral zone while maintaining their individual needs (i.e., food acquisition, thermoregulation, etc.), tasks likely unable to be achieved solely by one parent (White and Kinney 1974, Carey 1980, Hinsley and Ferns 1994).

Adaptive behaviors to alleviate heat stress are physiologically costly (i.e., increased energy expenditure; Hinsley and Ferns 1994) and could potentially increase predation risks for adults and nests, as adults performing these behaviors tend to be more conspicuous. Therefore, to lessen conspicuousness, Snowy Plovers should select nest sites that are both thermally favorable (e.g., high degree of cover/shading and cooler substrates; Kainady and Al-Dabbagh 1976, Page et al. 1985, Bergstrom 1989, Amat and Masero 2004a, Amat and Masero 2004b) and reduce predation risks to incubating adults and eggs. For example, nest sites with lower ambient temperatures should allow parents to alleviate heat stress during incubation by reducing both time spent performing conspicuous adaptive behaviors and associated negative costs (Kainady and Al-Dabbagh 1976, Page et al. 1985, Amat and Masero 2004a, Amat and Masero 2004b). However, selecting thermally favorable nest sites (especially nests sites with ample cover) can be costly as such nests experience greater predation rates than presumed less thermally suitable nests (Amat and Masero 2004b, see Chapters I and II). Selection of nest sites with little or no cover is likely an adaptive behavior that facilitates early detection of predators by incubating parents (Burger 1987, Götmark et al. 1995, Lauro and Nol 1995, Amat and Masero 2004b), but may be costly to thermoregulate. Therefore, only adults in good condition, able to compensate for, or withstand, high physiological incubation costs in a thermally stressful environment, may select nests in open areas (Amat and Masero 2004b). Furthermore, adult condition may influence nest temperatures, as better condition adults may be able to leave nests less frequently to perform thermoregulating behaviors, maintain eggs at more stable temperatures, initiate nesting earlier in the season (Perrins 1996) when ambient temperatures are less extreme, and/or outcompete individuals for more thermally favorable nest sites (i.e., shaded, cooler substrate, or closer to water sources).

In the Southern High Plains (SHP) of Texas, Snowy Plovers nest within a semi-arid, thermally stressful saline lake environment, where incubation temperatures and mechanisms by which Snowy Plovers alleviate thermal stress are unknown. No work in North America has quantified the heat stress intensity experienced by Snowy Plovers nesting in these habitats as related to adaptive behaviors and landscape features (i.e., surface water presence) that may alleviate thermal stress during incubation. How Snowy Plovers alleviate heat stress (e.g., selection of thermally favorable nest sites) may provide insight for developing enhanced regional habitat conservation guidelines. Therefore, the objectives of this study were to examine incubation temperatures of Snowy Plover nests on saline lakes within the SHP of Texas in relation to 1) ambient substrate (i.e., control) temperatures, 2) year, 3) month, 4) study site (i.e., saline lake), 5) nest site selection (i.e., substrate type and amount of cover), 6) nest success, 7) parental condition, and 8) time during incubation.

METHODS

Study Area

The SHP is an approximately 80,000 km^2 region occurring from the panhandle of Texas, into New Mexico, and south to Midland, Texas (Osterkamp and Wood 1987). Within this region, approximately 40 saline lakes (i.e., primary regional nesting location for Snowy Plovers; Conway et al. 2005) occur (Reeves and Temple 1986). Saline lakes are discharge wetlands containing freshwater springs fed by the Ogallala aquifer (Brune 2002), but having an overall saline water chemistry (often > 200g/L of dissolved solids; Osterkamp and Wood 1987). Three previously identified important (i.e., having consistent surface water throughout the nesting season and containing the majority of regional nesting Snowy Plovers) saline lakes (Conway et al. 2005) ranging in size from ~ 270 – 600 ha were used as study sites in 2008 and 2009 (Figure 1.1). To maintain landowner anonymity, study site lakes will be referred to as lake A, lake B, and lake C. Each study site lake contained two – six fresh to slightly saline springs distributed along lake margins (Brune 2002). The primary landuse practice immediately surrounding study site lakes was pasture/rangeland with some held within the Conservation Reserve/Permanent Cover Program. Other landuse practices occurring within surrounding areas included row-crop agriculture production (i.e., mostly cotton

[*Gossypium* spp.]), mineral excavation (e.g., caliche), and development (i.e., mostly small home/ranch developments).

Nest Surveys

Surveys were conducted ≥ 1 time per week at each lake during the breeding season (i.e., early April – mid August; Conway et al. 2005; see Chapter I) in 2008 – 2009 to locate new nests and/or scrapes or monitor known nests until nest fate was determined. Nests were located by observing adult Snowy Plovers incubating nests, flushing from or returning to nest sites, and searching appropriate habitat (Conway et al. 2005). If a nest was discovered with one egg, it was assumed that the nest was initiated the day of discovery; however if nests were discovered with two eggs, it was assumed that the nest was initiated the day prior to discovery. If nests were located after all three eggs (modal clutch size) were laid, eggs were floated to determine incubation stage (Hays and LeCroy 1971).

Nests were checked ≥ 1 time per week until nest fate was determined. A successful nest was defined as a nest in which ≥ 1 egg hatched (Mayfield 1975). Evidence of hatching included visually locating chicks in/near nest, breeding pair displaying distraction displays, and/or presence of egg shell fragments indicative of hatching (i.e., < 1 mm shell fragments found in scrape and/or top or bottom of egg shell located < 10 m from nest with membrane detached; Mabee 1997). Nests were considered failed when 1) eggs were absent prior to estimated hatching date, 2) presence of signs of predation or trampling, 3) evidence suggested nests were destroyed by weather (i.e., hail, wind, flooding, etc.), or 4) evidence suggested abandonment (i.e., eggs were present one week after estimated hatching date or when one egg was moved such that the smaller end pointed up and remained for > 24 hrs). If nest fate did not match these definitions, fate was classified as unknown (Manolis et al. 2000). After nest fate was determined, local habitat characteristics were measured and included classification of primary nest substrate (i.e., sand or pebble; see Chapter II for details).

Nest Temperature Determination

To estimate nest temperatures, Thermochron iButtons (Model DS1922L; Maxim Integrated Products, Inc., Sunnyvale, CA) were placed within a subset of nests upon discovery. Temperature probes were randomly distributed among study sites, nests, and laying dates throughout the nesting season. To estimate ambient substrate temperatures, iButtons were placed at nearby sites (i.e., hereafter referred to as control) < 10 m from nest with similar microhabitat (e.g., substrate type, vegetative cover, etc.). iButtons were attached to galvanized nails with Velcro similar to Schneider and McWilliams (2007) to deter removal by adults. All iButtons were placed just beneath (i.e., < 2 cm) the substrate in the nest (adjacent to or underneath eggs) or control location to eliminate any potential negative effects (i.e., predator detection, heat conductance, or disturbance to incubating birds) of iButtons being visible on the surface. iButtons were programmed to record temperatures at ≤ 1-hour intervals; however, to remain consistent among nests, only 1-hour intervals were included in analyses.

Capture and Handling

Adult Snowy Plovers were captured on nests using nest traps (Conway and Smith 2000) from early April – early August, 2008 – 2009. Adults were sexed in the field based upon plumage characteristics, where males generally have larger and darker breast and forehead patches as compared to females. All adults were banded with a uniquely numbered U.S. Fish and Wildlife Service aluminum band on the upper part (i.e., tibiotarsus) of their left leg, a dark green color band on the upper part of their right leg, and a unique combination of two color bands on both right and left lower legs. Upon capture, body mass (g) and the following morphological characteristics were measured for each adult (see Pyle et al. 1987 for descriptions): wing chord (mm), flattened wing chord (mm), tarsus (mm), tail (mm), culmen (mm), bill depth (mm), bill width (mm), and head length (mm). Mass was measured to the nearest 0.1 g with a digital scale (Ohaus® Scout Pro Balance, Pine Brook, NJ). Wing chord and flattened wing chord length were measured with a wing rule from the carpal joint to the tip of the longest primary, with wings pressed flat against a ruler for flattened wing chord measurement. Tarsus length was measured with calipers from the intertarsal joint to the distal end of the last leg scale.

Tail length was measured with a ruler parallel to the tail from the point of insertion to the tip of tail. Culmen, bill length, bill width, and head length were measured with calipers. Culmen was measured from the anterior end of the nostril to the tip of bill, bill depth from the anterior end of the nostrils to the lower mandible perpendicular to the bill length measurement, bill width perpendicular to the bill length measurement at the anterior end of the nostrils, and head length from the back to the front of the head.

DATA ANALYSIS

To include only nest temperature data during which parental incubation was known to occur, nest temperature data were truncated to 0700 h the last observed active day for nests that failed or to 0700 h the morning nests hatched. Temperature data were classified as day (0700 – 2059 h) or night (2100 – 0659 h), placed into 30-day periods during the breeding season (i.e., 1 May – 31 May, 1 June – 30 June, or 1 July – 31 July), and 10-day periods based upon time during incubation (i.e., early: 1 – 10 days, mid: 11 – 20 days, and late: 21 – 30 days), where first day of incubation corresponded with the day the first egg was laid. The effect of incubation/adult attendance on nest temperatures was calculated by subtracting paired control temperatures from nest temperatures (hereafter referred to as incubation value). Differences in day and night temperatures between control temperatures and nest temperatures were examined using repeated measures analysis of variance (ANOVA), repeated among temperature readings for paired nest and control temperatures with a compound symmetric covariance structure (PROC MIXED; SAS Institute 2002). Differences in 1) day nest temperatures, 2) night nest temperatures, 3) day control temperatures, 4) night control temperatures, 5) day incubation values, and 6) night incubation values were also examined between or among years (i.e., 2008 and 2009), lakes (i.e., lake A, lake B, and lake C), nest fate (i.e., success or failure), substrate type (i.e., pebble or sand), time during incubation (i.e., 1 – 10 days, 11 – 20 days, or 21 –

30 days), and time during season (1 May – 31 May, 1 June – 30 June, or 1 July – 31 July) using repeated measures ANOVA as described above (PROC MIXED; SAS Institute 2002).

To examine potential physiological costs of incubation, correlation between time of day an individual adult was captured on nest and body mass was calculated using Pearson correlation analysis (PROC CORR; SAS Institute 2002). Similarly, Pearson correlation analysis was used to examine the association between parental body mass and average night and day nest temperatures and incubation values for an individual nest. Due to low sample sizes within a specific sex and little variability between sexes, when more than one putative parent was captured from a given nest, the mean body mass for both parents was used for analyses. To examine the relationship between substrate type and parental body mass, an ANOVA was used (PROC GLM; SAS Institute 2002). To determine if laying date (i.e., month) influenced selection of a particular substrate, Chi-square analysis (PROC FREQ; SAS Institute 2002) was used. Since not all months had adequate sample size (i.e., 7 nests initiated in July), nests initiated in June and July were pooled for this analysis.

RESULTS

iButtons were placed in 104 nests and control sites (20 in 2008 and 84 2009; 22 in lake A, 65 in lake B, and 17 in lake C) between 12 June – 26 July 2008 and 1 May – 5 August 2009, and recorded 15,312 hrs of temperature data over 142 d. Placement of iButtons within nests did not negatively influence nest success, as nests with iButtons had slightly greater nest success (34% hatched) than nests without (22% hatched). Nest temperatures ranged from 12.2 – 47.2°C (12.2 – 47.2°C during day, 12.7 – 39.2°C during night), while control temperatures ranged from 6.7 – 54.0°C (6.7 – 54.0°C during day and 7.2 – 38.6°C during night). Nest temperatures mirrored control temperatures, but did not exhibit the extreme amplitude between high (day) and low (night) temperatures as controls (Figure 3.1). In fact, nest temperatures were greater ($P < 0.001$) at night and lower ($P < 0.001$) during day than control sites (Figure 3.2, Table 3.1).

Night nest ($P = 0.012$) and control ($P = 0.012$) temperatures varied between years, where nest and control temperatures were greater in 2008 than 2009 (Table 3.2). However, day nest and control temperatures, and day and night incubation values (i.e., difference between paired nest and control temperatures) were similar ($P > 0.05$) between years (Table 3.2). With years combined, night nest temperatures varied spatially ($P = 0.011$) among lakes, where lake A and B had greater night nest temperatures than lake C

(Table 3.3). However, lakes had similar ($P > 0.05$) night control temperatures, day nest and control temperatures, and day and night incubation values (Table 3.3).

As expected, both day and night nest and control temperatures increased over time within the nesting season ($P < 0.001$), where lower temperatures were recorded in May than June and July (Figure 3.3, Table 3.4). Day and night incubation values also varied seasonally ($P < 0.05$), with incubation having a greater effect (i.e., greater difference between nest and control temperatures) during the day in June and July as compared to May, and a greater effect during the night in May and July as compared to June (Figure 3.4, Table 3.4). Therefore, because ambient temperatures (i.e., control temperatures) were lower earlier in the season (i.e., May), incubating adults had a greater effect during the night, but less of an effect during the day. Despite incubation having an increased effect during the night, nest temperatures remained lower earlier in the season as compared to later.

Regardless of month, day and night nest and control temperatures increased as incubation progressed ($P < 0.05$) with the first 10 days of incubation having lower temperatures than the next two incubation periods (Figure 3.5, Tables 3.5 – 3.8). Day and night incubation values also varied as incubation progressed ($P < 0.05$), with incubation during early periods having a greater effect during day, but a lower effect during night, regardless of month (Figure 3.6, Tables 3.5 – 3.8). Therefore, incubating adults of older nests (i.e., > 11 days) had a greater effect during night, but lower effect during day, resulting in both day and night nest temperatures increasing as incubation progressed.

Only four nests were placed in shaded locations, but all nests were placed on either sand or pebble substrate (see Chapter II). With months combined, control temperatures during day were greater (*P* = 0.034) on sand than pebble substrate; however, control night temperatures were similar between substrates (*P* > 0.05; Table 3.9; Figure 3.7). Although day and night control temperatures were similar (*P* > 0.05) between substrates in May (Table 3.10), both day and night control temperatures were greater (*P* < 0.05) on sand substrate in June (Table 3.11) and July (Table 3.12) than pebble. Despite differences in control temperatures, nests placed on sand and pebble substrates had similar day and night temperatures with months combined (*P* > 0.05; Table 3.9; Figure 3.7). Day and night temperatures were also similar between substrate types in May (Table 3.10) and June (Table 3.11); however, in July (Table 3.12), nests placed on sand substrate had greater day (*P* = 0.023) and night (*P* = 0.018) temperatures than nests placed on pebble substrate. With months combined, incubation of nests placed on sand substrate had a greater (*P* = 0.004) effect during the day than nests on pebble substrate; however, night incubation values were similar (*P* = 0.339) between substrate types (Table 3.9; Figure 3.8). Similarly, in June, incubation had a greater effect during the day (*P* = 0.027), but a lower effect during night (*P* = 0.031) for nests placed on sand substrate as compared to nests placed on pebble substrate (Table 3.11). Therefore, because ambient (i.e., control) temperatures were warmer on sand than pebble substrate, incubating adults needed to have a greater incubation effect on sand during day, but a lower effect on sand at night. However, as the season progressed (i.e., July), incubation resulted in similar effects between substrate type, resulting in greater temperatures of nests placed on sand substrate.

Nests, regardless of fate, had similar day and night nest and control temperatures as well as day and night incubation values with months combined ($P > 0.05$; Table 3.13). Additionally, nest temperature ranges for successful and unsuccessful nests were similar (successful: 12.67 – 47.15°C; unsuccessful: 12.19 – 46.14°C). Among months (Tables 3.14 – 3.16), however, incubation of successful nests had a greater ($P = 0.011$) effect than unsuccessful nests in June (Table 3.15), and in July successful nests had greater ($P = 0.019$) night nest temperatures than unsuccessful nests (Table 3.16). Therefore, successful nests had greater incubation effects during night in June and higher night temperatures than unsuccessful nests in July.

Mean day and night nest temperatures, as well as incubation values were not correlated with mean parental body mass ($P > 0.05$). In addition, adult body mass was not correlated ($P > 0.05$) with time captured. Adults that selected nest sites on pebble substrate had greater mean body mass ($\bar{x} = 42.7$ g; $F_{1,62} = 4.83$; $P = 0.032$) than sand substrate ($\bar{x} = 40.6$ g). Parents selected pebble substrate at a greater percentage during all months; however, as the season progressed, parents tended to select pebble substrate at a greater rate than earlier (April = 57.6%; May = 52.3%; and June – July = 65.12%), but not significantly ($\chi^2 = 2.91$; df = 2; $P = 0.233$).

DISCUSSION

Nesting Snowy Plovers in the SHP of Texas are exposed to high ambient temperatures during the day (i.e., maximum air temperatures > 40°C and maximum control temperatures > 54°C), creating a very hot, thermally stressful nesting environment that necessitates incubating parents to cool eggs during daylight hours. Many studies have reported lethal egg temperatures for avian species occurring > 40°C (e.g., 45.6ºC in House Wren [*Troglodytes aedon*]: Baldwin and Kendeigh 1932, 43ºC in Heermann's Gull [*Larus heermanni*]: Bennett and Dawson 1979, 46ºC in Western Gulls [*Larus occidentalis*]: Bennett et al. 1981, 47.7ºC in Black-necked Stilt [*Himantopus mexicanus*]: Grant 1982), although there is obvious variation in both optimal and lethal temperatures among species (Webb 1987). In this study, nests reached temperatures > 47°C and still successfully hatched, suggesting that Snowy Plover embryos are able to survive greater temperature extremes than some species, at least for short periods of time (i.e., eggs were exposed to these extreme temperatures for < 30 min). Similar extreme temperatures were observed in Wilson's Plovers (*Charadrius wilsonia*) where substrate temperatures beneath eggs reached 48.5°C; however, viability of the eggs was not reported (Bergstrom 1989). It should be noted that egg temperatures were not documented in this study; therefore, recorded temperature extremes may not precisely reflect actual egg temperatures, but are indicative of egg temperatures.

To cope with individual heat stress and maintain eggs within the thermal neutral zone, Snowy Plovers performed adaptive behaviors (e.g., biparental care, shading nests, belly soaking, standing in water, and panting), especially during times of extremely high temperatures (> 38ºC; S. Saalfeld per. obs.). Although more females (50) were captured than males (20) on nests during day (i.e., 1000 – 1600 hrs), males were commonly observed sharing diurnal incubation duties, especially during these times of extremely high temperatures. Both sexes were observed shading nests, belly soaking (two females were caught with wet ventral plumage on nests), standing in water after leaving nests, and panting while incubating eggs (S. Saalfeld per. obs.). By performing these behaviors, Snowy Plovers may alleviate heat stress during the nesting season; however, such behaviors are costly (i.e., increased energy expenditure; Hinsley and Ferns 1994) and could increase predation risks.

To lessen risks associated with these adaptive behaviors, Snowy Plovers should select nest sites that are thermally favorable (e.g., high degree of cover/shading and cooler substrates; Kainady and Al-Dabbagh 1976, Page et al. 1985, Bergstrom 1989, Amat and Masero 2004a, Amat and Masero 2004b), reducing thermal stress, energy expenditure, and water loss (Wolf and Walsberg 1996). Shaded nests should maintain lower temperatures than nests in open areas, where adults would not be forced to engage in behaviors to alleviate stress (i.e., panting, gular fluttering, and wetting of belly feathers; Kainady and Al-Dabbagh 1976, Amat and Masero 2004a). However, only four nests occurred in areas with vegetative cover. Selection of open nest sites may be a function of predation rates, where nests with greater vegetative cover have greater predation risk due to presumed poorer predator detection by incubating adults (Burger 1987, Götmark et al. 1995, Amat and Masero 2004b). Despite the thermal advantages of placing nests near vegetative cover, nests close to plants experienced decreased nest success (see Chapter I), precluding selection by Snowy Plovers.

Selection of thermally favorable nest sites may not always be juxtaposed with increased predation rates. In this study, Snowy Plovers selected nest sites located on pebble substrate (see Chapter II), where nests are more camouflaged and may have lower predation rates than nests located on more homogeneous substrates (i.e., sand; Page et al. 1985, Colwell et al. 2005). Pebble substrate provides a thermally stable environment (Ackerman and Seagrave 1987, Mayer et al. 2009), as lower nest and control temperatures, and less incubation effects were documented for nests on pebble substrate in this study. Given that pebble substrates provide a more thermally favorable nesting environment, it would be expected that parents incubating nests on pebble substrate would behaviorally alleviate heat stress (i.e., biparental incubation, shading nests, belly soaking, standing in water, panting, and gular fluttering) less frequently. The benefits of reducing the frequency of these conspicuous behaviors would include escaping predator detection and reducing energy expenditures and physiological stress. This study generally confirms these notions as adults trapped on nests located on pebble substrate were in better condition than those trapped on nests located on sand substrate. Therefore, Snowy Plovers may alleviate heat stress during the nesting season without increasing predation rates by selecting pebble substrates.

In contrast to high ambient temperatures during day, low ambient temperatures were commonly recorded at night (minimum air temperatures < 10°C and minimum control temperatures < 8°C), reaching temperatures (i.e., 13°C) below the thermally moderate range (i.e., 31 – 40ºC; Purdue 1976b), but likely still within non-lethal zones (e.g., embryo mortality occurred < 10ºC in Western Gulls; Bennett et al. 1981). Wide ranging temperatures between day and night forces Snowy Plovers to be relatively plastic in incubation techniques, from heat application during night to egg cooling during day (see Figure 3.1). Such incubation strategies have been observed in other species nesting in similar climates, including Killdeer (*Charadrius vociferus*; Bergstrom 1989), Wilson's Plover (Bergstrom 1989), Crowned Plover *(Vanellus coronatus*; Downs and Ward 1997), Black-bellied Sandgrouse (*Pterocles orientalis*; Hinsley and Ferns 1994), and Pin-tailed Sandgrouse (*P. alchata*; Hinsley and Ferns 1994). Plasticity in incubation techniques may allow these species to exist in environments with dramatic thermal fluctuations, potentially providing additional habitat that may not be available to less plastic species. For example, few species (e.g., Killdeer, Black-necked Stilt, American Avocet [*Recurvirostra americana*], and Snowy Plover; Conway et al. 2005) successfully nest within saline lakes in the SHP of Texas, potentially due to the inability to compensate with fluctuating temperatures and thermal extremes.

Nest temperatures closely followed ambient temperatures, increasing as the season progressed (from May – July). As earlier egg laying dates frequently result in greater nest success (Perrins 1996), Snowy Plovers also benefit from nesting earlier (during a less thermally stressful time period) as daily nest survival rates declined over time (see Chapter I). However, complete shifts in nest initiation may not be feasible and are rarely documented. For example, Grant (1982) failed to document any shift in nest initiation dates, so that nesting could occur during less thermally stressful time periods among species nesting within the Salton Sea, California (i.e., Killdeer, Black-necked Stilt, American Avocet, Forster's Tern [*Sterna forsteri*], Lesser Nighthawk [*Chordeiles acutipennis*], Black Skimmer [*Rynchops niger*]). As egg formation is costly (i.e., energetically and physiologically), especially for precocial species, females may be unable to acquire necessary food and nutrients for egg formation at the most opportune time (i.e., early in the breeding season; Perrins 1996). However, if females posses the necessary nutrients for egg formation upon arrival to the SHP of Texas, they should have earlier egg laying dates (Perrins 1996). Although energetics and winter-migratory food habits and body condition estimates are unknown for Snowy Plovers, individuals in better condition tended to initiate egg laying earlier and nests laid earlier tended to have greater survival (see Chapter I). Therefore, survival and physiological benefits do exist for Snowy Plovers to arrive early for both the care-giving adults and the eggs they incubate.

Time during incubation shifted incubation routines, where incubation effects decreased during day, but increased during night as incubation progressed. Nest temperatures also increased as incubation progressed, where increased temperatures may reflect a combination of increased heat production of the embryo as it ages (Drent 1970), incubation routine shifts, and temperature increases over time during the breeding season. Increased nest temperatures as clutches near hatching may synchronize hatching. In most avian species, synchronized hatching is thought to be achieved by delaying incubation until the last egg is laid (Kendeigh 1952). However, species that nest within thermally stressful environments may not be able to delay incubation, because eggs must be incubated or shaded at least part of the time during egg laying to remain viable (Grant 1982). For example, at the Salton Sea, California, eggs must be incubated or shaded ≥ 10 hrs a day to prevent overheating in ground nesting species (Grant 1982). Therefore, several alternate mechanisms have been hypothesized to explain hatching synchronization, such as increased metabolic rates in later laid eggs (MacCluskie et al. 1997, Nicolai et al. 2004) and vocalization by chicks within earlier laid eggs stimulating later laid eggs to accelerate development (Freeman and Vince 1974, Persson and Andersson 1999). It has also been suggested that synchronization of hatching could be the result of parental behavior (MacCluskie et al. 1997). In general, greater incubation temperatures decrease incubation duration (Yogev et al. 1996), whereby, increasing incubation temperatures closer to hatching, parents may facilitate hatching synchronization by accelerating development of later laid eggs.

Another potential function of increased nest temperatures closer to hatching, especially night temperatures, could be to trigger hatching during a particular time (i.e., early morning). During this study, most nests were observed hatching before 1200 h (S. Saalfeld per. obs.). This strategy may be beneficial for Snowy Plovers due to lower temperatures during early morning hours. By hatching earlier in the day, chicks may perform physiologically costly behaviors (i.e., pecking/hatching) during times when temperatures are low. Once hatched, they can then quickly move to more protective, less thermally stressful areas (e.g., shallow water areas) before temperatures increase throughout the day. Therefore, incubation techniques that trigger hatching during early morning hours may provide a survival advantage to hatchlings.

Incubation techniques (i.e., application of heat and cooling of eggs) are often a trade off between maintaining eggs within the thermal neutral zone and increased energy demands of adults and predation rates of adults and nests. However, several alternative adaptations may allow nesting Snowy Plovers to mitigate heat stress within the SHP of Texas without increasing energy expenditure or predation rates. In particular, selecting pebble substrates for nests and laying eggs earlier in the season may allow Snowy Plovers to reduce thermal stress on eggs and adults while simultaneously lowering predation risk. However, habitat features necessary for mitigating heat stress (i.e., pebble substrate), thermoregulation (i.e., presence of surface water for belly soaking and standing in), and energy requirements (i.e., freshwater springs that support salt intolerant invertebrate prey; Andrei et al. 2009) are declining within regional saline lakes that support nesting Snowy Plovers. Therefore, conservation within this region should focus upon conserving pebble substrates as well as surface water availability. Specifically, promoting native vegetation cover in surrounding upland areas can reduce erosion rates and sand deposition, ultimately maintaining pebble substrate availability. Additionally, conserving freshwater springs discharging into saline lakes, as well as the Ogallala aquifer can increase surface water availability. However, because the Ogallala aquifer is recharged from playa wetlands (Osterkamp and Wood 1987, Bolen et al. 1989), it also remains important to conserve the entire complex of wetlands within the SHP of Texas (Andrei et al. 2008, Andrei et al. 2009).

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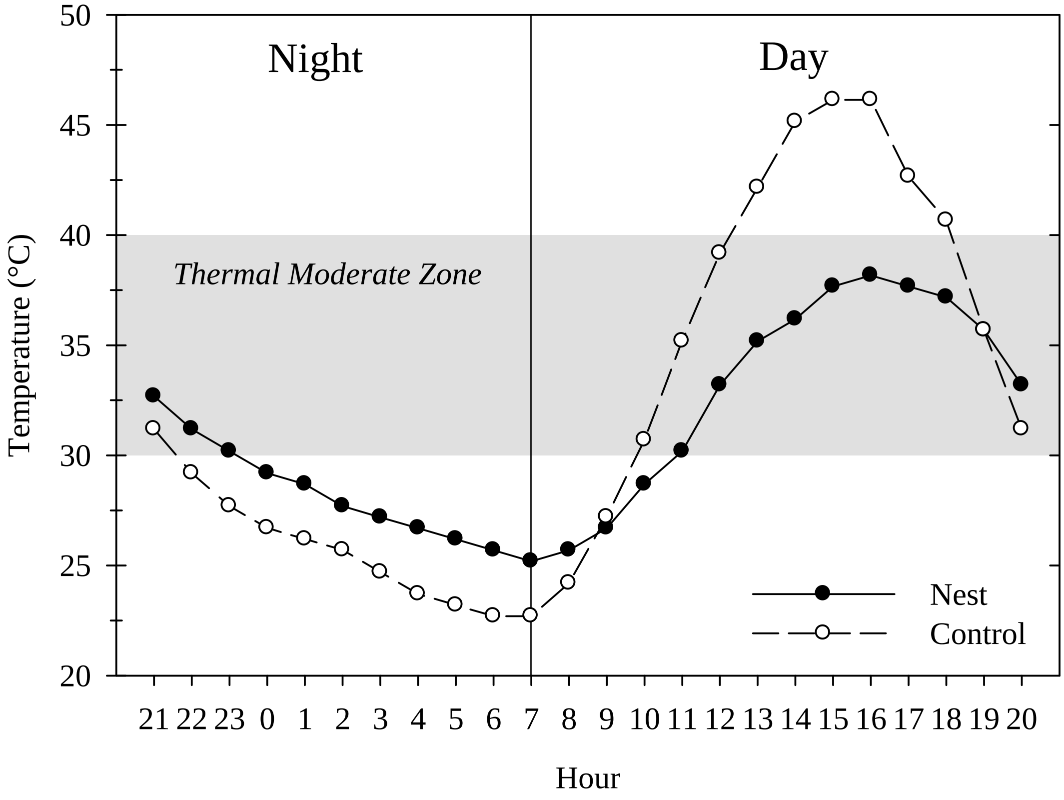

Figure 3.1. Day and night temperatures measured using iButtons on 17-18 June 2009 at a Snowy Plover nest and control site located on a saline lake within the Southern High Plains of Texas, USA. These data are representative of a typical relationship between nest temperatures and control temperatures for a 24-hour period.

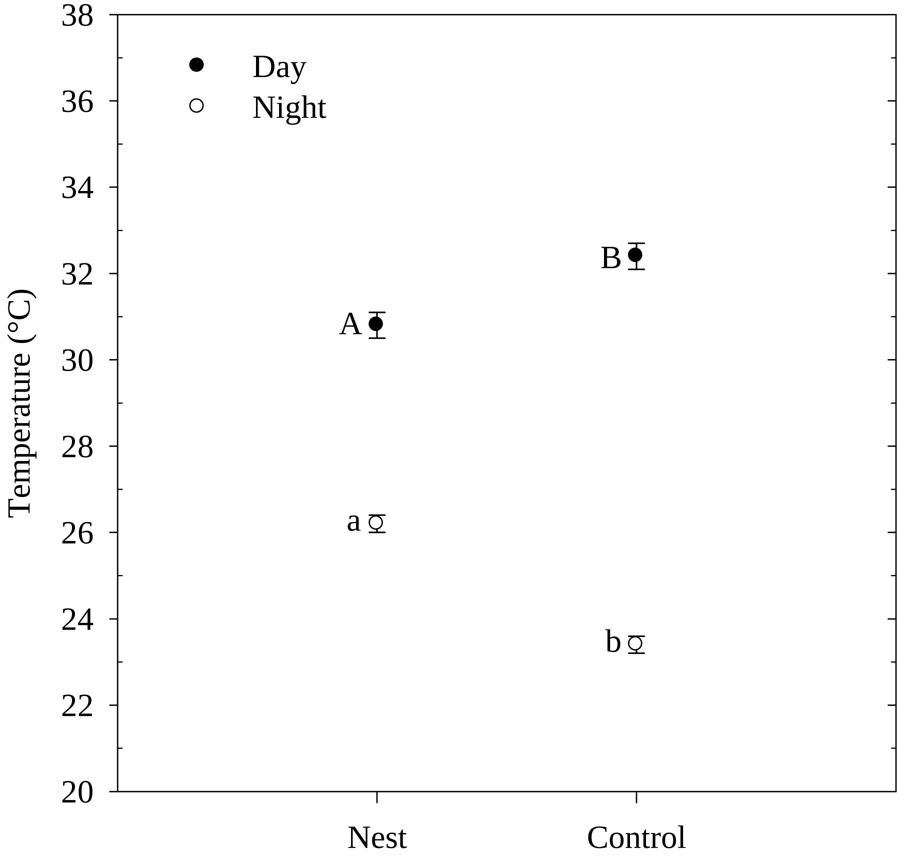

Figure 3.2. Least squares estimates and standard errors of Snowy Plover day and night nest and control temperatures on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. Estimates with same letters (of the same case) within a category (i.e., day or night) are not different ($P > 0.05$; least squares cross validation).

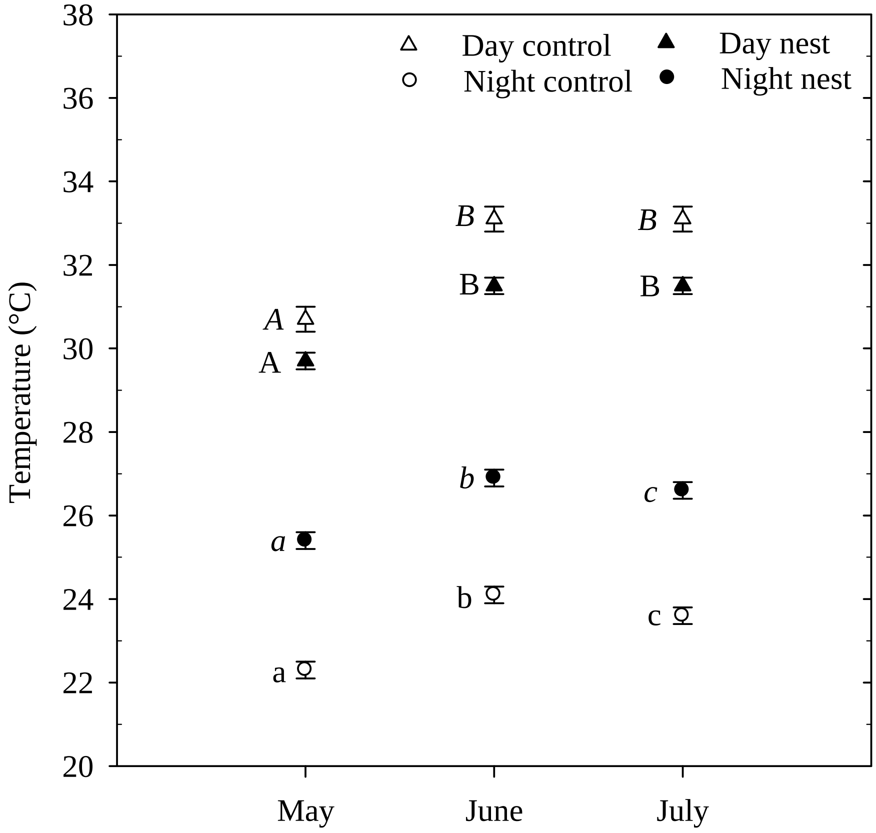

Figure 3.3. Least squares estimates and standard errors of Snowy Plover day and night nest and control temperatures by month on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. Estimates with same letters (of the same case and font) within a category (i.e., day or night nest or control) are not different ($P > 0.05$; least squares cross validation).

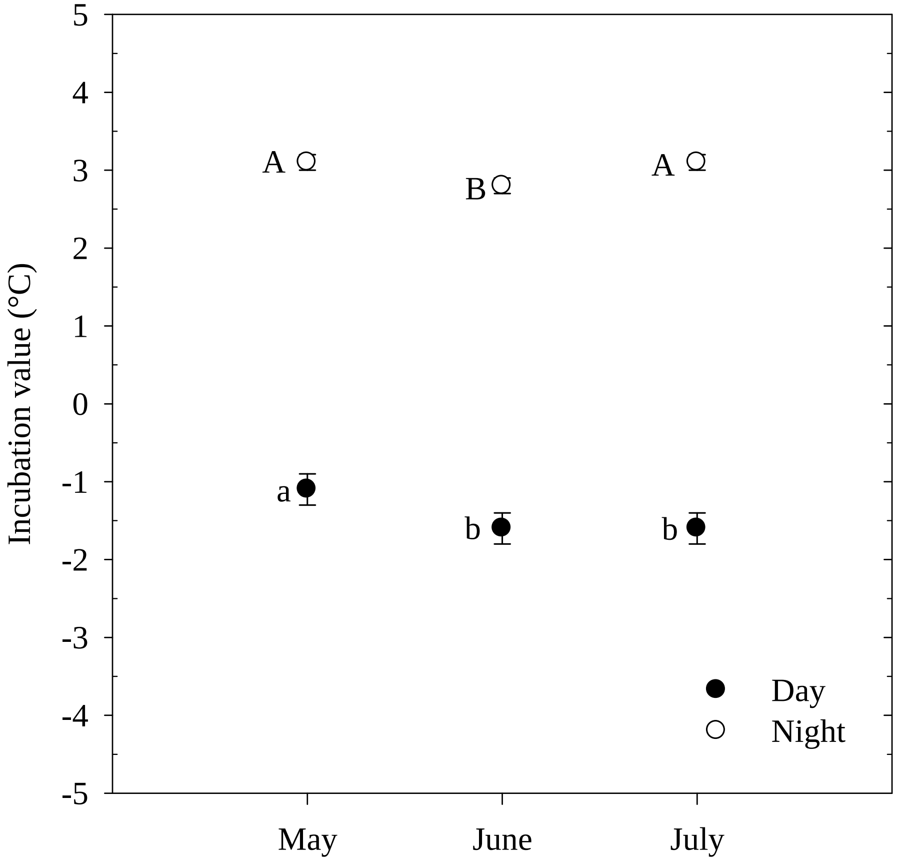

Figure 3.4. Least squares estimates and standard errors of Snowy Plover day and night incubation values (i.e., difference between paired nest and control temperature) by month on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. Estimates with same letters (of the same case) within a category (i.e., day or night) are not different (*P* > 0.05; least squares cross validation).

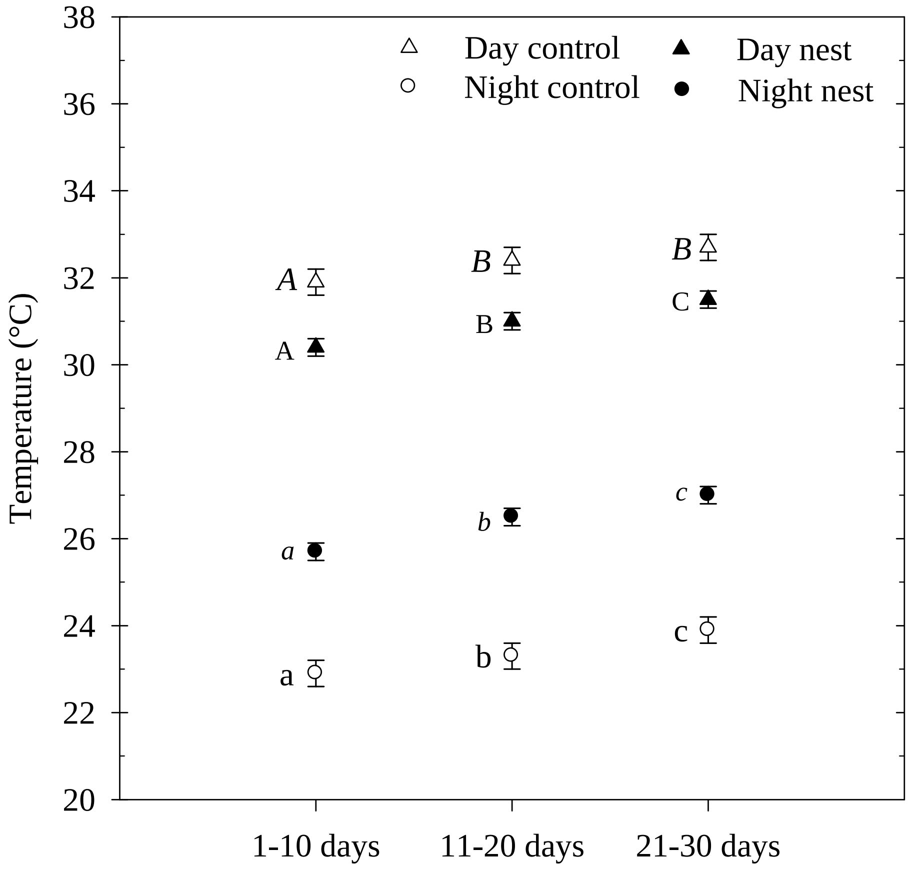

Figure 3.5. Least squares estimates and standard errors of Snowy Plover day and night nest and control temperatures by incubation period on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. Estimates with same letters (of the same case and font) within a category (i.e., day or night nest or control) are not different (*P* > 0.05; least squares cross validation).

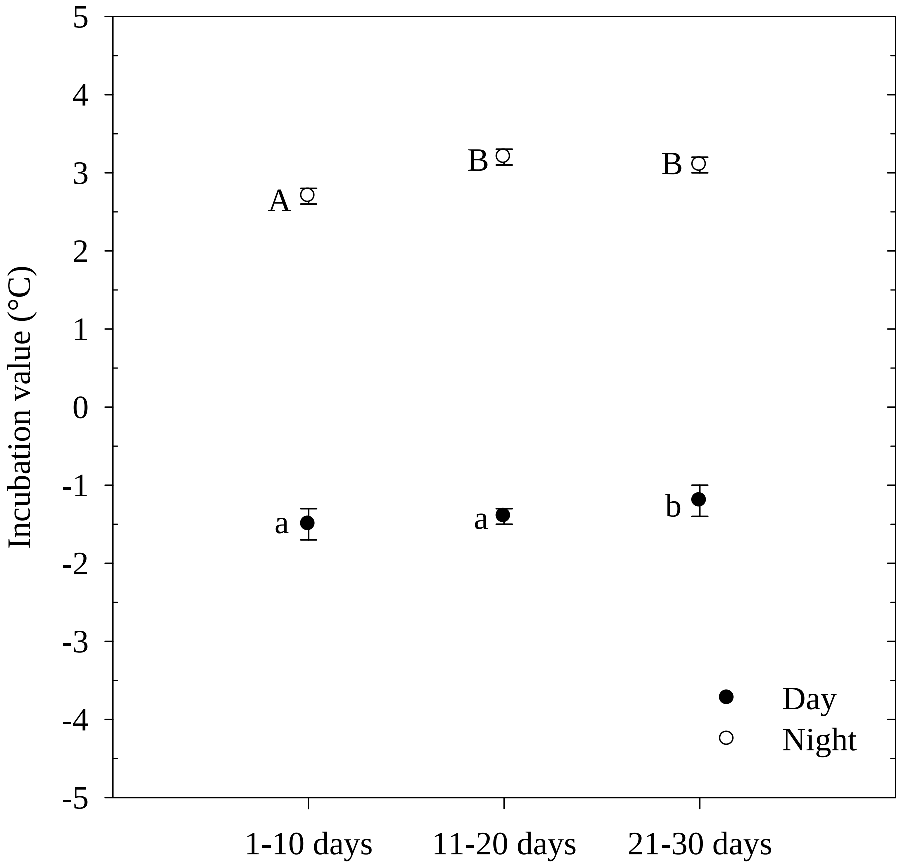

Figure 3.6. Least squares estimates and standard errors of Snowy Plover day and night incubation values (i.e., difference between paired nest and control temperature) by incubation period on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. Estimates with same letters (of the same case) within a category (i.e., day or night) are not different (*P* > 0.05; least squares cross validation).

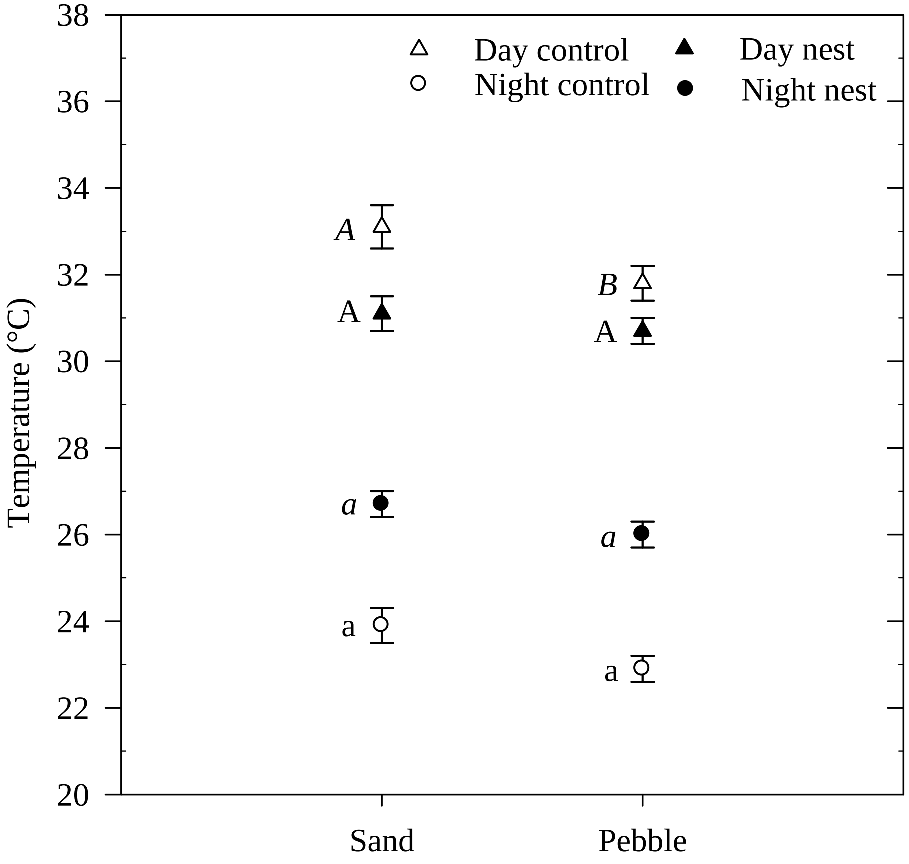

Figure 3.7. Least squares estimates and standard errors of Snowy Plover day and night nest and control temperatures by substrate type on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. Estimates with same letters (of the same case and font) within a category (i.e., day or night nest or control) are not different (*P* > 0.05; least squares cross validation).

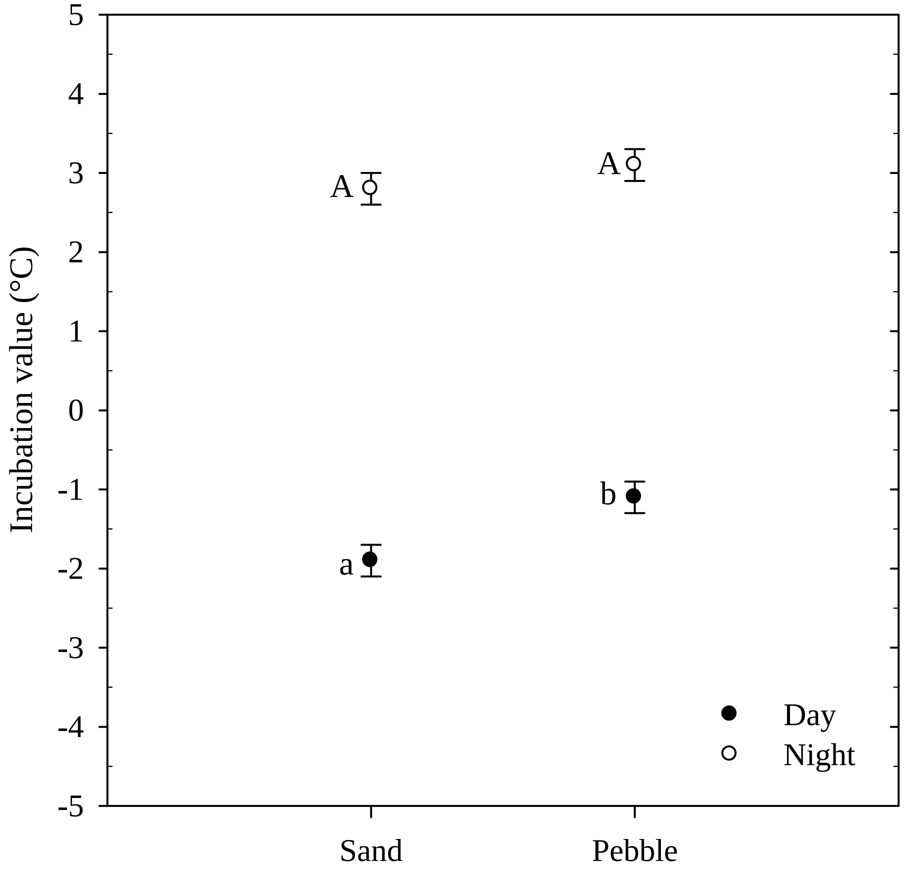

Figure 3.8. Least squares estimates and standard errors of Snowy Plover day and night incubation values (i.e., difference between paired nest and control temperature) by substrate type on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009. Estimates with same letters (of the same case) within a category (i.e., day or night) are not different ($P > 0.05$; least squares cross validation).

Table 3.1. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest and control temperatures on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Nest (*n* = 104)[a]		Control (*n* = 104)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (°C)	30.6 (30.8)	0.0 (0.3)	32.2 (32.4)	0.1 (0.3)	385.16	<0.001*
Night nest T (°C)	26.2 (26.2)	0.0 (0.2)	23.4 (23.4)	0.0 (0.2)	4263.67	<0.001*

[a] Number of nests or control sites.

* Significant *P*-value ($P < 0.05$).

Table 3.2. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) between years on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	2008 (n = 20)[a]		2009 (n = 84)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	30.8 (31.6)	0.1 (0.5)	30.6 (30.7)	0.1 (0.3)	2.39	0.126
Night nest T (ºC)	27.1 (27.4)	0.1 (0.5)	26.0 (26.0)	0.0 (0.2)	6.63	0.012*
Day control T (ºC)	32.1 (32.9)	0.1 (0.7)	32.3 (32.1)	0.1 (0.3)	0.93	0.338
Night control T (ºC)	24.5 (24.6)	0.1 (0.6)	23.1 (23.0)	0.0 (0.3)	6.53	0.012*
Day Inc. (ºC)	-1.3 (-1.3)	0.1 (0.3)	-1.7 (-1.4)	0.0 (0.2)	0.10	0.748
Night Inc. (ºC)	2.6 (2.8)	0.0 (0.3)	2.9 (3.0)	0.0 (0.2)	0.36	0.548

[a] Number of nests within year.

* Significant *P*-value ($P < 0.05$).

Table 3.3. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) among lakes on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Lake A (*n* = 22)[a]		Lake B (*n* = 65)		Lake C (*n* = 17)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	31.2 (31.4) a[b]	0.1 (0.5)	30.6 (30.9) a	0.1 (0.3)	29.6 (30.1) a	0.1 (0.6)	1.54	0.218
Night nest T (ºC)	26.9 (27.1) a	0.1 (0.5)	26.3 (26.3) a	0.0 (0.3)	24.6 (25.0) b	0.1 (0.5)	4.74	0.011*
Day control T (ºC)	33.0 (33.0) a	0.1 (0.6)	32.0 (32.1) a	0.1 (0.4)	31.6 (31.8) a	0.2 (0.7)	0.91	0.406
Night control T (ºC)	23.8 (23.7) a	0.1 (0.5)	23.6 (23.4) a	0.0 (0.3)	21.6 (22.1) a	0.1 (0.6)	2.37	0.098
Day Inc. (ºC)	-1.8 (-1.6) a	0.1 (0.3)	-1.4 (-1.3) a	0.0 (0.2)	-2.0 (-1.7) a	0.1 (0.4)	1.07	0.348
Night Inc. (ºC)	3.1 (3.4) a	0.0 (0.3)	2.7 (2.9) a	0.0 (0.2)	3.0 (2.9) a	0.0 (0.3)	1.17	0.314

[a] Number of nests within lake.

[b] Means with the same letter within a row are not different (*P* > 0.05; least squares cross validation).

* Significant *P*-value (*P* < 0.05).

Table 3.4. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) among months on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	May (*n* = 44)[a]		June (*n* = 56)		July (*n* = 37)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	29.2 (29.7) a[b]	0.1 (0.2)	31.2 (31.5) b	0.1 (0.2)	31.3 (31.5) b	0.1 (0.2)	43.93	<0.001*
Night nest T (ºC)	24.5 (25.4) a	0.1 (0.2)	26.6 (26.9) b	0.0 (0.2)	27.4 (26.6) c	0.1 (0.2)	55.69	<0.001*
Day control T (ºC)	30.5 (30.7) a	0.1 (0.3)	33.0 (33.1) b	0.1 (0.3)	32.9 (33.1) b	0.1 (0.3)	33.89	<0.001*
Night control T (ºC)	20.7 (22.3) a	0.1 (0.2)	24.2 (24.1) b	0.1 (0.2)	25.0 (23.6) c	0.1 (0.2)	75.21	<0.001*
Day Inc. (ºC)	-1.2 (-1.1) a	0.1 (0.2)	-1.8 (-1.6) b	0.0 (0.2)	-1.6 (-1.6) b	0.1 (0.2)	4.97	0.013*
Night Inc. (ºC)	3.8 (3.1) a	0.0 (0.1)	2.4 (2.8) b	0.0 (0.1)	2.5 (3.1) a	0.0 (0.1)	32.85	<0.001*

[a] Number of nests within month.

[b] Means with the same letter within a row are not different (*P* > 0.05; least squares cross validation).

* Significant *P*-value (*P* < 0.05).

Table 3.5. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) among incubation periods on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	1-10 days (n = 69)[a]		11-20 days (n = 84)		21-30 days (n = 47)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	30.3 (30.4) a[b]	0.1 (0.2)	30.7 (31.0) b	0.1 (0.2)	31.0 (31.5) c	0.1 (0.2)	30.41	<0.001*
Night nest T (ºC)	25.6 (25.7) a	0.1 (0.2)	26.4 (26.5) b	0.0 (0.2)	26.6 (27.0) c	0.1 (0.2)	99.13	<0.001*
Day control T (ºC)	32.1 (31.9) a	0.1 (0.3)	32.3 (32.4) b	0.1 (0.3)	32.3 (32.7) b	0.1 (0.3)	7.50	0.001*
Night control T (ºC)	23.4 (22.9) a	0.1 (0.3)	23.3 (23.3) b	0.1 (0.3)	23.5 (23.9) c	0.1 (0.3)	39.43	<0.001*
Day Inc. (ºC)	-1.8 (-1.5) a	0.0 (0.2)	-1.6 (-1.4) a	0.1 (0.1)	-1.3 (-1.2) b	0.1 (0.2)	4.85	0.010*
Night Inc. (ºC)	2.3 (2.7) a	0.0 (0.1)	3.1 (3.2) b	0.0 (0.1)	3.1 (3.1) b	0.0 (0.1)	99.19	<0.001*

[a] Number of nests within incubation period.

[b] Means with the same letter within a row are not different (*P* > 0.05; least squares cross validation).

* Significant *P*-value (*P* < 0.05).

Table 3.6. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) among incubation periods for May on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	1-10 days (*n* = 27)[a]		11-20 days (*n* = 32)		21-30 days (*n* = 15)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	28.6 (28.6) a[b]	0.1 (0.4)	29.5 (29.8) b	0.1 (0.4)	29.7 (30.7) c	0.2 (0.4)	19.53	<0.001*
Night nest T (ºC)	23.5 (23.9) a	0.1 (0.3)	25.1 (25.2) b	0.1 (0.3)	24.8 (25.6) c	0.1 (0.3)	38.90	<0.001*
Day control T (ºC)	30.4 (29.5) a	0.2 (0.5)	30.5 (30.6) b	0.2 (0.5)	30.3 (31.3) b	0.3 (0.6)	6.28	0.006*
Night control T (ºC)	20.6 (20.6) a	0.1 (0.3)	20.9 (21.0) a	0.1 (0.3)	20.3 (20.9) a	0.1 (0.3)	1.74	0.194
Day Inc. (ºC)	-1.8 (-0.9) a	0.1 (0.3)	-1.1 (-0.8) a	0.1 (0.3)	-0.7 (-0.8) a	0.1 (0.3)	0.04	0.957
Night Inc. (ºC)	3.0 (3.2) a	0.1 (0.2)	4.1 (4.2) b	0.0 (0.2)	4.4 (4.7) c	0.1 (0.2)	138.97	<0.001*

[a] Number of nests within incubation period.

[b] Means with the same letter within a row are not different ($P > 0.05$; least squares cross validation).

* Significant *P*-value ($P < 0.05$).

Table 3.7. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) among incubation periods for June on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	1-10 days (*n* = 38)[a]		11-20 days (*n* = 33)		21-30 days (*n* = 21)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	30.8 (31.3) a[b]	0.1 (0.3)	31.2 (31.4) a	0.1 (0.3)	32.1 (31.7) a	0.2 (0.3)	1.48	0.241
Night nest T (ºC)	26.4 (26.1) a	0.1 (0.2)	26.7 (26.8) b	0.1 (0.2)	27.0 (27.6) c	0.1 (0.3)	32.84	<0.001*
Day control T (ºC)	32.7 (33.3) a	0.2 (0.4)	33.0 (33.2) a	0.2 (0.4)	33.6 (33.0) a	0.2 (0.4)	0.24	0.787
Night control T (ºC)	24.4 (23.8) a	0.1 (0.3)	23.9 (24.2) b	0.1 (0.3)	24.3 (25.3) c	0.1 (0.3)	35.55	<0.001*
Day Inc. (ºC)	-1.9 (-2.1) a	0.1 (0.2)	-1.8 (-1.8) b	0.1 (0.2)	-1.5 (-1.2) c	0.1 (0.2)	12.92	<0.001*
Night Inc. (ºC)	1.9 (2.4) a	0.0 (0.2)	2.8 (2.6) b	0.0 (0.2)	2.6 (2.2) c	0.0 (0.2)	29.06	<0.001*

[a] Number of nests within incubation period.

[b] Means with the same letter within a row are not different (*P* > 0.05; least squares cross validation).

* Significant *P*-value (*P* < 0.05).

Table 3.8. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) among incubation periods for July on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	1-10 days (n = 17)[a]		11-20 days (n = 29)		21-30 days (n = 17)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	31.8 (30.5) a[b]	0.2 (0.4)	31.3 (31.4) b	0.1 (0.4)	30.9 (31.7) b	0.1 (0.4)	6.79	0.005*
Night nest T (ºC)	27.5 (26.2) a	0.1 (0.4)	27.4 (27.2) b	0.1 (0.4)	27.4 (27.8) c	0.1 (0.4)	31.31	<0.001*
Day control T (ºC)	33.4 (32.5) a	0.3 (0.6)	33.0 (32.8) a	0.2 (0.5)	32.5 (33.1) a	0.2 (0.5)	0.74	0.486
Night control T (ºC)	25.4 (24.1) a	0.1 (0.4)	24.9 (24.7) b	0.1 (0.4)	24.8 (25.3) c	0.1 (0.4)	15.02	<0.001*
Day Inc. (ºC)	-1.6 (-1.9) a	0.1 (0.3)	-1.7 (-1.4) a	0.1 (0.2)	-1.6 (-1.4) a	0.1 (0.2)	2.77	0.082
Night Inc. (ºC)	2.1 (2.2) a	0.1 (0.2)	2.5 (2.6) b	0.0 (0.2)	2.6 (2.5) b	0.0 (0.2)	17.10	<0.001*

[a] Number of nests within incubation period.

[b] Means with the same letter within a row are not different (*P* > 0.05; least squares cross validation).

* Significant *P*-value (*P* < 0.05).

Table 3.9. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) between substrate type (i.e., sand or pebble) on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Sand (*n* = 40)[a]		Pebble (*n* = 63)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	30.8 (31.1)	0.1 (0.4)	30.5 (30.7)	0.1 (0.3)	0.97	0.326
Night nest T (ºC)	26.4 (26.7)	0.1 (0.3)	26.0 (26.0)	0.0 (0.3)	2.29	0.134
Day control T (ºC)	32.9 (33.1)	0.1 (0.5)	31.6 (31.8)	0.1 (0.4)	4.63	0.034*
Night control T (ºC)	23.8 (23.9)	0.1 (0.4)	23.0 (22.9)	0.0 (0.3)	3.37	0.069
Day Inc. (ºC)	-2.1 (-1.9)	0.0 (0.2)	-1.2 (-1.1)	0.0 (0.2)	8.56	0.004*
Night Inc. (ºC)	2.6 (2.8)	0.0 (0.2)	3.0 (3.1)	0.0 (0.2)	0.92	0.339

[a] Number of nests within substrate type.

* Significant *P*-value ($P < 0.05$).

Table 3.10. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) between substrate type (i.e., sand or pebble) for May on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Sand (*n* = 17)[a]		Pebble (*n* = 27)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	28.9 (29.1)	0.1 (0.5)	29.6 (29.7)	0.1 (0.4)	1.09	0.303
Night nest T (ºC)	24.7 (24.8)	0.1 (0.5)	24.2 (24.7)	0.1 (0.4)	0.09	0.767
Day control T (ºC)	30.5 (30.4)	0.2 (0.6)	30.3 (30.2)	0.2 (0.5)	0.06	0.815
Night control T (ºC)	20.8 (20.9)	0.1 (0.4)	20.5 (20.8)	0.1 (0.3)	0.01	0.905
Day Inc. (ºC)	-1.6 (-1.3)	0.1 (0.4)	-0.7 (-0.5)	0.1 (0.3)	2.56	0.117
Night Inc. (ºC)	3.9 (3.9)	0.0 (0.3)	3.7 (3.8)	0.0 (0.3)	0.05	0.832

[a] Number of nests within substrate type.

* Significant *P*-value ($P < 0.05$).

Table 3.11. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) between substrate type (i.e., sand or pebble) for June on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Sand (*n* = 24)[a]		Pebble (*n* = 31)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	31.9 (31.9)	0.1 (0.4)	30.8 (31.1)	0.1 (0.3)	2.78	0.101
Night nest T (ºC)	26.9 (26.8)	0.1 (0.3)	26.4 (26.4)	0.1 (0.3)	0.90	0.347
Day control T (ºC)	34.2 (34.1)	0.2 (0.4)	32.3 (32.6)	0.1 (0.4)	7.11	0.010*
Night control T (ºC)	25.0 (24.8)	0.1 (0.3)	23.7 (23.7)	0.1 (0.3)	6.47	0.014*
Day Inc. (ºC)	-2.3 (-2.2)	0.1 (0.2)	-1.5 (-1.5)	0.1 (0.2)	5.18	0.027*
Night Inc. (ºC)	1.9 (2.0)	0.0 (0.2)	2.7 (2.7)	0.0 (0.2)	4.89	0.031*

[a] Number of nests within substrate type.

* Significant *P*-value ($P < 0.05$).

Table 3.12. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) between substrate type (i.e., sand or pebble) for July on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Sand (*n* = 14)[a]		Pebble (*n* = 23)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	31.9 (32.3)	0.1 (0.6)	30.6 (30.6)	0.1 (0.4)	5.64	0.023*
Night nest T (ºC)	27.9 (28.2)	0.1 (0.5)	26.9 (26.6)	0.1 (0.4)	6.14	0.018*
Day control T (ºC)	34.3 (34.4)	0.2 (0.7)	31.5 (31.9)	0.2 (0.5)	7.76	0.009*
Night control T (ºC)	25.9 (26.0)	0.1 (0.5)	24.0 (24.0)	0.1 (0.4)	10.46	0.003*
Day Inc. (ºC)	-2.4 (-2.0)	0.1 (0.3)	-0.9 (-1.2)	0.1 (0.3)	3.62	0.066
Night Inc. (ºC)	2.0 (2.2)	0.0 (0.3)	2.9 (2.6)	0.0 (0.2)	1.39	0.246

[a] Number of nests within substrate type.

* Significant *P*-value ($P < 0.05$).

Table 3.13. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) between nest fate (i.e., successful and unsuccessful) and on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Successful (n = 35)[a]		Unsuccessful (n = 68)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	30.5 (30.9)	0.1 (0.4)	30.7 (30.8)	0.1 (0.3)	0.09	0.762
Night nest T (ºC)	26.2 (26.8)	0.0 (0.4)	26.2 (26.0)	0.0 (0.3)	2.79	0.098
Day control T (ºC)	31.9 (32.4)	0.1 (0.5)	32.5 (32.2)	0.1 (0.4)	0.17	0.677
Night control T (ºC)	22.9 (23.6)	0.1 (0.4)	23.7 (23.1)	0.1 (0.3)	0.79	0.376
Day Inc. (ºC)	-1.4 (1.5)	0.0 (0.2)	-1.8 (-1.4)	0.0 (0.2)	0.14	0.712
Night Inc. (ºC)	3.3 (3.2)	0.0 (0.2)	2.4 (2.9)	0.0 (0.2)	0.88	0.351

[a] Number of nests within success category.

* Significant *P*-value ($P < 0.05$).

Table 3.14. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) between nest fate (i.e., successful and unsuccessful) for May on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Successful (n = 13)[a]		Unsuccessful (n = 30)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	29.0 (29.0)	0.1 (0.5)	29.4 (29.6)	0.1 (0.4)	0.93	0.340
Night nest T (ºC)	24.2 (24.2)	0.1 (0.5)	24.7 (24.9)	0.1 (0.4)	1.21	0.277
Day control T (ºC)	30.3 (30.3)	0.2 (0.7)	30.6 (30.1)	0.2 (0.5)	0.04	0.838
Night control T (ºC)	20.3 (20.2)	0.1 (0.4)	21.1 (21.0)	0.1 (0.3)	2.71	0.107
Day Inc. (ºC)	-1.3 (-1.4)	0.1 (0.4)	-1.1 (-0.6)	0.1 (0.3)	2.15	0.150
Night Inc. (ºC)	4.0 (4.0)	0.0 (0.4)	3.6 (3.8)	0.0 (0.3)	0.13	0.718

[a] Number of nests within success category.

* Significant *P*-value ($P < 0.05$).

Table 3.15. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) between nest fate (i.e., successful and unsuccessful) for June on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Successful (*n* = 17)[a]		Unsuccessful (*n* = 38)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Day nest T (ºC)	31.3 (31.2)	0.1 (0.4)	31.1 (31.5)	0.1 (0.3)	0.27	0.607
Night nest T (ºC)	26.8 (26.8)	0.1 (0.4)	26.5 (26.6)	0.1 (0.3)	0.19	0.668
Day control T (ºC)	32.8 (32.6)	0.1 (0.5)	33.2 (33.5)	0.1 (0.4)	1.70	0.198
Night control T (ºC)	23.9 (23.8)	0.1 (0.4)	24.5 (24.4)	0.1 (0.3)	1.87	0.177
Day Inc. (ºC)	-1.5 (-1.4)	0.1 (0.3)	-2.0 (-2.0)	0.1 (0.2)	3.67	0.061
Night Inc. (ºC)	2.9 (3.0)	0.0 (0.3)	2.0 (2.1)	0.0 (0.2)	6.88	0.011*

[a] Number of nests within success category.

* Significant *P*-value ($P < 0.05$).

Table 3.16. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and F and P-values resulting from repeated measures analysis of variance of Snowy Plover day and night nest temperatures (T), control temperatures (T), and incubation values (Inc.; difference between paired nest and control temperature) between nest fate (i.e., successful and unsuccessful) for July on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

	Successful (n = 16)[a]		Unsuccessful (n = 21)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	F	P
Day nest T (ºC)	31.3 (31.8)	0.1 (0.5)	31.2 (30.8)	0.1(0.5)	2.09	0.157
Night nest T (ºC)	27.9 (28.1)	0.1 (0.5)	27.0 (26.5)	0.1 (0.4)	6.06	0.019*
Day control T (ºC)	32.7 (33.5)	0.2 (0.7)	33.1 (32.3)	0.2 (0.6)	1.56	0.220
Night control T (ºC)	24.9 (25.3)	0.1 (0.5)	25.0 (24.3)	0.1 (0.4)	1.97	0.169
Day Inc. (ºC)	-1.3 (-1.6)	0.1 (0.3)	-1.9 (-1.5)	0.1 (0.3)	0.11	0.738
Night Inc. (ºC)	3.0 (2.8)	0.0 (0.2)	2.0 (2.2)	0.0 (0.2)	3.55	0.068

[a] Number of nests within success category.

* Significant P-value ($P < 0.05$).

CHAPTER IV

SNOWY PLOVER OFFSPRING SEX RATIOS IN THE SOUTHERN HIGH PLAINS OF TEXAS

INTRODUCTION

Fisher (1930) predicted that when costs of producing male and female offspring are equal, offspring sex ratio should not differ from parity, with equal production of both sexes. However, if one sex is more costly to produce, excess of the less costly sex would be expected. Additionally, females may enhance lifetime fitness by producing the sex with the greatest potential reproductive value (Trivers and Willard 1973). Until recently, accurate sexing of monomorphic birds, particularly juveniles (i.e., hatching to fledging), has been nearly impossible. However advancements in molecular sexing techniques (Ellegren and Sheldon 1997, Griffiths et al. 1998) allows for accurate identification of birds and eggs, resulting in a vast increase in studies investigating sex ratio manipulation. In birds, offspring sex ratios rarely differ from parity (Clutton-Brock 1986), but deviations have been correlated with environmental, conditional, and social factors for a number of avian species (see Gowaty 1993, Pike and Petrie 2003). Some factors potentially influencing offspring sex ratios include maternal condition (Nager et al. 1999, Korpimäki et al. 2000), parental age (Blank and Nolan 1983, Cooch et al. 1997), mate attractiveness (Burley 1981, Ellegren et al. 1996, Sheldon et al. 1999), laying/hatching date (Howe 1977, Dijkstra et al. 1990, Zijlstra et al. 1992, Daan et al. 1996, Smallwood and Smallwood 1998, Székely et al. 2004), and laying/hatching sequence (Ankney 1982, Bednarz and Hayden 1991). Despite wide-spread associations between these factors and sex ratios, no mechanism has been identified causing skewed sex ratios in birds (Krackow 1995, Pike and Petrie 2003, Alonso-Alvarez 2006).

Female condition is suspected to influence offspring sex ratios, as poor condition females may not be able to withstand the physiological stress of producing the more costly sex (Myers 1978, Landete-Castillejos et al. 2004). In most species, females are generally the less expensive sex, as females typically require less maternal investment due to their smaller size and slower growth rates (see Landete-Castillejos et al. 2004). Therefore, females in poor condition may produce more daughters, as daughters can be successfully produced even while care-giving females are in poor condition. Trivers and Willard (1973) proposed that females in good condition would attain greater lifetime fitness by producing sons, as mother’s condition would more strongly influence future reproductive success of sons than daughters. Conversely, females in poor condition would attain greater lifetime fitness by producing daughters, as female offspring require less maternal investment and will likely attain some lifelong fitness, regardless of maternal condition. As a corollary to this, poor quality male offspring will likely not develop the physical characteristics necessary to compete successfully for females, furthering the notion that females in poor condition should produce daughters. The Trivers and Willard hypothesis assumes that offspring condition is correlated with care-giving female condition after the parental investment period, condition of the young following the parental investment period will carry over to adulthood, and conditional advantages will differentially benefit male offspring in reproductive success (Trivers and

Willard 1973). Maternal condition, however, may vary depending upon habitat conditions and prey availability, where poor habitat conditions and subsequent poor female condition result in female-biased offspring sex ratios (Howe 1977, Myers 1978, Wiebe and Bortolotti 1992, Korpimäki et al. 2000).

Laying/hatching date may also influence offspring sex ratio, with many avian taxa exhibiting seasonal variation in sex ratios, including shorebirds (Andersson et al. 2003, Székely et al. 2004), raptors, (Dijkstra et al. 1990, Olsen and Cockburn 1991, Tella et al. 1996, Smallwood and Smallwood 1998, Pen et al. 1999, Korpimäki et al. 2000, Byholm et al. 2002, Griggio et al. 2002), and passerines (Cordero et al. 2001, McIntosh et al. 2003). Most studies have reported male-biased sex ratios from broods hatching earlier in the season and female-biased sex ratios later in the season (Dijkstra et al. 1990, Tella et al. 1996, Smallwood and Smallwood 1998, Korpimäki et al. 2000, Byholm et al. 2002, Griggio et al. 2002, Andersson et al. 2003, Székely et al. 2004). In theory, in species that exhibit male resource defense and competition for mates, and/or breed within their first year, males born earlier have a developmental and fitness-based advantage (either born during times of greater food availability or have longer to obtain food) over later born individuals, as earlier born males are more likely to find and defend territories, successfully compete for mates, and breed within their first year (Trivers and Willard 1973, Daan et al. 1996). However, developmental advantages of hatching early are inconsequential to females, as females are likely to breed regardless of condition (Trivers and Willard 1973, Daan et al. 1996). Conversely, in species with alternate breeding strategies (e.g., female resource defense and compete for mates and/or do not breed within their first year), female-biased sex ratios were observed earlier in the season (Howe 1977, Olsen and Cockburn 1991, Zijlstra et al. 1992, Daan et al. 1996, Cordero et al. 2001, McIntosh et al. 2003). Here, females were hypothesized to have a reproductive advantage over males, as earlier born females were more likely to find suitable breeding locations, find and defend territories, and/or compete for mates. Varying offspring sex ratios according to hatching date has adaptive advantages to mothers via fitness benefits gained from successfully reproducing offspring, whereby the sex that gains greatest advantages by hatching earlier should be favored in early hatching dates.

Snowy Plovers (*Charadrius alexandrinus*) exhibit unique characteristics (e.g., determinant layer of odd modal clutch size [i.e., three eggs] and variable mating systems) that make examining sex allocation of particular interest within this species. For example, production of an odd modal clutch size forces individuals to invest differentially in a particular offspring sex. Although the genetic mating system of Kentish Plovers (*Charadrius alexandrinus*) is predominantly monogamous (Küpper et al. 2004), the social mating system of Snowy and Kentish Plovers varies within and among populations and has been described as facultatively polygynous, monogamous, and polyandrous (Page et al. 2009), with both parents capable of initiating second nesting attempts (Boyd 1972, Lessells 1984, Warriner et al. 1986, Székely and Lessells 1993, Székely and Williams 1994, Székely and Williams 1995, Amat et al. 1999). However, females typically renest at greater rates than males, as males are typically the care-giving parent during brood rearing (Lessells 1984, Warriner et al. 1986, Székely and Lessells 1993, Székely and Cuthill 1999, Székely et al. 1999, Székely and Cuthill 2000). This mating system is possible only if individuals are able to find and acquire a new mate after their first nesting attempt.

Snowy Plover populations have experienced declines throughout their range in the United States and are currently listed as threatened by the U.S. Fish and Wildlife Service along the Pacific Coast (U.S. Fish and Wildlife Service 1993) and as endangered, threatened, or of special concern in several states (see Page et al. 2009). Although no data exist on current population trends in interior regions, this study suggests a > 50% regional population decline in nesting Snowy Plovers in the Southern High Plains (SHP) of Texas (see Chapter VI). In species with low reproductive rates (i.e., few offspring produced per female) and relatively high adult survivorship, sex ratios can have important implications for long-term population stability. Therefore, examining sex ratios and sex allocation theory can provide insight into potential limitations of population growth rates as well as provide data for population demographic models. Therefore, the objectives of this study were to 1) document offspring sex ratios of Snowy Plovers in the SHP of Texas, 2) determine potential costs (i.e., hatchling and egg size) of producing offspring of different sexes, and 3) evaluate sex ratio adjustment based upon maternal condition, habitat, and hatching date.

METHODS

Study Area

The SHP is an approximately 80,000 km^2 region occurring from the panhandle of Texas, into New Mexico, and south to Midland, Texas (Osterkamp and Wood 1987). Within this region, approximately 40 saline lakes (i.e., primary regional nesting location for Snowy Plovers; Conway et al. 2005a) occur (Reeves and Temple 1986). Saline lakes are discharge wetlands containing freshwater springs fed by the Ogallala aquifer (Brune 2002), but having an overall saline water chemistry (often > 200g/L of dissolved solids; Osterkamp and Wood 1987). Two – three previously identified important (i.e., having consistent surface water throughout the nesting season and containing the majority of regional nesting Snowy Plovers) saline lakes (Conway et al. 2005a) ranging in size from ~ 270 – 600 ha were used as study sites in 1999 – 2000 and 2008 – 2009 (Figure 1.1). To maintain landowner anonymity, study site lakes will be referred to as lake A, lake B, and lake C. Each study site lake contained two – six fresh to slightly saline springs distributed along lake margins (Brune 2002). The primary landuse practice immediately surrounding study site lakes was pasture/rangeland with some held within the Conservation Reserve/Permanent Cover Program. Other landuse practices occurring within surrounding areas included row-crop agriculture production (i.e., mostly cotton

[*Gossypium* spp.]), mineral excavation (e.g., caliche), and development (i.e., mostly small home/ranch developments).

Nest Surveys

Surveys were conducted ≥ 1 time per week at each lake during the breeding season (i.e., early April – mid August; Conway et al. 2005a) in 1999 – 2000 and 2008 – 2009 to locate new nests. Nests were located by observing adult Snowy Plovers incubating nests, flushing from or returning to nest sites, and searching appropriate habitat (Conway et al. 2005a). Upon discovery, in 2008 – 2009, length (mm) and breadth (mm) of all eggs were measured with calipers (Coulson 1963). Egg volume (V_e; a measure of parental quality) was calculated similar to Amat et al. (2001) using the equation $V_e = K_v LW^2$, where K_v corrects for variation in egg shape and is calculated by $K_v = 0.5236 – [0.5236*2(L/W)/100]$, with L = egg length (cm) and W = egg width (cm).

During weekly surveys in 2008 – 2009, ocular estimates of percent dry ground, wet mud (areas wet from spring flow rather than rainwater), shallow water (1 – 5 cm deep; shallow enough for wading Snowy Plover), medium water (5 – 15 cm deep; too deep for wading Snowy Plover, but shallow enough for wading American Avocet [*Recurvirostra americana*]), and deep water (> 15 cm deep; too deep for wading American Avocet) were recorded to determine availability of surface water for nesting plovers throughout the breeding season. Specifically, during weekly surveys, locations of above categories were drawn on 2004 NAIP digital orthophoto quarter-quadrangle (DOQQ) aerial photographs (Texas Natural Resources Information System 2004) to estimate percent composition. To obtain total surface water availability, percent wet mud, shallow water, medium water, and deep water were summed for each survey. Mean percent surface water availability was then determined for each nest during the time the nest was active (i.e., from time first egg was laid until hatching or failure).

Nest Habitat Measurements

Habitat measurements were obtained at each lake in 2008 – 2009. Once a nest was located, primary nest substrate (i.e., sand or pebble) was recorded and 120 GPS positions were obtained per nest using a Trimble GeoXH GPS unit (Trimble Navigation Ltd, Sunnyvale, CA). All GPS positions were differentially corrected using GPS Pathfinder Office software (Trimble Navigation Ltd, Sunnyvale, CA) from six base stations and averaged to obtain one position for each nest. The differentially corrected positions were imported into ArcGIS 9.2 (ESRI, Redlands, CA) and mapped. Distance (m) to nearest active (i.e., day first egg was laid to day hatched or failed) nest was determined using Hawth's Analysis Tools (Beyer 2004).

Capture and Handling

Adult Snowy Plovers were captured on nests using nest traps (Conway and Smith 2000) from early April – early August, 1999 – 2000 and 2008 – 2009. Adults were sexed in the field based upon plumage characteristics (but verified by molecular sexing techniques; see below), where males generally have larger and darker breast and forehead patches as compared to females. All adults were banded with a uniquely numbered U.S. Fish and Wildlife Service aluminum band on the upper part (i.e., tibiotarsus) of their left leg, a dark green color band on the upper part of their right leg, and a unique combination of two color bands on both right and left lower legs. Upon capture, body mass (g) and the following morphological characteristics were measured for each adult (see Pyle et al. 1987 for descriptions): wing chord (mm), flattened wing chord (mm), tarsus (mm), tail (mm), culmen (mm), bill depth (mm), bill width (mm), and head length (mm). Mass was measured to the nearest 0.1 g with a digital scale (Ohaus® Scout Pro Balance, Pine Brook, NJ). Wing chord and flattened wing chord length were measured with a wing rule from the carpal joint to the tip of the longest primary, with wings pressed flat against a ruler for flattened wing chord measurement. Tarsus length was measured with calipers from the intertarsal joint to the distal end of the last leg scale. Tail length was measured with a ruler parallel to the tail from the point of insertion to the tip of tail. Culmen, bill length, bill width, and head length were measured with calipers. Culmen was measured from the anterior end of the nostril to the tip of bill, bill depth from the anterior end of the nostrils to the lower mandible perpendicular to the bill length measurement, bill width perpendicular to the bill length measurement at the anterior end of the nostrils, and head length from the back to the front of the head. In addition, a 200 μl blood sample was collected from each adult using brachial veinopuncture, stored in 10 ml of lysis buffer, and refrigerated or kept cool in coolers with ice packs while in the field (Longmire et al. 1997).

In 1999 – 2000 and 2008 – 2009, Snowy Plover chicks were captured by hand in nests at hatching. The same handling techniques as adults were used for chicks, where each bird was banded with a U.S. Fish and Wildlife Service aluminum band on the left upper leg, a dark green color band on right upper leg, and a unique combination of color bands on the lower legs. The same morphological characteristics as adults were also measured. In addition, a 200 μl blood sample was collected from each individual by puncturing the vein at the tibia-knee joint, stored in 10 ml of lysis buffer, and refrigerated or kept cool in coolers with ice packs while in the field (Longmire et al. 1997).

Molecular Sexing

Blood stored in lysis buffer was extracted using phenol-chloroform extraction following Longmire et al. (1997). Polymerase chain reaction (PCR) was performed following Conway et al. (2004) using CHD primers (Griffiths et al. 1996) P2—5’-TCT GCA TCG CTA AAT CCT TT-3’ and labeled primer P8-6FAM—5’-CTC CCA AGG

ATG AGR AAY TG-3’ (Applied Biosystems, Foster City, California). The CHD gene was amplified in 25 µL reactions that consisted of 20 – 50 ng DNA, 2X PCR buffer, 0.8 mM dNTPs (0.2 mM each), 2mM MgCl2, 0.3 µM of each primer, and 0.02 U *Taq* polymerase. Thermal cycler parameters followed Conway et al. (2004) with an initial denature of 95°C for 2 min; followed by 36 cycles of denaturation at 95°C for 1 min, anneal at 45°C for 1 min, and 72°C for 1 min; followed by a final extension of 72°C for 2 min. Reactions were performed on a 3100-*Avant* Genetic Analyzer (ABI) using 1 µL of PCR product with a mixture of 0.5 µL of Genescan-400HD ROX size standard (Applied Biosystems) and 12.5 µL formamide. Fragments were visualized using GeneMapper version 4.0 software (Applied Biosystems).

DATA ANALYSIS

To determine if offspring sex ratios (total number of males divided by total number of chicks) differed from parity within years (i.e., 1999, 2000, 2008, and 2009) and with years combined, a Chi-square analysis (PROC FREQ; SAS Institute 2002) was used. To investigate seasonal differences in offspring sex ratios, offspring were subdivided into 10-day intervals (i.e., time periods) based upon the range of hatching dates (i.e., 4 May – 11 August) similar to Smallwood and Smallwood (1998). Because not all time periods had adequate sample sizes (see Figure 4.1), time periods with samples sizes < 10 individuals were pooled. This resulted in the pooling of dates prior to 23 May and after 23 July for all years.

Because all chicks were not captured for majority of clutches (i.e., failure to locate precocial chicks that left nest prior to capture), proportion of males within a clutch was not used as the response variable. Rather, the probability a given individual was male was modeled using repeated measures logistic regression. Variables influencing offspring sex were examined using generalized estimating equations (GEE) repeated among clutches with binomial error and logit function (PROC GENMOD; SAS Institute 2002). GEEs are an extension of generalized linear models that account for the covariance structure of response variables (Hardin and Hilbe 2003). Sex of offspring was modeled using the following explanatory variables: lake, year, linear time period trend (i.e., probability of producing a male within a time period [10-day interval periods] was linearly related to time), female body mass (sex of incubating parent was determined by molecular techniques), substrate type, mean egg volume of clutch, distance to nearest active nest, brood size, and percent surface water available during the week eggs were laid. Due to visual evidence of a nonlinear distribution of sex ratios (Figure 4.1), a quadratic time period trend and a fourth-degree polynomial time period trend were also evaluated as explanatory variables. Because there were missing covariate data for individuals (e.g., habitat data only collected in 2008 – 2009), the quasi-likelihood criterion (QIC_u; a modified version of Akaike's Information Criterion corrected for small sample size that can be used with GEEs) could not be used to rank models. Therefore, models were evaluated based upon significance of explanatory variables, where parameter estimates, standard errors, and *P*-values are presented. To examine differences in offspring size between sexes, body measurements (i.e., tarsus length, wing chord length, and culmen length) and mass between male and female offspring were examined using repeated measures analysis of variance (ANOVA) repeated among clutches with a compound symmetric covariance structure (PROC MIXED; SAS Institute 2002).

RESULTS

A total of 245 chicks (45 in 1999, 87 in 2000, 38 in 2008, and 75 in 2009) were captured and sexed from 118 clutches during the study. Although offspring sex ratio (i.e., total number of males divided by total number of chicks) was slightly male-biased (53.8%) for the entire study, it did not deviate from parity ($X^2 = 1.47$; df = 1; $P = 0.225$). Additionally, offspring sex ratio did not deviate ($P > 0.05$) from parity within years, but was slightly male-biased in 1999, 2000, and 2009 (1999 = 55.6; 2000 = 58.6; 2008 = 44.7; 2009 = 52.0). From clutches in which all three chicks were captured ($n = 36$), offspring sex ratio was slightly male biased (57.4%), with few ($n = 9$; 25%) producing solely one sex (three produced all females; six produced all males) and the majority producing combinations of both sexes (10 produced one male and two females; 17 produced two males and one female).

Among explanatory variables, the fourth order polynomial time period trend and mean egg volume per clutch were significant ($P < 0.05$; Table 4.1), suggesting that the probability of being male was bimodal, where more males were produced earlier and later in the season as compared to the middle of the season (Figures 4.1, 4.2). Also, the probability of being male increased as mean clutch egg volume increased (Figure 4.3).

No other covariates influenced offspring sex ratios, where lake, year, linear time period trend, quadratic time period trend, female body mass, substrate type, distance to nearest active nest, brood size, and percent surface water available during the week eggs were laid did not affect the probability of a male offspring being produced ($P > 0.05$; Table 4.1). Male offspring were generally larger than female offspring, however, only significant for tarsus length ($P = 0.005$; Table 4.2).

DISCUSSION

Despite an odd modal clutch size, offspring sex ratios did not deviate from parity, suggesting an equal investment of males and females at a population level, despite sex-biased clutches. These results are consistent with a previous study on Kentish Plovers, where an unbiased offspring sex ratio was observed (0.46; Székely et al. 2004). Therefore, biased mating opportunities are not facilitated by biased offspring sex ratios. Although the degree of female brood desertion is unknown within this population, several females did initiate second breeding attempts after first nests successfully hatched (W. Conway and S. Saalfeld per. obs.). However, equal offspring and adult sex ratios within this population (Conway 2001) may preclude females from finding mates following initial breeding attempts.

Although offspring sex ratios did not differ from parity, slightly more males were produced in most years, and as males are more costly to produce (as indicated by larger body size and mean egg size of clutch), these results are inconsistent with existing theory that predicts excess production of the less costly sex (i.e., females; Fisher 1930). Although mechanisms causing skewed sex ratios in birds remain unknown (Krackow 1995, Pike and Petrie 2003, Alonso-Alvarez 2006), biased offspring sex ratios may arise if females with specific brood sex ratio characteristics produce the majority of offspring (Olsen and Cockburn 1991). For example, females in better condition may positively influence nest success by producing larger eggs, compensating for or withstanding high physiological costs of incubation, occupying nest sites of better quality (i.e., lower predation risks, lower risks of destruction from weather events, and/or closer to optimal foraging areas), and better defending nests from predation risks (Blomqvist et al. 1997). Furthermore, Snowy Plovers are capable of producing more than one clutch within a given season; however, only females in good condition will likely initiate these second nesting attempts, as only good condition females will be able to meet energy demands required for production of more than one clutch. In both instances, good condition females may produce a greater proportion of offspring within a given year compared to poor condition females. Therefore, if good condition females produce mostly male offspring (Trivers and Willard 1973), sex ratios may become male-biased. However, female body mass did not influence offspring sex in this study. Female body mass exhibits low variation among individuals (e.g., 35 – 54 g) and can vary diurnally, with female Kentish Plovers losing 8.4% body mass between morning and afternoon from depletion of stored body fat and/or evaporation of water (Szentirmai et al. 2001). Therefore, body mass of individuals captured at different times may not be indicative of an individual's condition and may preclude detection of significant trends.

Similar to a previous study on Kentish Plovers (Székely et al. 2004), offspring sex varied based upon hatching date, suggesting benefits for females that seasonally adjust offspring sex ratio. Although earlier births could be beneficial to both sexes, because Snowy Plovers exhibit male resource defense and both sexes attempt to breed within their first year (Warriner et al. 1986, Sandercock et al. 2005; W. Conway and S. Saalfeld per. obs.), fitness gains would potentially be greater for males than females. Individuals born earlier have a longer season in which to acquire food prior to migration, a fitness advantage that may carry over into following breeding season(s) (Andersson et al. 2003). Because male Snowy Plovers compete for and defend nesting territories, differential breeding success likely occurs between the sexes, although estimates of actual fitness gains by males born earlier in the season remain unknown (Székely et al. 2004). In Snowy Plovers, males are the more costly sex to produce, as male offspring are larger than females (as indicated by tarsus length) and likely require additional energy input (as indicated by larger mean egg volume for males). Therefore, females in better condition, able to withstand the energetic costs should produce males (Trivers and Willard 1973, Clark 1978, Myers 1978). Seasonally biased offspring sex ratios may arise if females with specific brood sex ratio characteristics breed at different times during the season (Székely et al. 2004). For example, females able to acquire necessary food and nutrients for egg formation, tend to initiate nests earlier in the season (Perrins 1996); therefore, nests initiated earlier by better condition females may produce more male offspring (Andersson et al. 2003).

More male offspring were also born late in the season. Although not observed in Kentish Plovers (Székely et al. 2004), this late season male bias trend was apparent in American Kestrels (*Falco sparverius*), although low sample size precluded statistical analysis (Smallwood and Smallwood 1998). Furthermore, bimodal distribution of sex ratios was observed in Red-winged Blackbirds (*Agelaius phoeniceus*), where more males were produced in middle time periods when food abundance was likely to be greatest (Weatherhead 1983). In the SHP of Texas, surface water availability and subsequent food availability vary unpredictably (within and between years) throughout the season, depending upon weather. As offspring sex ratio may vary based upon food availability (Howe 1977, Myers 1978, Wiebe and Bortolotti 1992, Korpimäki et al. 2000), sex ratios within this region may exhibit unpredictable seasonal variation. For example, nests initiated following a severe weather event late in the season in 1999 (that greatly increased surface water availability in June) produced more male offspring (S. Saalfeld unpublished data). These results suggest that sex ratio manipulation in unpredictable environments may not be straightforward, following nonlinear models and/or trends varying annually. Rather, offspring sex ratios may follow unpredictable surface water patterns, where more male offspring are produced when perceived food availability is high, regardless of time during a given nesting season.

Nests hatching late in the season (i.e., after 3 July) are likely second breeding attempts rather than first breeding attempts by late nesters. For example, following a severe weather event in June 1999, numerous individuals were observed initiating second breeding attempts. Therefore, if sex ratio manipulation is controlled by females with specific brood sex ratio characteristics breeding at different times during the season (Székely et al. 2004), good condition females breeding late in the season will produce an excess of male offspring. Producing male offspring late in the season may have selective advantages for females nesting at these times. Because males have faster growth rates than females (Székely et al. 2004), and may fledge earlier, producing males late in the season may allow parents to migrate earlier or focus upon acquiring food prior to migration. Therefore, production of males late in the season could provide fitness and survival benefits for parents. Late born chicks may also have survival advantages to early born chicks. For example, the majority (i.e., 15 out of 16) of male offspring returning the following nesting season were born late in the season (i.e., after 3 July; S. Saalfeld unpublished data). Although chick survival (from hatching to fledging) was not determined in this study, late hatching could result in greater chick survival if fewer devastating weather events occur later in the season (Colwell et al. 2007), greater surface water is available (although unpredictable and variable from year to year), and/or there are lower predation rates due to other species being present (e.g., migrant sandpipers; Colwell et al. 2007). However, these potential factors influencing seasonal survival rates may vary annually and provide inconsistent advantages to chicks born at specific times. While both sexes may benefit by being born late in the season, males may have a differential survival advantage due to faster growth rates (Székely et al. 2004), potentially allowing males to fledge faster than females, migrate earlier, and/or have longer times to increase body condition prior to migration.

Within the SHP of Texas, Snowy Plover populations have declined within the past 10 years (see Chapter VI), suggesting the need for conservation efforts within this region. For conservation to be successful, understanding current dynamics (e.g., population size, mortality rates, recruitment rates, sex ratios, etc.) influencing population growth rates remains important. This study suggests a slightly male-biased offspring sex ratio that may limit population growth rates as well as reduce population stability. Therefore, conservation efforts within this region should focus upon maintaining as well as increasing current population size. This population appears to have seasonal shifts in sex ratios, which may be related to female condition as well as differential advantages of sexes being born at specific times. Currently, the mechanism for seasonal variation in sex ratios remains unknown (Krackow 1995, Pike and Petrie 2003, Alonso-Alvarez 2006) as well as the effects such changes in sex ratios may have on population growth and stability.

One of the primary conservation concerns within this region is surface water availability (see Chapter I). Saline lakes are discharge wetlands containing freshwater springs fed by the Ogallala aquifer that, at least historically, provided reliable surface water during the nesting season (Brune 2002). However, declining spring flow due to decreasing water table levels of the aquifer has occurred since the 1950s (Brune 2002). This, along with irrigation during the breeding season, has resulted in shortened hydroperiods and increased salinity. Because freshwater springs not only provide reliable surface water during the breeding season, a necessary landscape feature for nesting Snowy Plovers (Conway et al. 2005b), but also support salt intolerant invertebrate prey (Andrei et al. 2009), declining spring flow may decrease suitability of saline lakes for nesting shorebirds as well as decrease food availability during the nesting season, resulting in poor condition of nesting individuals. Long-term reduction in food availability and subsequent condition of nesting females may result in significant changes in offspring sex ratios (Cooch et al. 1997). Because poor condition females are likely to produce more females (Trivers and Willard 1973), if conditions continue to decline within this region, sex ratios may become more female-biased, having potentially dramatic affects on population growth and stability. Therefore, it remains important to provide quality habitat for nesting Snowy Plovers in the SHP of Texas. As surface water availability is the main factor influencing habitat quality in this region, conserving freshwater springs discharging into saline lakes, as well as the Ogallala aquifer can increase surface water availability and habitat quality. However, because the Ogallala aquifer is recharged from playa wetlands (Osterkamp and Wood 1987, Bolen et al. 1989), it also remains important to conserve the entire complex of wetlands within the SHP of Texas (Andrei et al. 2008, Andrei et al. 2009).

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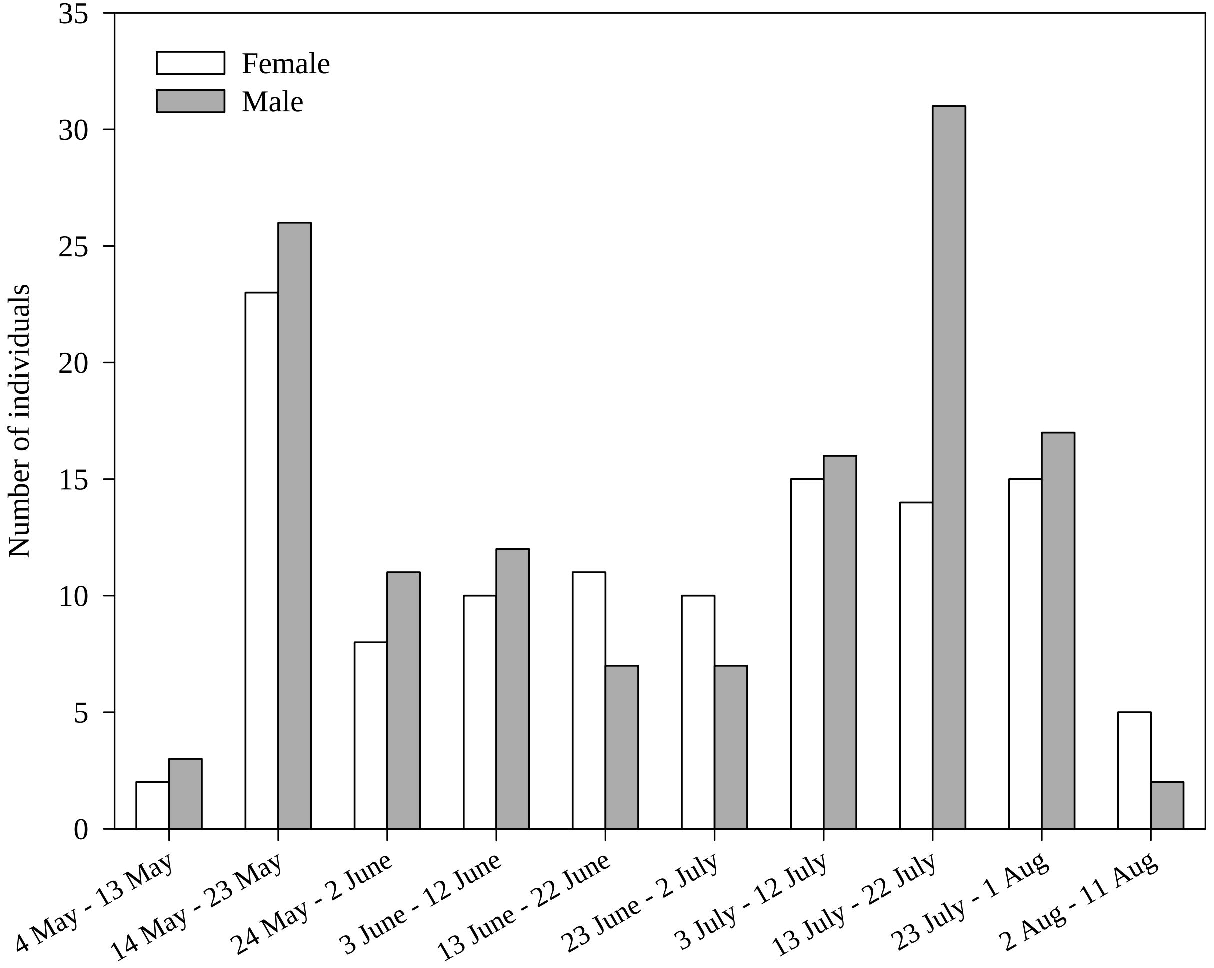

Figure 4.1. Number of male and female Snowy Plover offspring produced within 10-day time periods on saline lakes within the Southern High Plains of Texas, USA, 1999 – 2000 and 2008 – 2009.

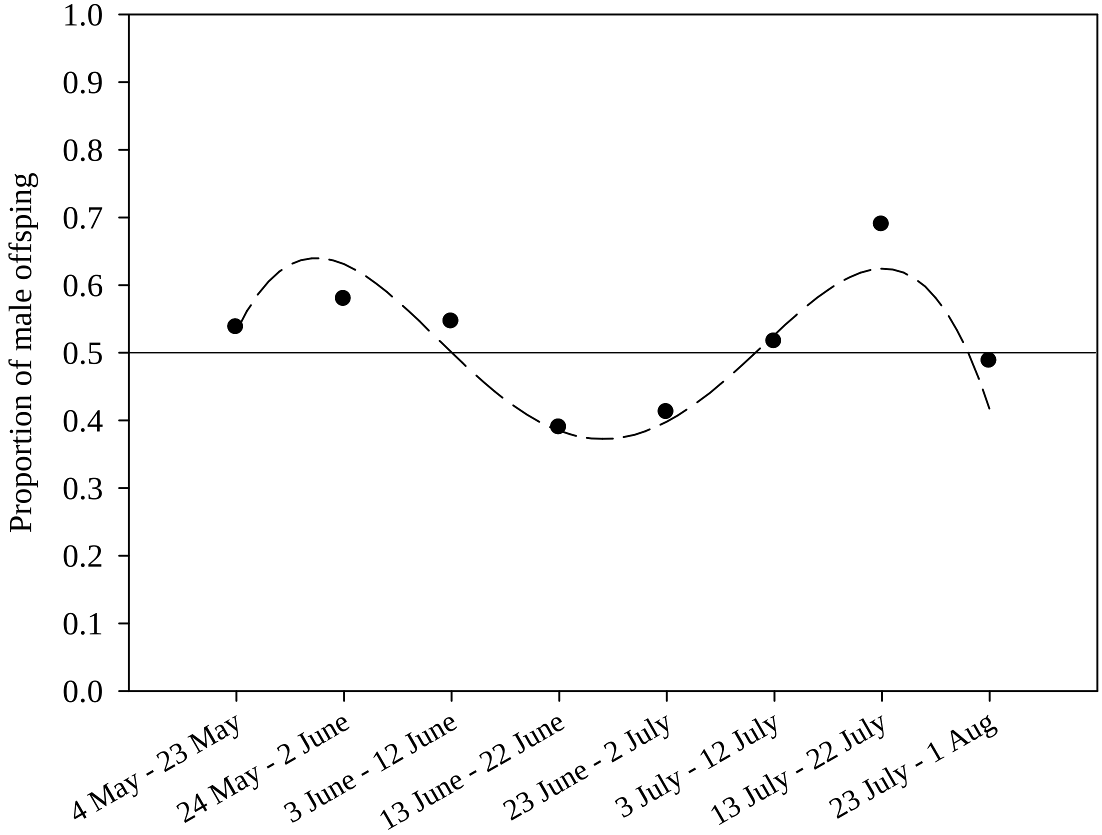

Figure 4.2. Proportion of male Snowy Plover chicks produced within 10-day time periods and fitted line from repeated measures logistic regression (model = fourth order time period trend) estimating probability of Snowy Plover offspring being male on saline lakes within the Southern High Plains of Texas, USA, 1999 – 2000 and 2008 – 2009.

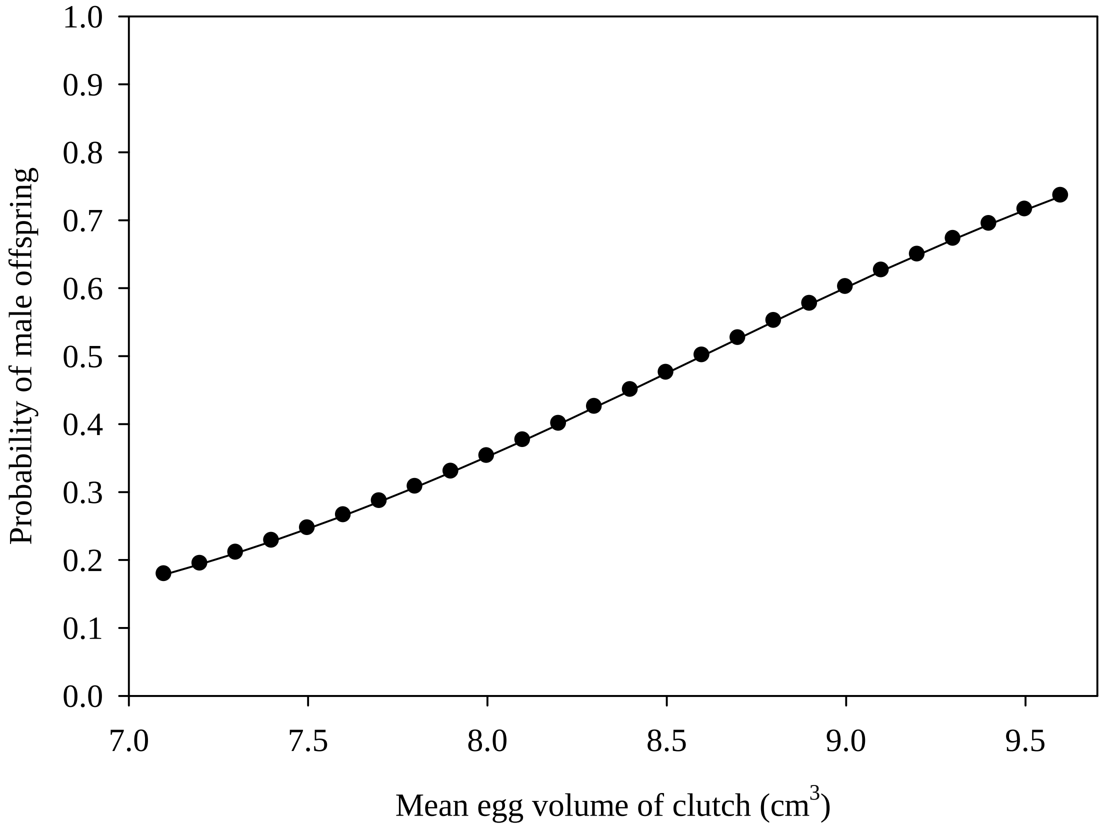

Figure 4.3. Probability of Snowy Plover offspring being male estimated from repeated measures logistic regression (model = mean egg volume) on saline lakes within the Southern High Plains of Texas, USA, 1999 – 2000 and 2008 – 2009.

Table 4.1. Repeated measures logistic regression models estimating probability of Snowy Plover offspring being male on saline lakes within the Southern High Plains of Texas, USA, 1999 – 2000 and 2008 – 2009.

Model	Parameter	Estimate	SE	*Z*	*P*
Lake[a]	Lake A	0.10	0.17	0.59	0.553
	Lake B	0.26	0.20	1.27	0.203
	Lake C	0.18	0.60	0.30	0.761
Year[a]	1999	0.22	0.34	0.66	0.511
	2000	0.35	0.22	1.57	0.116
	2008	-0.21	0.31	-0.69	0.493
	2009	0.08	0.22	0.36	0.721
Linear time period trend[a]	Intercept	0.07	0.29	0.26	0.798
	Time period	0.02	0.05	0.33	0.740
Quadratic time period trend[a]	Intercept	0.27	0.50	0.54	0.590
	Time period	-0.12	0.26	-0.45	0.652
	Time period^2	0.02	0.03	0.54	0.589

Table 4.1. Continued.

Model	Parameter	Estimate	SE	*Z*	*P*
Fourth order time period trend[a]	Intercept	-2.74	1.66	-1.65	0.099
	Time period	4.74	2.27	2.09	0.036*
	Time period^2	-2.24	0.96	-2.34	0.019*
	Time period^3	0.39	0.16	2.48	0.013*
	Time period^4	-0.02	0.01	-2.55	0.011*
Female body mass[b]	Intercept	-1.25	2.40	-0.52	0.604
	Female body mass	0.03	0.06	0.60	0.551
Substrate[c]	Pebble	0.12	0.19	0.64	0.525
	Sand	-0.38	0.40	-0.94	0.348
Mean egg volume[c]	Intercept	-8.77	3.04	-2.88	0.004*
	Mean egg volume	1.02	0.35	2.88	0.004*

Table 4.1. Continued.

Model	Parameter	Estimate	SE	Z	P
Distance to nearest active nest[c]	Intercept	0.01	0.23	0.04	0.965
	Distance nest	0.00	0.00	-0.29	0.772
Brood size[a]	Brood size 2	-0.41	0.30	-1.35	0.177
	Brood size 3	0.21	0.14	1.47	0.142
Percent surface water availability[d]	Intercept	0.44	0.42	1.07	0.286
	Percent water	-0.01	0.01	-1.05	0.292

[a] $n = 245$ chicks from 118 clutches.

[b] $n = 157$ chicks from 78 clutches.

[c] $n = 113$ chicks from 59 clutches.

[d] $n = 110$ chicks from 57 clutches.

* Significant P-value ($P < 0.05$).

Table 4.2. Means ($\bar{x}$), standard errors (SE), least squares (LS) estimates and SE, and *F* and *P*-values resulting from repeated measures analyses of variance of Snowy Plover chick body measurements on saline lakes within the Southern High Plains of Texas, USA, 1999 – 2000 and 2008 – 2009.

	Females (*n* = 112)		Males (*n* = 131)			
	$\bar{x}$ (LS)	SE (LS)	$\bar{x}$ (LS)	SE (LS)	*F*	*P*
Body mass (g)	5.85 (5.88)	0.08 (0.08)	5.93 (5.92)	0.08 (0.08)	0.15	0.702
Tarsus length (mm)	17.68 (17.63)	0.20 (0.21)	17.71 (17.98)	0.20 (0.21)	8.86	0.005*
Wing chord length (mm)	11.00 (11.02)	0.09 (0.10)	11.18 (11.20)	0.09 (0.09)	2.13	0.151
Culmen length (mm)	3.90 (3.88)	0.06 (0.07)	4.02 (4.00)	0.07 (0.07)	3.35	0.073

* Significant *P*-value ($P < 0.05$).

CHAPTER V

APPARENT SURVIVAL OF ADULT AND JUVENILE SNOWY PLOVERS IN THE SOUTHERN HIGH PLAINS OF TEXAS

INTRODUCTION

Population growth is dependent upon several key components including adult and juvenile survival, fecundity, immigration, and emigration. In species such as Snowy Plovers (*Charadrius alexandrinus*) with low reproductive rates (i.e., few offspring produced per female) and relatively high adult survivorship, declines in adult survival can dramatically influence population growth, causing formerly stable populations to decline (Hitchcock and Gratto-Trevor 1997, Plissner and Haig 2000, Sandercock 2003). Therefore, estimating current population vital rates such as reproductive success, adult and juvenile survival, and breeding and natal site fidelity are key elements for long-term monitoring and conservation of Snowy Plovers throughout their geographic range. Although continental populations of Snowy Plovers have received considerable conservation attention due to declines, particularly along the Pacific coast (see Wilson-Jacobs and Meslow 1984, Wilson-Jacobs and Dorsey 1985, Warriner et al. 1986, Palacios et al. 1994, Powell and Collier 2000, Powell 2001, Powell et al. 2002, Ruhlen et al. 2003, Neuman et al. 2004, Colwell et al. 2005, Lafferty et al. 2006, Mullin et al. 2010), few data exist (Conway et al. 2005a) to evaluate the current status and threats to Snowy Plovers nesting within the Southern High Plains (SHP) of Texas. Estimating metrics influencing regionally specific population growth (e.g., survival and natal and breeding site fidelity) is crucial for both regional and continental conservation and management.

Moreover, estimates of adult and juvenile apparent survival can be used to determine recruitment thresholds needed to maintain a stable population within this region (Ricklefs 1973, Page et al. 1983, Trine 1998, Mullin et al. 2010). In conjunction with current recruitment estimates, these thresholds can be used to understand current population growth and stability and evaluate source-sink dynamics (Ricklefs 1973, Page et al. 1983, Trine 1998, Mullin et al. 2010), important metrics to understand when implementing conservation actions and management plans for at risk species.

To obtain robust estimates of survival, Cormack-Jolly-Seber (CJS) models can be used to estimate apparent survival; the product of true survival and site fidelity (Cormack 1964, Jolly 1965, Seber 1965). Beyond estimating apparent survival rates within populations, understanding yearly variation in such metrics may also provide important information for long-term conservation. In many shorebird species, yearly variation in predation rates of nests, chicks, and adults (Stenzel et al. 1994, Badzinski 2000, Stenzel et al. 2007), nest success (Redmond and Jenni 1982, Gratto et al. 1985, Reed and Oring 1993, Flynn et al. 1999, Badzinski 2000), and available nesting habitat (Haig and Oring 1988, Wiens and Cuthbert 1988, Stenzel et al. 1994) affect both true survival and site fidelity. In general, increased predation rates and poor habitat conditions may result in greater mortality and/or dispersal of adults and juveniles. Furthermore, following unsuccessful nesting attempts, individuals may be more likely to disperse to alternate breeding locations (Redmond and Jenni 1982, Gratto et al. 1985, Reed and Oring 1993, Flynn et al. 1999).

Apparent survival may also vary based upon sex and age (i.e., juvenile and adults), although true survival is likely similar between sexes in Snowy Plovers (Warriner et al. 1986, Paton 1994b, Sandercock et al. 2005). Conversely, breeding and natal site fidelity can vary dramatically between sexes, where dispersal patterns are typically linked to social mating systems, as related to resource defense (Greenwood 1980, Greenwood and Harvey 1982). For example, in species with male resource defense, males have greater breeding site fidelity due to increased familiarity with vital resources, allowing them to successfully compete for access to limited nest territories and/or mates (Greenwood 1980, Greenwood and Harvey 1982). Conversely, females are typically the dispersing sex, and by dispersing further may find better habitat, access more potential mates, and decrease inbreeding risks (Greenwood 1980, Paton 1994a). Such female-biased dispersal is more common than male-biased dispersal in Snowy Plovers (Page et al. 1983, Warriner et al. 1986, Paton 1994a, Stenzel et al. 1994, Paton and Edwards 1996, Powell and Collier 2000, Colwell et al. 2007).

Within the SHP of Texas, Snowy Plovers nest primarily on edges of saline lakes (Conway et al. 2005a), discharge wetlands containing springs fed by the Ogallala aquifer, which historically, provided a reliable source of freshwater during the breeding season (Brune 2002). However, declining spring flow due to increasing water use and subsequent decreasing water table levels of the aquifer has occurred since the 1950s (Brune 2002), resulting in shortened hydroperiods and increased salinity, frequently making saline lakes unsuitable for migrant (Andrei et al. 2008) and nesting shorebirds.

As spring flow declines, surface water availability within these lakes will become more reliant upon unpredictable weather events, exaggerating nesting habitat variability within and between seasons. Therefore, the ability to move (potentially) long distances may be important in allowing Snowy Plovers to nest successfully in unpredictable environments (Stenzel et al. 1994). Additionally, familiarity with multiple breeding sites could allow individuals flexibility to make discrete choices to nest in alternate sites if habitats becomes unsuitable on short temporal scales (Stenzel et al. 1994). Therefore, it remains important to not only estimate metrics influencing population growth (e.g., survival and natal and breeding site fidelity), but also determine the relative importance of movements within and between breeding seasons. Therefore, the objectives of this study were to 1) compare estimates of adult and juvenile apparent survival of Snowy Plovers nesting in the SHP of Texas between 1999 – 2000 and 2008 – 2010, 2) quantify sex and age specific differences in Snowy Plover apparent survival and encounter rates from 2008 – 2010, 3) document and estimate the relative importance of adult and juvenile movements within and between seasons, and 4) determine recruitment thresholds needed to maintain a stable population.

METHODS

Study Area

The SHP is an approximately 80,000 km^2 region occurring from the panhandle of Texas, into New Mexico, and south to Midland, Texas (Osterkamp and Wood 1987). Within this region, approximately 40 saline lakes (i.e., primary regional nesting location for Snowy Plovers; Conway et al. 2005a) occur (Reeves and Temple 1986). Saline lakes are discharge wetlands containing freshwater springs fed by the Ogallala aquifer (Brune 2002), but having an overall saline water chemistry (often > 200g/L of dissolved solids; Osterkamp and Wood 1987). Two – three previously identified important (i.e., having consistent surface water throughout the nesting season and containing the majority of regional nesting Snowy Plovers) saline lakes (Conway et al. 2005a) ranging in size from ~ 270 – 600 ha were used as study sites in 1999 – 2000 and 2008 – 2010 (Figure 1.1). To maintain landowner anonymity, study site lakes will be referred to as lake A, lake B, and lake C. Each study site lake contained two – six fresh to slightly saline springs distributed along lake margins (Brune 2002). The primary landuse practice immediately surrounding study site lakes was pasture/rangeland with some held within the Conservation Reserve/Permanent Cover Program. Other landuse practices occurring within surrounding areas included row-crop agriculture production (i.e., mostly cotton

[*Gossypium* spp.]), mineral excavation (e.g., caliche), and development (i.e., mostly small home/ranch developments).

Capture and Handling

Adult Snowy Plovers were captured at feeding locations using mist nets and on nests using nest traps (Conway and Smith 2000) in early April – early August in 1999 – 2000 and 2008 – 2009. Adults were sexed in the field based upon plumage characteristics (but verified by molecular sexing techniques; see below), where males generally have larger and darker breast and forehead patches as compared to females. All adults were banded with a uniquely numbered U.S. Fish and Wildlife Service aluminum band on the upper part (i.e., tibiotarsus) of their left leg, a dark green color band on the upper part of their right leg, and a unique combination of two color bands on both right and left lower legs (i.e., red, blue, purple, light green, orange, pink, white, and yellow color bands). All females were banded with a red color band on the right lower leg and males with a blue color band on the right lower leg (example female band combination: upper right leg: dark green, lower right leg: red/yellow, upper left leg: USFWS band, lower left leg: white/orange). In addition, a 200 μl blood sample was collected from each adult using brachial veinopuncture, stored in 10 ml of lysis buffer, and refrigerated or kept cool in coolers with ice packs while in the field (Longmire et al. 1997).

In 1999 – 2000 and 2008 – 2009, Snowy Plover chicks were captured by hand in nests at hatching or with adult(s) after hatching. The same handling techniques as adults were used for chicks, where each individual received a U.S. Fish and Wildlife Service aluminum band on the left upper leg, a dark green color band on right upper leg, a purple color band on the right lower leg, and a unique combination of color bands on lower legs. In addition, a 200 µl blood sample was collected from each individual by puncturing the vein at the tibia-knee joint, stored in 10 ml of lysis buffer, and refrigerated or kept cool in coolers with ice packs while in the field (Longmire et al. 1997).

Molecular Sexing

Blood stored in lysis buffer was extracted using phenol-chloroform extraction following Longmire et al. (1997). Polymerase chain reaction (PCR) was performed following Conway et al. (2004) using CHD primers (Griffiths et al. 1996) P2—5’-TCT GCA TCG CTA AAT CCT TT-3’ and labeled primer P8-6FAM—5’-CTC CCA AGG ATG AGR AAY TG-3’ (Applied Biosystems, Foster City, California). The CHD gene was amplified in 25 µL reactions that consisted of 20 – 50 ng DNA, 2X PCR buffer, 0.8 mM dNTPs (0.2 mM each), 2mM MgCl2, 0.3 µM of each primer, and 0.02 U *Taq* polymerase. Thermal cycler parameters followed Conway et al. (2004) with an initial denature of 95°C for 2 min; followed by 36 cycles of denaturation at 95°C for 1 min, anneal at 45°C for 1 min, and 72°C for 1 min; followed by a final extension of 72°C for 2 min. Reactions were run on a 3100-*Avant* Genetic Analyzer (ABI) using 1 µL of PCR product with a mixture of 0.5 µL of Genescan-400HD ROX size standard (Applied Biosystems) and 12.5 µL formamide. Fragments were visualized using GeneMapper version 4.0 software (Applied Biosystems).

Bird Surveys

1999 – 2000

Approximately weekly surveys were conducted at lakes A and B during the breeding season (3 March – 31 July) as part of a previous research project (Conway 2001). During each survey, observers traveled (by foot) similar survey routes as 2008 – 2009 (see below) prior to 1200 hrs, and located Snowy Plovers by sight and sound. Once located, all individuals were recorded and inspected for presence of color bands. If color bands were present, band combinations were recorded for individual identification.

2008 – 2009

Weekly surveys were performed at lakes A, B, and C during the breeding season (10 April – 25 July) in 2008 – 2009. A route was delineated within each lake, where during each survey observers traveled (by foot) the same route prior to 1200 hrs, and located Snowy Plovers by sight and sound. Once located, all individuals were recorded and inspected for presence of color bands. If color bands were present, band combinations were recorded for individual identification.

2010

Three surveys were conducted at lakes A, B, and C spaced throughout the breeding season (1 May – 2 May, 29 May – 30 May, and 15 July – 16 July). During each survey, observers traveled (by foot) the same survey routes as 2008 – 2009 prior to 1200 hrs, and located Snowy Plovers by sight and sound. Once located, all individuals were recorded and inspected for presence of color bands. If color bands were present, band combinations were recorded for individual identification.

DATA ANALYSIS

Adult and juvenile (i.e., interval from hatching to first year of adulthood) return rates were determined for each study (i.e., 1999 – 2000 study and 2008 – 2010 study) using a standard proportion (i.e., number of adults observed ≥ 1 year following capture divided by total number of adults captured). Differences in adult and juvenile return rates between sexes and studies were examined using a Chi-square analysis (PROC FREQ; SAS Institute 2002). Because only one year of resighting data was obtained during the 1999 – 2000 study, yearly apparent survival from only 2008 – 2010 was estimated in Program Mark using CJS models (Cormack 1964, Jolly 1965, Seber 1965). Candidate models for apparent survival were performed separately for adults and juveniles. Similar to Sandercock et al. (2005), models included combinations of apparent survival (φ) and encounter rates (p) that were allowed to 1) vary over time (i.e., φ_t or p_t: two parameters were entered into the model representing a separate estimate of apparent survival and/or encounter rates between years), 2) vary with sex (i.e., φ_{sex} or p_{sex}: two parameters were entered into the model representing a separate estimate of apparent survival and/or encounter rates between males and females), and/or 3) remain constant (i.e., φ_c or p_c: one parameter was entered into the model representing a constant estimate of apparent survival and/or encounter rates between years). Juvenile apparent survival was modeled based upon age class, where survival during their first year (i.e., interval from hatching to first year of adulthood; φ^1) was modeled separately from survival during their second year (i.e., interval from first year of adulthood to second year of adulthood; φ^2). Akaike's Information Criterion corrected for small sample size (AIC_c) was used to rank candidate models. An individual model was considered plausible when $\Delta AIC_c < 2$ (Burnham and Anderson 2002). To check for over-dispersion (i.e., goodness-of-fit), median $\hat{c}$ procedure in Program MARK was used (Cooch and White 2002).

Finally, recruitment thresholds required to maintain a stable population without immigration were compared between studies (i.e., 1999 – 2000 study and 2008 – 2010 study) using the following equation: recruitment threshold = 2*(adult mortality) / (1 – juvenile mortality) (Ricklefs 1973, Page et al. 1983, Trine 1998, Mullin et al. 2010).

RESULTS

Return Rates

In 1999 and 2000, 151 adult and 174 juvenile Snowy Plovers were individually marked from lakes A and B (Table 5.1), where in 2000, 94 adults and 17 juveniles were resighted (Table 5.1). Return rate of adult Snowy Plovers banded in 1999 was 77% (94 of 122). Although slightly more males (82% [49 of 60]) returned than females (73% [45 of 62]), there was no sex bias in return rates ($\chi^2 = 1.42$; df = 1; $P = 0.233$). Movements between saline lakes (i.e., lake A and B) appeared to be uncommon in 1999 – 2000, as few adults were recorded changing primary locations (i.e., saline lakes) between (i.e., eight males and eight females; Table 5.2) or within years (i.e., two males from lake B were observed on lake A in June 1999, one female from lake B was observed on lake A in July 2000, and two females from lake A were observed on lake B in May 2000).

In 2008 and 2009, 73 adult and 118 juvenile Snowy Plovers were individually marked from lakes A, B, and C (Table 5.1), where in 2009 and 2010, 42 adults and 10 juveniles were resighted ≥ 1 year following capture (Table 5.1). Return rate of adult Snowy Plovers banded in 2008 and 2009 was 58% (42 of 73), 25% lower than return rates in 2000 ($\chi^2 = 8.24$; df = 1; $P = 0.004$). Although a greater percentage of males (70% [16 of 23]) returned than females (52% [26 of 50]), there was no sex bias in return rates in 2009 – 2010 (χ^2 = 1.99; df = 1; P = 0.158). Movements among saline lakes (i.e., lake A, B, and C) also appeared to be uncommon in 2008 – 2010, as few adults were observed changing primary locations (i.e., saline lakes) between years (i.e., three females; Table 5.3) or within years (i.e., one female from lake C was observed on lake B in July 2008). Furthermore, one individual banded as an adult at lake A in 1999 was recaptured at lake A in 2009.

In 2000, return rate of first year adult Snowy Plovers banded as chicks in 1999 was 22% (17 of 77; Table 5.1). Return rates were similar among first year males (24% [10 of 41]) and females (19% [7 of 36]; χ^2 = 0.27; df = 1; P = 0.602). Movements among saline lakes (i.e., lake A, B, and C) were rare for juveniles as well in 1999 – 2000, as four (i.e., two males and two females) first year adults were observed changing primary locations (i.e., saline lakes) from natal sites (Table 5.2). In 2008 – 2010, return rate of first year adult Snowy Plovers was 9% (10 of 118; Table 5.1), 60% lower than return rate in 2000 (χ^2 = 7.23; df = 1; P = 0.007). No sex bias in return rates was observed between first year males (10% [6 of 60]) and females (7% [4 of 58]; χ^2 = 0.37; df =1; P = 0.545). Movements among saline lakes (i.e., lake A, B, and C) were also uncommon for juveniles in 2008 – 2010, as four (one male and two females) first year adults were observed changing primary locations (i.e., saline lakes) from natal sites (Table 5.3). Furthermore, three individuals banded as chicks at lake A in 1999 – 2000 were recaptured at lake A in 2008 – 2009.

Apparent Survival

Among 13 candidate CJS models for adult Snowy Plover apparent survival, the first four models should be considered plausible (i.e., $\Delta AIC_c < 2$; Table 5.4). The top-ranked model contained constant apparent survival and encounter rates varying between sexes; however, models containing apparent survival varying between years and sexes were equally plausible (Table 5.4). From the top-ranked model, apparent annual survival for adults was estimated to be 0.65 ± 0.07, where female encounter rates (0.70 ± 0.13) were lower than males (1.00 ± 0.00; Table 5.5). Competing models also suggest that apparent survival was lower in 2008 – 2009 than in 2009 – 2010, and greater for males than females (Table 5.5). Goodness of fit statistic from the general model indicated that the model fit the data well (median $\hat{c} = 1.15$).

Among 17 candidate CJS models for juvenile Snowy Plover apparent survival, the first six ranked models should be considered plausible (i.e., $\Delta AIC_c < 2$; Table 5.6). The top-ranked model contained constant apparent survival and encounter rates; however, models containing apparent survival varying between years and sexes and encounter rates varying between sexes, years, and the interaction were equally plausible (Table 5.6). From the top-ranked model, apparent survival for juveniles was estimated to be 0.12 ± 0.06, with encounter rates estimated as 0.62 ± 0.30 (Table 5.7). Apparent survival during second year of adulthood (i.e., φ^2) was estimated to be 0.80 ± 0.48 (Table 5.7); however, this estimate was based upon few individuals for one year and is therefore not a robust estimate. Competing models also suggest that both apparent survival and encounter rates were lower in 2008 – 2009 than in 2009 – 2010, and greater for males than females (Table 5.7). Goodness of fit statistic from the general model indicated that the model fit the data well (median $\hat{c} = 1.42$).

Recruitment Threshold

Using return rates for adults (0.77) and juveniles (0.22), recruitment threshold for 1999 – 2000 was 2.1 hatchlings per adult. Using apparent survival rates for adults (0.65) and juveniles (0.12) obtained from the top-ranked CJS models, recruitment threshold for 2008 – 2010 was 5.8 hatchlings per adult. However, using return rates for adults (0.58) and juveniles (0.09), recruitment threshold for 2008 – 2010 was 9.3 hatchlings per adult.

DISCUSSION

Adult yearly apparent survival rates from 2008 – 2010 (58% using return rates and 65% using CJS models) were 16 – 25% lower than 10 years prior (77% using return rates), and similar to or lower than most other estimates reported for temperate congeners: Snowy/Kentish Plover (*Charadrius alexandrinus*): (74% using return rates in Page et al. 1983, 73 – 79% using return rates in Warriner et al. 1986, 69% using Jolly-Seber models in Paton 1994b, 58% using CJS in Sandercock et al. 2005, 69% using Barker models in Stenzel et al. 2007, 50 – 61% using CJS in Mullin et al. 2010), Piping Plover (*C. melodus*): (66% using Jolly-Seber in Root et al. 1992, 74% using CJS in Larson et al. 2000), and Semipalmated Plover (*C. semipalmatus*): (40 – 59% using return rates in Flynn et al. 1999, 71% using CJS in Badzinski 2000, 87% using CJS in Nol et al. 2010). Similarly, juvenile yearly apparent survival estimates (9% using return rates and 12% using CJS models) were 45 – 60% lower than 10 years prior (22% using return rates) and lower than a previous study on Snowy Plovers (18% using Barker models; Stenzel et al. 2007), but similar to Kentish Plovers (9% using CJS in Sandercock et al. 2005) and higher than Semipalmated Plovers (2% using return rates in Flynn et al. 1999, 5% using CJS in Nol et al. 2010). Along with declining nest success (see Chapter I), decreased apparent survival rates of adults and juveniles can have dramatic affects on population growth rates and appear to be the main factors driving current population declines within this region (see Chapter VI).

Lower apparent survival of both adults and juveniles may be related to increased mortality or dispersal (to alternate breeding locations [e.g., saline lakes] either within or outside the SHP of Texas), as these two factors cannot be separated from these estimates. Increased mortality and/or dispersal rates may be due to declining habitat quality (Haig and Oring 1988, Wiens and Cuthbert 1988, Stenzel et al. 1994), poor nest success (Redmond and Jenni 1982, Gratto et al. 1985, Reed and Oring 1993, Flynn et al. 1999, Badzinski 2000), and/or increased predation rates (Stenzel et al. 1994, Badzinski 2000, Stenzel et al. 2007). Within the SHP of Texas, declines in aquifer levels and spring integrity have degraded habitat conditions (i.e., amount and salinity of surface water available) of saline lakes since the 1950s (Brune 2002). Because surface water is a necessary landscape feature for nesting Snowy Plovers within this region (Conway et al. 2005b), surface water availability upon arrival may influence regional fidelity rates, where site fidelity decreases when surface water is low. Furthermore, as the breeding season advances, greater ambient temperatures and evaporation rates may exacerbate poor habitat conditions (i.e., declining surface water and prey availability), resulting in declines of Snowy Plover condition (see Chapter I). For example, current low juvenile return rates may be from greater mortality between hatching and fledging than previously estimated. If chicks cannot find the necessary food resources after hatching, increased mortality may occur as a result of stress and high energy requirements needed for growth.

Furthermore, both juveniles and adults need to obtain sufficient energy requirements prior to migration (Bairlein and Gwinner 1994); however, if resources are unavailable, greater mortality rates may occur during this physiologically and energetically costly time period (Alerstam et al. 2003).

Besides declining habitat quality and unpredictable surface water availability, nest predation rates have dramatically increased (from 27% to 40%) since 1998 (see Chapter I). Decreased nest success (see Chapter I) may be a good predictor of apparent survival, where greater predation (or lower nest success) may increase mortality and/or force adult dispersal (Redmond and Jenni 1982, Gratto et al. 1985, Reed and Oring 1993, Flynn et al. 1999, Badzinski 2000). For example, in Semipalmated Plovers, nest success was a good predictor of adult survival, where increased predator densities caused greater adult mortality and nest failures and triggered adult emigration (Badzinski 2000). As most Snowy Plover nest failures were due to predation (see Chapter I), moving to a new nesting area, undiscovered by predators, may increase individual reproductive success (Stenzel et al. 1994). Such within season movement occurs in the Great Salt Lake, Utah, where females dispersed at greater rates when they were unsuccessful (Paton 1994a, Paton and Edwards 1996). However, few adults (i.e., 6 out of 224) were observed moving between saline lakes within a breeding season.

Current declines of apparent Snowy Plover survival within this region may be a result of factors occurring during the breeding season; however, factors occurring outside of the breeding season are also likely important. Although current survival rates and causes of mortality during the nonbreeding season (i.e., migration and wintering) remain unknown for this population, catastrophic events (e.g., hurricanes) in wintering regions (presumed to be between upper Texas coast and Yucatán peninsula, as the majority of Snowy Plovers winter within this region; Mabee et al. 2001, Gorman and Haig 2002, Elliott-Smith et al. 2004) and poor wintering habitat may increase mortality. For example, during August – September 2007, four hurricanes made landfall between the Texas coast and Yucatán Peninsula, potentially resulting in dramatic population declines between 2007 and 2008 (see Chapter VI). Furthermore, wintering coastal populations are threatened by habitat loss and degradation, coastal development, and disturbance from human recreation (Mabee et al. 2001, Elliott-Smith et al. 2004).

Males had greater apparent survival rates than females regardless of age. In contrast to previous work, this study is one of only a few estimating sex related survival and fidelity rates using molecularly sexed individuals. However, results obtained in this study are consistent with previous observations on Snowy Plovers (Page et al. 1983, Warriner et al. 1986, Paton 1994a, Stenzel et al. 1994, Paton and Edwards 1996, Powell and Collier 2000, Colwell et al. 2007). Therefore, if true survival rates are similar between sexes (see Warriner et al. 1986, Paton 1994b, Sandercock et al. 2005), sex-biased apparent survival rates are likely a factor of breeding and natal site fidelity, where males have greater site fidelity than females. In species with male resource defense, such as Snowy Plovers, males may increase annual and/or lifetime reproductive fitness by returning to the same (familiar) sites where they successfully acquire limited nest territories and/or mates (Greenwood 1980, Greenwood and Harvey 1982).

Beyond behavioral influences on sex-biased dispersal, male-biased encounter rates were also observed, similar to previous resighting estimates of Snowy (Paton 1994b), Kentish (Sandercock et al. 2005), and Semipalmated Plovers (Badzinski 2000). Males may have a greater detection probability than females due to conspicuous behavior, as females spend more time incubating nests (e.g., 71% of birds captured on nests were female; S. Saalfeld unpublished data) and remain relatively inconspicuous when off nests (Sandercock et al. 2005). Male-biased detection rates may also be estimated if females temporarily emigrate from nesting areas due to failure of previous breeding attempts, poor habitat conditions, and/or increased mortality risks (see Badzinski 2000). Therefore, decreased nest success and increased predation rates, along with seasonal variation in surface water levels observed in this study (see Chapter I) may result in females temporarily emigrating to better locations (e.g., saline lakes either within or outside the SHP of Texas) either between or within years. However, identification of alternate breeding locations is difficult, as no color banded individuals were resighted during the breeding season outside of the SHP of Texas (although > 500 adults and juveniles were banded during 1999 – 2010) and few individuals were observed moving among saline lakes within the SHP of Texas.

Despite the potential for emigration to alternate breeding locations, strong adult breeding site fidelity has been reported in several shorebird species including many

Charadiid and Scolopacid species (see Haig and Oring 1988, Wiens and Cuthbert 1988). Similarly, Snowy Plovers within this region tend to have high breeding site fidelity with few individuals documented dispersing either within or between nesting seasons, returning to the same lakes even 10 years after initial capture. High breeding site fidelity may be a function of widely spaced and patchily distributed interior nesting habitat (Boyd 1981, Gorman and Haig 2002) as well as poor suitability of alternate nesting locations (e.g., poor habitat quality of other saline lakes within this region due to low surface water availability and spring flow), reducing the potential for dispersal among nesting sites. For example, in regions with few available nest sites in close proximity to one another, Piping Plovers had relatively high site fidelity, as individuals had few possibilities to disperse to alternate breeding locations without traveling great distances (Haig and Oring 1988). However, within the SHP of Texas, because of aquifer and freshwater spring decline, nesting habitat is becoming more variable within and between seasons. Therefore, the ability to move (potentially) long distances and be familiar with multiple breeding sites may be important for Snowy Plovers to nest successfully in unpredictable environments (Stenzel et al. 1994). However, it remains unknown if Snowy Plovers are behaviorally plastic enough to move to alternate locations either within or between nesting seasons. If Snowy Plovers are unable to cope with unpredictability of surface water levels within this region, populations may continue to decline (see Chapter VI).

Current estimates of adult and juvenile apparent survival rates indicate that 5.8 hatchlings per adult are needed to maintain the current population, without immigration.

However, 10 years prior, when apparent survival of adults and juveniles was greater, only 2.3 hatchlings per adult were needed to maintain a stable population. Snowy Plovers are a determinant layer with a modal clutch size of three eggs. Therefore, to produce > 5 hatchlings per adult, each pair needs to successfully hatch > 3 clutches each year. This is not physiologically possible, nor is there enough time during the nesting season for > 3 clutches per pair to successfully hatch. For example, it takes ~ 60 days (30 day incubation period; see Chapter I, and 30 day fledging period; see Page et al. 2009) from egg laying to fledging (requiring 150 days to successfully hatch three clutches); however, only a 112 (see Chapter I) to 119 (Conway et al. 2005a) day nesting season exists for this population. In California, Page et al. (1983) estimated only ≥ 0.8 fledglings per adult were necessary for population maintenance; however, Mullin et al. (2010) estimated ≥ 2.7 fledglings per adult were necessary to maintain a stable population. Although estimates obtained in this study (based upon hatchlings) are not directly comparable to those of previous studies (based on fledglings), these estimates suggest that current populations in California and the SHP of Texas are currently unstable and, without immigration, will continue to decline (see Chapter VI) if adult and/or juvenile survival remain at current levels.

Current conservation actions for Snowy Plovers focus upon increasing nest success (e.g., predator exclosures, predator control, and reduction of human disturbance around nest sites; Page et al. 2009); however, current rates of adult and juvenile mortality cannot be reversed by increased nest success. Therefore, conservation efforts must focus on increasing adult and juvenile survival on both breeding and wintering grounds, but this can be extremely difficult (Mullin et al. 2010). Moreover, techniques are lacking that improve either adult or juvenile survival, further exacerbating this problem for regional Snowy Plover populations. In the SHP of Texas, Snowy Plover juvenile survival has dramatically declined (45 – 60% decline) in the past 10 years, where potential causes of juvenile mortality include increased predation rates and poor habitat quality. As nest predation rates have increased from 27% to 40% in the past 10 years (see Chapter I), chick predation has likely increased as well. Current range expansion of both Common (*Corvus corax*) and Chihuahuan Ravens (*C. cryptoleucus*; Boarman and Heinrich 1999, Bednarz and Raitt 2002) may have serious impacts on juvenile survival rates within this region. As anthropogenic factors (e.g., increased nesting habitat due to woody vegetation encroachment and additional anthropogenic food sources) have likely played a role in this expansion, current management should focus upon habitat restoration to native grasslands and elimination of nesting trees (e.g., salt cedar [*Tamarix* spp.]) along edges of saline lakes. Furthermore, surface water availability has declined within the past 10 years, potentially resulting in reduction of food availability and juveniles having to travel further to reach suitable foraging areas. If juveniles cannot find necessary food resources after hatching and prior to migration, increased mortality will occur. Therefore, within this region, it remains important to conserve saline lake habitat, especially freshwater springs discharging into saline lakes. However, because the Ogallala aquifer is recharged from playa wetlands (Osterkamp and Wood 1987, Bolen et al. 1989), it also remains important to conserve the entire complex of wetlands within the SHP of Texas (Andrei et al. 2008, Andrei et al. 2009).

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Table 5.1. Captures and resightings of adult and juvenile Snowy Plovers on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2010.

Location	Year	Sex[a]	Capture[b]	Resighting[c]
Adults				
Lake A	1999	Female	60	----
Lake A	2000	Female	10	42
Lake A	2008	Female	6	----
Lake A	2009	Female	8	3
Lake A	2010	Female	----	3
Lake A	1999	Male	52	----
Lake A	2000	Male	11	46
Lake A	2008	Male	7	----
Lake A	2009	Male	4	5
Lake A	2010	Male	----	7
Lake B	1999	Female	2	----
Lake B	2000	Female	5	8
Lake B	2008	Female	18	----
Lake B	2009	Female	10	7
Lake B	2010	Female	----	8
Lake B	1999	Male	8	----
Lake B	2000	Male	3	10
Lake B	2008	Male	4	----

Table 5.1. Continued.

Location	Year	Sex[a]	Capture[b]	Resighting[c]
Lake B	2009	Male	4	2
Lake B	2010	Male	----	3
Lake C	2008	Female	6	----
Lake C	2009	Female	2	2
Lake C	2010	Female	-----	7
Lake C	2008	Male	0	-----
Lake C	2009	Male	4	0
Lake C	2010	Male	-----	4
Juveniles				
Lake A	1999	Female	36	----
Lake A	2000	Female	39	5
Lake A	2008	Female	6	-----
Lake A	2009	Female	14	0
Lake A	2010	Female	-----	1
Lake A	1999	Male	41	----
Lake A	2000	Male	54	10
Lake A	2008	Male	2	-----
Lake A	2009	Male	8	1
Lake A	2010	Male	-----	2

Table 5.1. Continued.

Location	Year	Sex[a]	Capture[b]	Resighting[c]
Lake B	1999	Female	0	----
Lake B	2000	Female	1	2
Lake B	2008	Female	15	-----
Lake B	2009	Female	19	0
Lake B	2010	Female	-----	2
Lake B	1999	Male	0	----
Lake B	2000	Male	3	2
Lake B	2008	Male	16	-----
Lake B	2009	Male	27	1
Lake B	2010	Male	-----	3
Lake C	2008	Female	1	-----
Lake C	2009	Female	3	0
Lake C	2010	Female	-----	1
Lake C	2008	Male	2	-----
Lake C	2009	Male	5	0

Table 5.1. Continued.

Location	Year	Sex[a]	Capture[b]	Resighting[c]
Lake C	2010	Male	-----	0

[a] Sex determined by molecular sexing techniques.

[b] Number of individuals banded at the given location.

[c] Number of individuals banded in previous years observed at given location, regardless of banding location.

Table 5.2. Encounter histories of adult and juvenile Snowy Plovers during the breeding season (i.e., 3 March – 31 July) on saline lakes within the Southern High Plains of Texas, USA, 1999 – 2000.

Sex[a]	Lake banded on in 1999	Lake resighted on in 2000	Number of individuals
Adults			
Female	Lake A	Lake A	41
Female	Lake A	Lake B	7*
Female	Lake B	Lake B	1
Female	Lake B	Lake A	1*
Male	Lake A	Lake A	43
Male	Lake A	Lake B	5*
Male	Lake B	Lake B	5
Male	Lake B	Lake A	3*
Juveniles			
Female	Lake A	Lake A	5
Female	Lake A	Lake B	2*
Male	Lake A	Lake A	10
Male	Lake A	Lake B	2*

[a] Sex determined by molecular sexing techniques.

* Individuals observed switching locations between years.

Table 5.3. Encounter histories of adult and juvenile Snowy Plovers during the breeding season (i.e., 10 April – 25 July) on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2010.

Sex[a]	Lake banded on in 2008	Lake banded on in 2009	Lake resighted on in 2009	Lake resighted on in 2010	Number of individuals
Adults					
Female	Lake A	-----	Lake A	Lake A	1
Female	Lake A	-----	Lake A	-----	1
Female	Lake B	-----	Lake B	-----	7
Female	Lake B	-----	-----	Lake B	1
Female	Lake B	-----	Lake A	Lake C	1*
Female	Lake C	-----	Lake C	Lake C	2
Female	Lake C	-----	-----	Lake C	1
Female	-----	Lake A	-----	Lake A	2
Female	-----	Lake A	-----	Lake B	1*
Female	-----	Lake B	-----	Lake B	6
Female	-----	Lake B	-----	Lake C	1*

Table 5.3. Continued.

Sex[a]	Lake banded on in 2008	Lake banded on in 2009	Lake resighted on in 2009	Lake resighted on in 2010	Number of individuals
Female	-----	Lake C	-----	Lake C	2
Male	Lake A	-----	Lake A	Lake A	4
Male	Lake A	-----	Lake A	-----	1
Male	Lake B	-----	Lake B	Lake B	1
Male	Lake B	-----	Lake B	-----	1
Male	-----	Lake A	-----	Lake A	3
Male	-----	Lake B	-----	Lake B	2
Male	-----	Lake C	-----	Lake C	4
Juveniles					
Female	Lake B	-----	-----	Lake C	1*
Female	-----	Lake A	-----	Lake A	1
Female	-----	Lake A	-----	Lake B	1*

Table 5.3. Continued.

Sex[a]	Lake banded on in 2008	Lake banded on in 2009	Lake resighted on in 2009	Lake resighted on in 2010	Number of individuals
Female	-----	Lake B	-----	Lake B	1
Male	Lake B	-----	Lake B	-----	1
Male	Lake B	-----	Lake A	Lake A	1*
Male	-----	Lake A	-----	Lake A	1
Male	-----	Lake B	-----	Lake B	3

[a] Sex determined by molecular sexing techniques.

* Individuals observed switching locations between years.

Table 5.4. Cormack-Jolly-Seber models from Program MARK to estimate apparent survival (φ) and encounter rates (p) of adult Snowy Plovers on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2010.

Model structure[a]		Model statistics		
φ	p	No. parameters	ΔAIC_c[b]	AIC_w[c]
c	*sex*	3	0.00	0.28
t	*sex*	4	0.89	0.18
sex	*sex*	4	1.46	0.13
sex	*c*	3	1.88	0.11
sex	*t*	4	2.88	0.07
c	*c*	2	3.11	0.06
t	*c*	3	3.82	0.04
c	*t*	3	3.95	0.04
c	*sex*t* [d]	5	4.30	0.03
*sex*t*	*c*	5	5.01	0.02
*sex*t*	*sex*	6	5.03	0.02
sex	*sex*t*	6	5.36	0.02

[a] Model factors included *c* = φ or *p* remained constant among years, *t* = φ or *p* showed annual variation, and *sex* = φ or *p* varied between males and females.

[b] Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[c] AIC_c relative weight attributed to model.

[d] Model of additive effects of sex and time and the interaction between them.

Table 5.5. Characteristics of top-ranked Cormack-Jolly-Seber models from Program MARK modeling apparent survival (φ) and encounter rates (p) of adult Snowy Plovers on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2010.

			95% CI	
Parameter	Estimate	SE	Lower	Upper
Top-ranked model				
φ (constant)	0.655	0.072	0.503	0.780
p (female)	0.697	0.132	0.404	0.887
p (male)	1.000	0.000	1.000	1.000
Second-ranked model				
φ (2008-2009)	0.579	0.096	0.389	0.748
φ (2009-2010)	0.722	0.091	0.516	0.863
p (female)	0.699	0.123	0.425	0.879
p (male)	1.000	0.000	1.000	1.000
Third-ranked model				
φ (female)	0.587	0.094	0.398	0.753
φ (male)	0.700	0.084	0.517	0.836
p (female)	0.770	0.137	0.423	0.939
p (male)	1.000	0.000	1.000	1.000
Forth-ranked model				
φ (female)	0.544	0.074	0.400	0.681
φ (male)	0.756	0.096	0.528	0.895

Table 5.5. Continued.

Parameter	Estimate	SE	95% CI	
			Lower	Upper
p (constant)	0.872	0.082	0.616	0.966

Table 5.6. Cormack-Jolly-Seber models from Program MARK to estimate apparent survival for interval between hatching and first year (φ^1), interval between first year and second year (φ^2), and encounter rates (p) of juvenile Snowy Plovers on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2010.

Model structure[a]			Model statistics		
φ^1	φ^2	p	No. parameters	ΔAIC_c [b]	AIC_w [c]
c	*c*	*c*	3	0.00	0.20
c	*c*	*sex*	4	0.78	0.14
t	*c*	*c*	4	1.33	0.10
c	*c*	*t*	4	1.33	0.10
c	*c*	*sex*t* [d]	6	1.37	0.10
sex	*c*	*c*	4	1.74	0.08
sex	*c*	*sex*	5	2.28	0.06
t	*c*	*sex*	5	2.66	0.05
sex	*c*	*t*	5	3.16	0.04
sex	*sex*	*c*	5	3.51	0.03
sex	*sex*	*sex*	6	4.33	0.02
sex	*sex*	*t*	6	4.64	0.02
*sex*t*	*c*	*c*	6	5.18	0.02
*sex*t*	*c*	*sex*	7	5.77	0.01
*sex*t*	*sex*	*c*	7	7.15	0.01

Table 5.6. Continued.

Model structure[a]			Model statistics		
φ^1	φ^2	p	No. parameters	ΔAIC_c[b]	AIC_w[c]
*sex*t*	*sex*	*sex*	8	7.39	0.00

[a] Model factors included $c = \varphi^1$, φ^2, or p remained constant among years, $t = \varphi^1$ or p showed annual variation, and $sex = \varphi^1$, φ^2, or p varied between males and females.

[b] Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[c] AIC_c relative weight attributed to model.

[d] Model of additive effects of sex and time and the interaction between them.

Table 5.7. Characteristics of top-ranked Cormack-Jolly-Seber models from Program MARK modeling apparent survival for interval between hatching and first year (φ^1), interval between first year and second year (φ^2), and encounter rates (p) of juvenile Snowy Plovers on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2010.

			95% CI	
Parameter	Estimate	SE	Lower	Upper
Top-ranked model				
φ^1 (constant)	0.122	0.061	0.044	0.297
φ^2 (constant)	0.803	0.475	0.011	0.999
p (constant)	0.623	0.297	0.122	0.952
Second-ranked model				
φ^1 (constant)	0.109	0.037	0.054	0.205
φ^2 (constant)	0.618	0.288	0.129	0.947
p (female)	0.486	0.264	0.107	0.882
p (male)	1.000	0.000	1.000	1.000
Third-ranked model				
φ^1 (2008-2009)	0.095	0.066	0.023	0.319
φ^1 (2009-2010)	0.184	0.139	0.036	0.580
φ^2 (constant)	1.000	0.503	0.000	1.000
p (constant)	0.500	0.331	0.069	0.931

Table 5.7. Continued.

Parameter	Estimate	SE	95% CI Lower	95% CI Upper
Forth-ranked model				
φ^1 (constant)	0.095	0.066	0.023	0.319
φ^2 (constant)	0.517	0.402	0.043	0.962
p (2008-2009)	0.500	0.354	0.059	0.941
p (2009-2010)	0.967	0.753	0.000	1.000
Fifth-ranked model				
φ^1 (constant)	0.102	0.061	0.030	0.296
φ^2 (constant)	0.521	0.406	0.043	0.963
p (2008-2009 female)[a]	.	.	.	.
p (2009-2010 female)	0.829	0.711	0.000	1.000
p (2008-2009 male)	1.000	0.000	1.000	1.000
p (2009-2010 male)	0.976	0.680	0.000	1.000
Sixth-ranked model				
φ^1 (female)	0.099	0.062	0.028	0.299
φ^1 (male)	0.146	0.081	0.045	0.381
φ^2 (constant)	0.807	0.478	0.010	0.999
p (constant)	0.619	0.298	0.120	0.951

[a] Unestimatable.

CHAPTER VI

SNOWY PLOVER POPULATION TRENDS IN THE SOUTHERN HIGH PLAINS OF TEXAS

INTRODUCTION

Numerous shorebird species have exhibited population declines in recent years (Morrison et al. 2006), with nearly a quarter of the world's shorebird species in danger of extinction (Piersma et al. 1997). Therefore, understanding and characterizing long-term population trends of both currently imperiled and stable shorebird populations remains important for long-term conservation efforts. Snowy Plover (*Charadrius alexandrinus*) is a cosmopolitan species nesting within America, Europe, Asia, and Africa (Page et al. 2009). Currently, in the United States, Snowy Plovers are listed as threatened by the U.S. Fish and Wildlife Service along the Pacific Coast (U.S. Fish and Wildlife Service 1993) and as endangered, threatened, or of special concern in several states including Washington, Oregon, California, Mississippi, Florida, Puerto Rico, and Kansas (see Page et al. 2009). Western Snowy Plovers (*C. a. nivosus*) have suffered declines due to human recreational use of beaches, beach development, and habitat degradation, resulting in decreased nest success (Page and Stenzel 1981, Page et al. 1991, U.S. Fish and Wildlife Service 1993). Similar declines have been observed in Europe, with primary causes of declines attributed to loss of breeding habitat and anthropogenic disturbance during the nesting season (Montalvo and Figuerola 2006).

Snowy Plover population and/or subspecies designation within the United States has long been unclear, but is important relative to understanding current population trends, and population structuring (e.g., conservation units). Recent genetic analyses reveal only one Snowy Plover subspecies in the continental United States (i.e., western Snowy Plover [*C. a. nivosus*]; Gorman 2000, Funk et al. 2007). However, further subdivision into management and/or population groups east and west of the Rocky Mountains may be warranted (Gorman 2000), as little connectivity exists between these regions. However, no studies have clearly documented nor identified wintering grounds for interior populations, which are generally thought to winter along the Gulf of Mexico from Texas to Yucatán Peninsula (Mabee et al. 2001, Gorman and Haig 2002, Elliott-Smith et al. 2004), while Pacific coast populations winter along the Pacific coast and Gulf of California (Page et al. 1995).

Currently, the population of western Snowy Plovers is estimated at 4,300 along the Pacific coast and 12,400 in interior areas (Morrison et al. 2006). These estimates are greater along the Pacific coast (2,000), but lower in interior areas (13,235) than estimates 5 years earlier (Morrison et al. 2001), but are still within current target population sizes (i.e., 13,200 in interior and 3,000 on Pacific coast; Brown et al. 2001). Because the majority (i.e., ~ 74%; Morrison et al. 2006) of the continental population exists within inland regions, interior populations are crucial for maintaining continental populations (Paton 1999). Data exist concerning local population trends for Pacific Coast populations (Page et al. 1991), but virtually no trend data exist anywhere in the interior portion of the United States.

Identifying and delineating factors influencing population sizes, trends, and detection probabilities is crucial for these inland populations. For example, in the Southern High Plains (SHP) of Texas, where Snowy Plovers principally depend on habitats associated with saline lakes, number of Snowy Plovers located on individual survey routes may vary seasonally depending upon breeding stage (i.e., pre-nesting, nesting, post-nesting, and second-breeding attempts). However, discrete separation among breeding stages is not always evident, as multiple breeding attempts may be initiated by individuals and nesting is rarely synchronized within a year or saline lake (S. Saalfeld unpublished data). Furthermore, surface water availability in inland saline lakes influences both regional Snowy Plover population size and detection probability (Boyd 1981).

Surface water presence on saline lakes in the SHP of Texas during the breeding season is not only a necessary landscape feature for nesting Snowy Plovers (Conway et al. 2005b), but also supports invertebrate prey (Andrei et al. 2009) and provides an important means to alleviate heat stress (e.g., belly soaking and standing in water; Maclean 1975, Purdue 1976, Amat and Masero 2004, Amat and Masero 2007, Amat and Masero 2009; see Chapter III). However, surface water availability fluctuates weekly (see Chapter I) due to unpredictable rain events, evapotranspiration, and reduced freshwater spring flow (S. Saalfeld per. obs.), all of which exhibit more exaggerated fluctuations today than historically. Moreover, Snowy Plovers may not be behaviorally plastic enough to move between nesting locations when suitable nesting habitat becomes compromised (e.g., low surface water availability; see Chapter V). Therefore, it is vital to document long-term population trends as well as understand population changes within and among years as related to surface water availability in this inland region. Identifying relevant factors influencing local population estimates may allow researchers to conduct surveys during opportune times and/or account for variability among surveys due to regionally important factors (e.g., surface water availability), ultimately resulting in more accurate and comparable surveys. Therefore, the objectives of this study were to 1) determine long-term population trends (i.e., 1998 to 2010) of adult Snowy Plovers nesting within the SHP of Texas and 2) evaluate potential factors influencing weekly population estimates of adult Snowy Plovers in the SHP of Texas in 2008 and 2009.

METHODS

Study Area

The SHP is an approximately 80,000 km^2 region occurring from the panhandle of Texas, into New Mexico, and south to Midland, Texas (Osterkamp and Wood 1987). Within this region, approximately 40 saline lakes (i.e., primary regional nesting location for Snowy Plovers; Conway et al. 2005a) occur (Reeves and Temple 1986). Saline lakes are discharge wetlands containing freshwater springs fed by the Ogallala aquifer (Brune 2002), but having an overall saline water chemistry (often > 200g/L of dissolved solids; Osterkamp and Wood 1987). Two – three previously identified important (i.e., having consistent surface water throughout the nesting season and containing the majority of regional nesting Snowy Plovers) saline lakes (Conway et al. 2005a) ranging in size from ~ 270 – 600 ha were surveyed in 1998 – 2000 and 2007 – 2010 (Figure 1.1). To maintain landowner anonymity, study site lakes will be referred to as lake A, lake B, and lake C. Each study site lake contained two – six fresh to slightly saline springs distributed along lake margins (Brune 2002). The primary landuse practice immediately surrounding study site lakes was pasture/rangeland with some held within the Conservation Reserve/Permanent Cover Program. Other landuse practices occurring within surrounding areas included row-crop agriculture production (i.e., mostly cotton

[*Gossypium* spp.]), mineral excavation (e.g., caliche), and development (i.e., mostly small home/ranch developments).

Capture and Handling

Adult Snowy Plovers were captured at feeding locations using mist nets and on nests using nest traps (Conway and Smith 2000) in early April – early August in 1999 – 2000 and 2008 – 2009. Adults were sexed in the field based upon plumage characteristics, where males generally have larger and darker breast and forehead patches as compared to females. All adults were banded with a uniquely numbered U.S. Fish and Wildlife Service aluminum band on the upper part (i.e., tibiotarsus) of their left leg, a dark green color band on the upper part of their right leg, and a unique combination of two color bands on both right and left lower legs (i.e., red, blue, purple, light green, orange, pink, white, and yellow color bands). All females were banded with a red color band on the right lower leg and males with a blue color band on the right lower leg (example female band combination: upper right leg: dark green, lower right leg: red/yellow, upper left leg: USFWS band, lower left leg: white/orange).

Snowy Plover chicks were captured by hand in nests at hatching or with adult(s) after hatching. The same handling techniques were used as adults for chicks, where each individual received a U.S. Fish and Wildlife Service aluminum band on the left upper leg, a dark green color band on right upper leg, a purple color band on the right lower leg, and a unique combination of color bands on lower legs. Because few chicks were resighted during weekly surveys, chicks were not included in the following analyses. However, if an individual banded as a chick returned as an adult, these individuals were included in surveys.

Bird Surveys

1998 – 2000

Approximately weekly surveys were conducted at lakes A and B during the breeding season (3 April – 30 July) as part of a previous research project (Conway 2001). During each survey, observers traveled (by foot) similar survey routes as 2008 – 2009 (see below) prior to 1200 hrs, and located Snowy Plovers by sight and sound. Once located, all individuals were recorded.

2007

Surveys were conducted at lakes A, B, and C as part of the International Snowy Plover Survey (U.S. Fish and Wildlife Service 2007). Two surveys were conducted at lakes A and C and one at lake B during 14 – 22 May 2007. During each survey, observers traveled (by foot) similar survey routes as 2008 – 2009 (see below) prior to 1200 hrs, and located Snowy Plovers by sight and sound. Once located, all individuals were recorded.

2008 – 2009

Weekly surveys were performed at lakes A, B, and C during the breeding season (10 April – 25 July) in 2008 – 2009. A route was delineated within each lake, where during each survey observers traveled (by foot) the same route prior to 1200 hrs, and located Snowy Plovers by sight and sound. Once located, all individuals were recorded and inspected for presence of color bands. If color bands were present, band combinations were recorded for individual identification. The proportion of banded individuals observed on each survey was calculated by dividing the number of banded individuals observed by the total number of banded individuals in the population at the time of survey execution (i.e., number of birds banded on a given lake at time of survey execution + number of adults banded in previous year that were resighted at least once on a given lake during the breeding season).

During weekly surveys, ocular estimates of percent dry ground, wet mud (areas wet from spring flow rather than rainwater), shallow water (1 – 5 cm deep; shallow enough for wading Snowy Plover), medium water (5 – 15 cm deep; too deep for wading Snowy Plover, but shallow enough for wading American Avocet [*Recurvirostra americana*]), and deep water (> 15 cm deep; too deep for wading American Avocet) were recorded to determine availability of surface water for nesting plovers throughout the breeding season. Specifically, during weekly surveys, locations of above categories were drawn on 2004 NAIP digital orthophoto quarter-quadrangle (DOQQ) aerial photographs (Texas Natural Resources Information System 2004) to estimate percent composition. To obtain total surface water availability, percent wet mud, shallow water, medium water, and deep water were summed for each survey.

2010

Only two surveys were conducted at lakes A, B, and C during the breeding season (1 May – 2 May and 29 May – 30 May), as a high water event in July 2010, precluded access to survey routes, reducing surveys to documentation of banded birds (see Chapter V). During each survey, observers traveled (by foot) the same survey routes as 2008 – 2009 prior to 1200 hrs, and located Snowy Plovers by sight and sound. Once located, all individuals were recorded.

DATA ANALYSIS

Due to insufficient sample sizes (i.e., markings and resightings), population size and resighting probabilities could not be estimated using Mark-Resight models in Program MARK (Pradel 1996). Detection probabilities in surveyed areas were assumed to be close or equal to 1.0 due to open nature of saline lakes (e.g., little to no vegetation, few view obstructions, and flat topography) and conspicuous behaviors of nesting Snowy Plovers (e.g., distraction displays). Direct evidence supporting this assumption comes from surveying lakes A and C on consecutive days in 2007, where counts differed by one – four individuals, respectively, suggesting detection probabilities close to 1.0.

Complete detection of all individuals within a lake was not assumed, because individuals may be located within areas of the lake not covered by the survey route. Therefore, number of Snowy Plovers observed during a survey was the number of individuals using the portion of the lake surveyed rather than the total number of birds on a lake. Therefore, changes in number of individuals observed on a survey route were assumed to be due to individuals leaving locations along a route (i.e., either moving to locations within the same lake not covered by the survey route or moving to locations outside the lake) rather than failure to detect individuals along a route.

Population Trends

Months were used to divide the nesting season into discrete windows, where April generally corresponded to pre-nesting, May to early nesting, June to nesting and post-nesting, and July to post-nesting and second-nesting attempts (Conway et al. 2005a; see Chapter I). An analysis of variance (PROC GLM; SAS Institute 2002) was used to examine differences in mean number of Snowy Plovers observed during each month among survey years (i.e., 1998 – 2000 and 2008 – 2009) for each lake (i.e., lakes A, B, and C).

Factors Influencing Counts

The following analyses used only data obtained in 2008 – 2009, as surface water level estimates were only obtained during these years. Because the response variable was a count, number of adult Snowy Plovers detected during weekly surveys was initially modeled using the Poisson distribution (PROC GENMOD; SAS Institute 2002). However, overdispersion was high (i.e., deviance/degrees of freedom [df] > 4) using this distribution. Therefore, the negative binomial distribution (PROC GENMOD; SAS Institute 2002) was used to model number of adult Snowy Plovers observed during weekly surveys. To determine variable(s) (i.e., year, lake, percent surface water, and Julian date) most influencing number of adult Snowy Plovers detected during weekly surveys, 30 candidate models were developed *a priori*, consisting of biologically relevant combinations of variables, where correlated ($P \leq 0.05$) variables were excluded from entering the same model. When interaction terms were added, negative effects of multicollinearity were observed (e.g., variance inflation and changes in sign of parameter estimates). To reduce the effects of multicollinearity, data for percent surface water and Julian date were centered (i.e., mean subtracted from each datum; where mean Julian date = 150.11 and mean percent surface water = 51.87). Akaike's Information Criterion corrected for small sample size (AIC_c) was used to rank candidate models, where an individual model was considered plausible when $\Delta AIC_c < 2$ (Burnham and Anderson 2002). Parameter estimates, standard errors, and confidence intervals are presented from the top-ranked model. Parameter likelihoods were determined using model averaging (i.e., sum of model weights for models that included a given parameter; Burnham and Anderson 2004). Goodness-of-fit was estimated using deviance/degrees of freedom (SAS Institute 2002).

RESULTS

From 1998 – 2010, 184 surveys were conducted, 23 in 1998, 45 in 1999, 32 in 2000, 5 in 2007, 40 in 2008, 33 in 2009, and 6 in 2010 (Tables 6.1 – 6.3). From 1998 – 2010, mean survey counts of adult Snowy Plovers in May generally declined at lakes A and B, with the most dramatic declines occurring between 2007 and 2008 and 1998 and 1999 (Figure 6.1). Mean survey counts varied among months; however, mean survey counts were generally lower in 2008 – 2009 than in 1998 – 2000 (Figures 6.2 – 6.4, Tables 6.1 – 6.3). With all months combined, mean survey counts in 1998 – 2000 had more ($P < 0.001$) adult birds sighted than 2008 – 2009 at lake A (Figure 6.5, Table 6.1), while mean survey counts in 1998 had more ($P = 0.006$) adult birds sighted than all other years at lake B (Figure 6.5, Table 6.2). With all months combined, mean survey counts in 2008 – 2009 ($\bar{x}$ = 28.3 adults; range: 0 – 59 adults) declined ($F_{1,147} = 35.14$; $P < 0.001$) by 55% at lakes A and B since 1998 – 2000 ($\bar{x}$ = 62.7 adults; range: 7 – 194 adults).

Survey counts (i.e., total number of adults [banded and unbanded] and percent banded observed) in 2008 – 2009 tended to vary with surface water levels and time during the season, where more birds were sighted during periods of high water levels and earlier in the season at lakes A and C, but later in the season at lake B (Figures 6.6 – 6.17). Among 30 candidate models (Table 6.4), the model best predicting number of

Snowy Plovers on weekly surveys was the model containing the interaction between lake and Julian date and the additive effect of percent surface water (Table 6.4). From the top-ranked model, (Figures 6.18 – 6.20, Table 6.5), more adult Snowy Plovers were predicted to occur on weekly surveys at lake B as compared to lakes A and C. Additionally, number of adult Snowy Plovers observed was positively influenced by Julian date at lake B, but negatively influenced at lakes A and C (although the 95% confidence interval overlapped zero for lake A; Figures 6.18 – 6.20, Table 6.5). At all lakes, number of adult Snowy Plovers observed during surveys declined as percent surface water declined (Figures 6.18 – 6.20, Table 6.5). Parameter likelihoods also indicated that the interaction between Julian date and lake (likelihood = 0.96) and percent surface water (likelihood = 0.91) were the most important variables included in the top-ranked models. Goodness of fit statistic from the top-ranked model indicated that the model fit the data well (deviance/df = 1.33).

DISCUSSION

Western Snowy Plovers have experienced population declines throughout their range in the United States, with the primary cause being attributed to decreased nest success (U.S. Fish and Wildlife Service 1993). For example, an approximate 20% population decline in California, Oregon, Washington, and Nevada was estimated between the late 1970s and late 1980s (Page et al. 1991). Over the last decade, the regional population of Snowy Plovers in the SHP of Texas has declined by 55%, with nest success declines of 31% (see Chapter I), and adult and juvenile apparent survival declines of 25% and 60%, respectively (see Chapter V). These data indicate that without conservation efforts directed towards offsetting low nest success rates and improving apparent survival rates, regional populations will continue to decline.

Snowy Plovers within this region are also susceptible to dramatic annual population variation (e.g., 2007 – 2008 at lake A and 1998 – 1999 at lake B). For example, populations within a saline lake may fluctuate annually due to inadequate habitat conditions (e.g., low surface water availability) and catastrophic events (e.g., hail storms and hurricanes) resulting in considerable adult mortality. Regionally, saline lake surface water availability is the most important component in determining local breeding abundance and site fidelity, as surface water presence is necessary for nesting Snowy Plovers (Conway et al. 2005b). Therefore, if surface water is not present upon arrival, individuals may seek alternate breeding locations, ultimately reducing both local (saline lake level) and regional populations for a given nesting season (Boyd 1981). For example, drought conditions (cumulative rainfall in the city of Tahoka [Lynn County, Texas] from January – July 2008 estimated at 10.5 cm below long-term average; National Climate Data Center; http://cdo.ncdc.noaa.gov) and lack of surface water at lake A in 2008 may have prevented birds from stopping at, or quickly dispersing from that lake upon arrival. Conversely, regional declines in surface water availability may concentrate birds within a limited number of saline lakes with suitable habitat conditions. For example, in 1998, drought conditions (cumulative rainfall in the city of Tahoka [Lynn County, Texas] from January – July 1998 estimated at 11.8 cm below average; National Climate Data Center; http://cdo.ncdc.noaa.gov) likely concentrated birds within lakes A and B, as most other lakes within the region were completely dry by early June (W. Conway per. obs.), contributing to the high population estimates observed in that year.

Although shorebirds such as Snowy Plovers tend to be long-lived species, with relatively high adult survival (Sandercock et al. 2005), catastrophic events (e.g., hail storms and hurricanes) may cause locally severe impacts. For example, hail storms during the nesting season can cause direct mortality to both incubating adults and eggs (Conway 2001). Furthermore, hurricanes can cause both direct and indirect mortality to shorebird populations from excessive wind, rain, and floods, that not only kill adult individuals, but also reduce prey availability and alter habitat conditions (Marsh and Wilkinson 1991, Michener et al. 1997). During August – September 2007, four hurricanes (i.e., Hurricane Dean, Hurricane Erin, Hurricane Humberto, and Hurricane Lorentzo) made landfall between the Texas coast and Yucatán Peninsula. This region is the presumed winter location of this inland nesting Snowy Plover population, as the majority of Snowy Plovers are thought to winter within this region (Mabee et al. 2001, Gorman and Haig 2002, Elliott-Smith et al. 2004). Combined, these hurricanes may have caused direct and indirect mortality to wintering populations of Snowy Plovers within these areas, resulting in the dramatic population declines observed between 2007 and 2008 nesting seasons. Although devastating impacts from such catastrophic weather events during winter cannot be prevented, negative effects to populations may be mitigated by improving nest success and/or survival. However, successful techniques to improve nest success and survival are often difficult to implement or do not exist.

Current climate change models for the SHP of Texas suggest drier summers and more severe and frequent extreme weather events as the result of global warming (Matthews 2008). With such changes, adult and juvenile mortality due to severe weather events will increase within this region, exacerbating current declines of Snowy Plovers. Along with this, drier summers will reduce surface water availability during the nesting season, negatively impacting breeding and natal site fidelity, nest success, and juvenile and adult survival.

Regardless of the cause of regional population declines, recovery of Snowy Plover populations may be restricted by limited (or lack of) immigration from other populations. Within this region, Snowy Plovers exhibit high breeding site fidelity (e.g., 58 – 77% return rates of adults banded in 1999, 2008, and 2009; see Chapter V), with immigration occurring, presumably from other regional saline lakes (see Chapter V). Furthermore, most (82%) individuals returned to the same saline lake in subsequent years, even 10 years following capture (see Chapter V), and no color banded individuals were resighted in other regions during the breeding season. Because interior nesting habitat is widely spaced and patchily distributed (Boyd 1981, Gorman and Haig 2002), immigration between locations may be lmiited. Therefore, population declines observed in this region likely cannot be offset by immigration, making conservation of local populations within the SHP of Texas extremely important.

To properly monitor local populations and assess apparent population declines, regularly occurring regional survey counts need to be conducted. However, several factors may influence accuracy and comparability of counts. For example, surface water availability in regional saline lakes and time during the nesting season influenced number of Snowy Plovers observed during surveys. Weekly population fluctuations based upon surface water availability are likely the result of movements within a given lake rather than movements among lakes, as very few individuals were ever confirmed to move between lakes within a year (see Chapter V). Moreover, it appears that most individuals located during surveys were nesting and were unlikely to abandon nests to leave a particular lake on a weekly time frame. When surface water was low, Snowy Plovers may have needed to move further within a lake to obtain food and/or water, resulting in individuals occurring in areas not visible from survey routes. Therefore, population estimates may vary considerably if surveys are not standardized to account for changes in surface water availability, or if multiple surveys are not conducted throughout the breeding season to account for variation in surface water levels. Furthermore, maintaining consistent survey routes within and among years may reduce variability among surveys and provide consistent estimates for long-term comparisons.

Unlike surface water availability, time during the nesting season likely affected population size within a given lake, as consistent declines (i.e., lakes A and C) or increases (i.e., lake B) rather than fluctuations, were observed over time. Within season movements of Snowy Plovers have been attributed to habitat quality and predator densities, where individuals initiating second nests may disperse to areas of better quality or with fewer predators after first nesting attempts (Stenzel et al. 1994). Similarly, seasonal declines in number of Snowy Plovers at lakes A and C in 2008 – 2009 may be a result of low nest success (see Chapter I) and surface water availability (see Figures 6.6 – 6.17). Because few adult Snowy Plovers had chicks to attend to (i.e., few nests hatched) and surface water was low, individuals may have left lakes A and C sooner than lake B. Conversely, at lake B, number of adult Snowy Plovers increased as the season progressed in 2008 – 2009, likely due to greater nest success (see Chapter I) and surface water availability (see Figures 6.6 – 6.17). Because of consistent surface water levels, lake B may also have functioned as a migratory stopover location for birds from regional (e.g., local saline lakes) and/or distant locations (e.g., individuals nesting further north than the SHP). Therefore, population estimates may not be directly comparable if surveys are not conducted during similar time period within the breeding season.

Regional declines in nesting Snowy Plovers combined with apparently high breeding site fidelity illustrate the need for concerted regional conservation efforts. The primary regional conservation concern is presence of surface water within saline lakes during the nesting season. Surface water availability is not only a necessary landscape feature for nesting Snowy Plovers (Conway et al. 2005b), but reliable surface water presence may increase nest success (see Chapter I) and adult and juvenile survival (see Chapter V). Although surface water is partially dependent upon unpredictable weather events, spring flow on saline lakes historically provided reliable surface water during the nesting season (Brune 2002). However, several anthropogenic factors including presence of exotic invasive plants (e.g., salt cedar [*Tamarix* spp.]), groundwater uptake, and irrigation negatively affect spring flow and ultimately reliability of surface water for nesting Snowy Plovers (see Chapter I). Therefore, to conserve subsurface and surface water in saline lakes, salt cedar should be removed from areas surrounding lakes, and especially near freshwater springs. Furthermore, crop irrigation relying on the same aquifer during the nesting season has decreased the amount of freshwater input of functioning springs into saline lakes and resulted in permanent drying of most springs in saline lakes within this region (Conway et al. 2005a). Therefore, to conserve freshwater springs discharging into saline lakes within this region, as well as the Ogallala aquifer, irrigation within areas surrounding saline lakes should be reduced. However, in instances where spring flow has completely ceased, it may be necessary to artificially pump surface water onto saline lakes to create additional suitable nesting habitat for regional Snowy Plovers. Because the Ogallala aquifer is recharged from playa wetlands (Osterkamp and Wood 1987, Bolen et al. 1989), it also remains important to conserve the entire complex of wetlands within the SHP of Texas (Andrei et al. 2008, Andrei et al. 2009).

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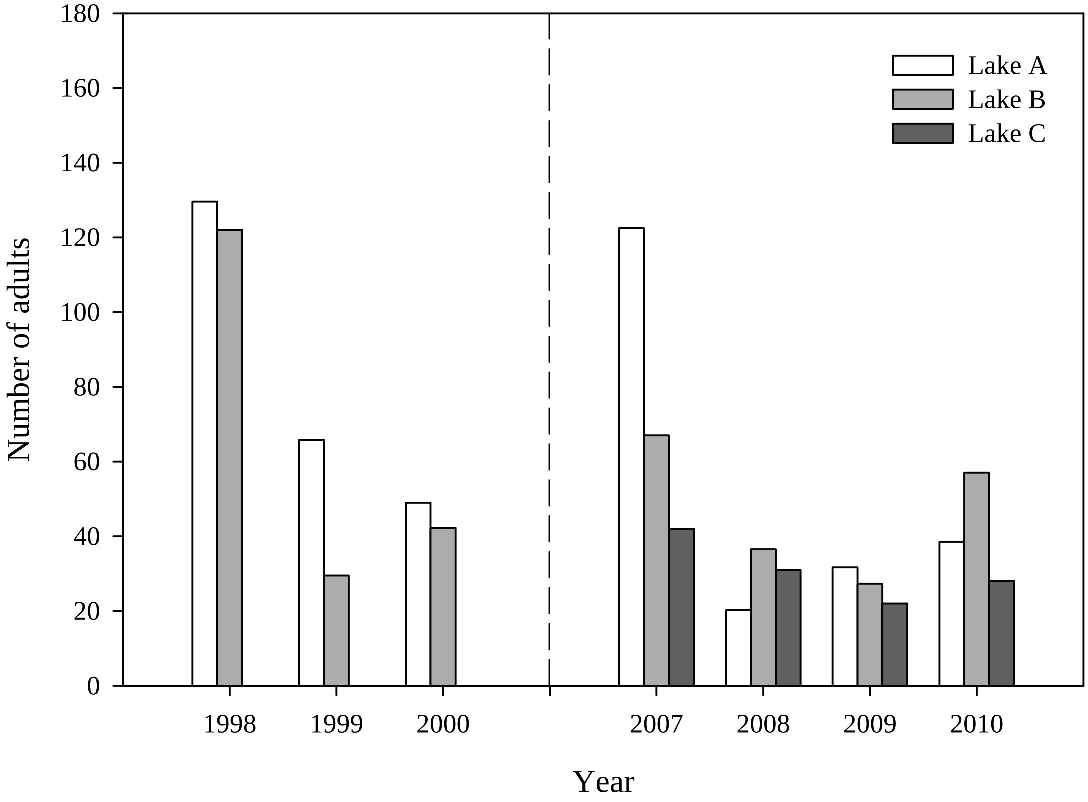

Figure 6.1. Mean survey counts during May (as May was only surveyed in 2007 and 2010) of adult Snowy Plovers observed on saline lakes within the Southern High Plains of Texas, USA, 1998 – 2010.

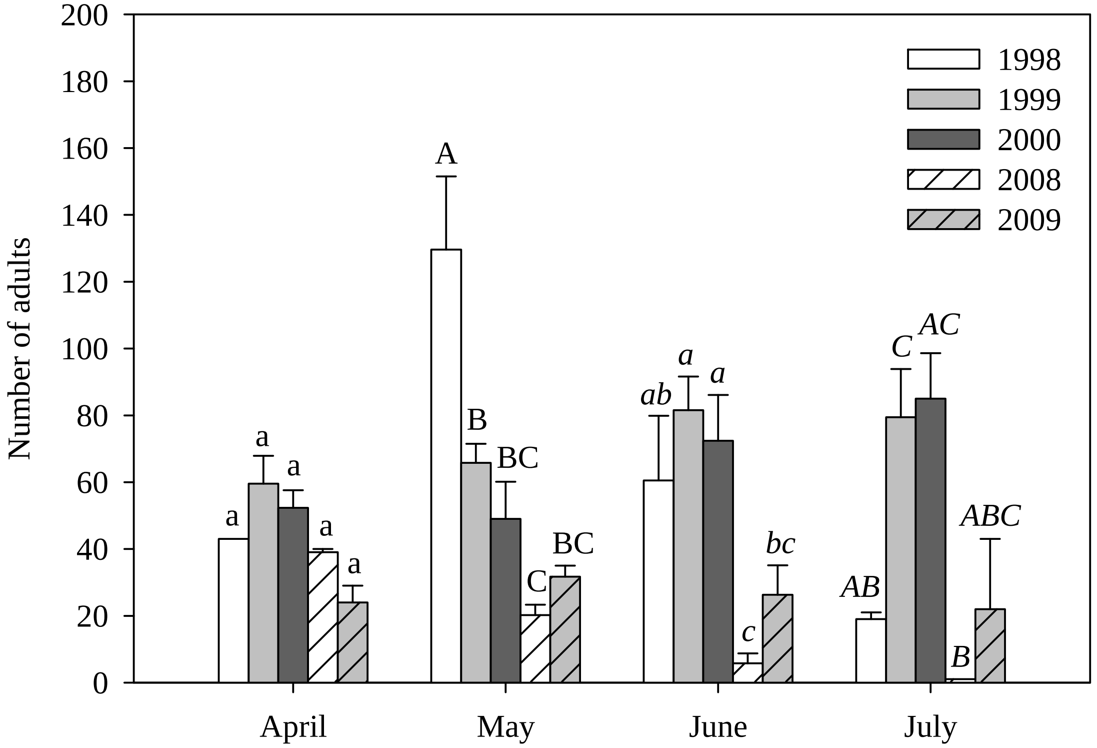

Figure 6.2. Mean monthly survey counts of adult Snowy Plovers observed on lake A within the Southern High Plains of Texas, USA, 1998 – 2009. Years with the same letter within a month are not different (*P* > 0.05; least squares cross validation).

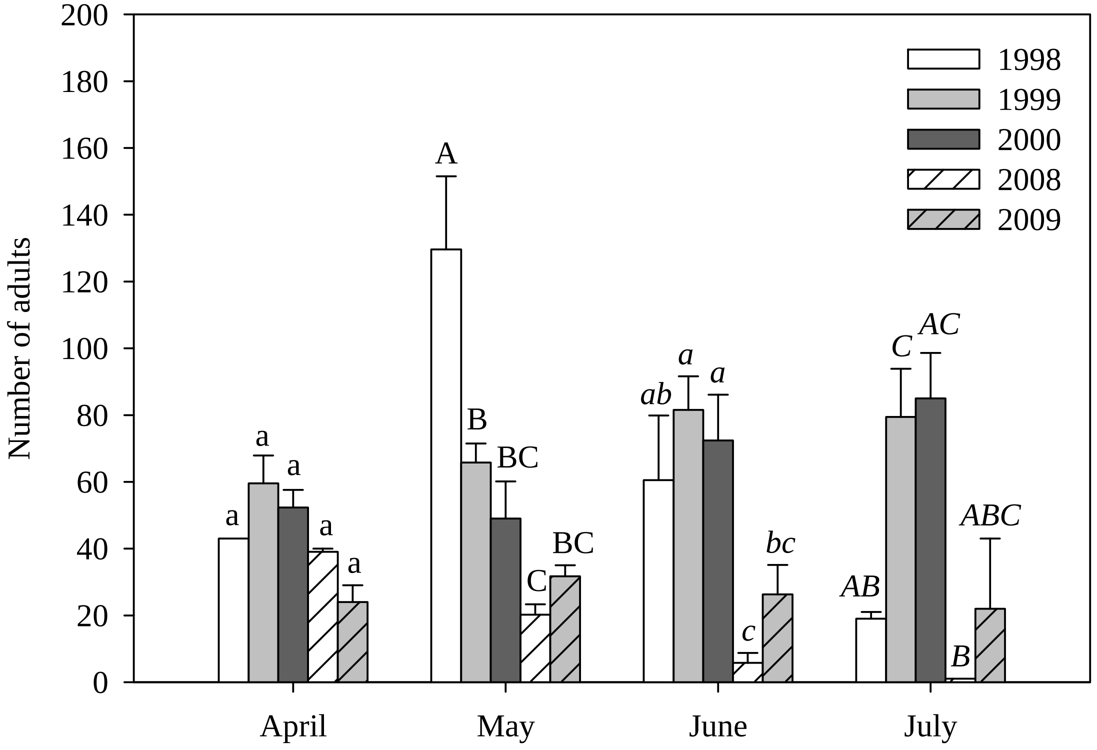

Figure 6.3. Mean monthly survey counts of adult Snowy Plovers observed on lake B within the Southern High Plains of Texas, USA, 1998 – 2009. Years with the same letter within a month are not different (*P* > 0.05; least squares cross validation).

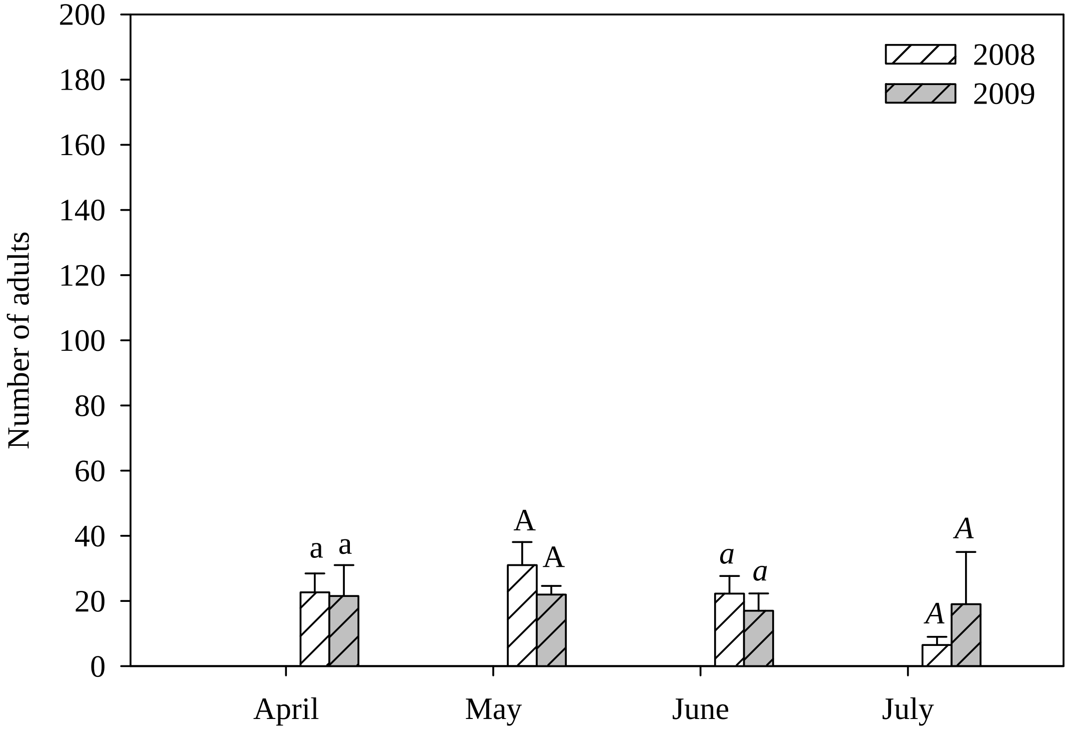

Figure 6.4. Mean monthly survey counts of adult Snowy Plovers observed on lake C within the Southern High Plains of Texas, USA, 1998 – 2009. Years with the same letter within a month are not different ($P > 0.05$; least squares cross validation).

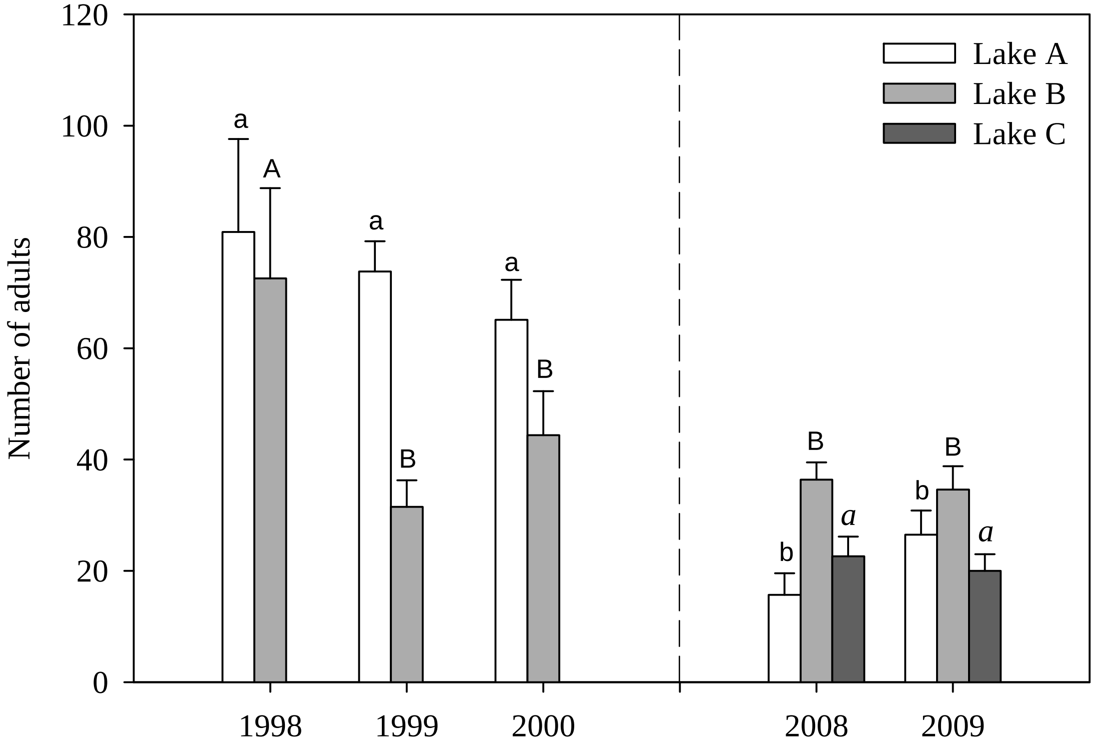

Figure 6.5. Mean survey counts of adult Snowy Plovers observed on saline lakes within the Southern High Plains of Texas, USA, 1998 – 2009. Years with the same letter within a lake are not different (*P* > 0.05; least squares cross validation).

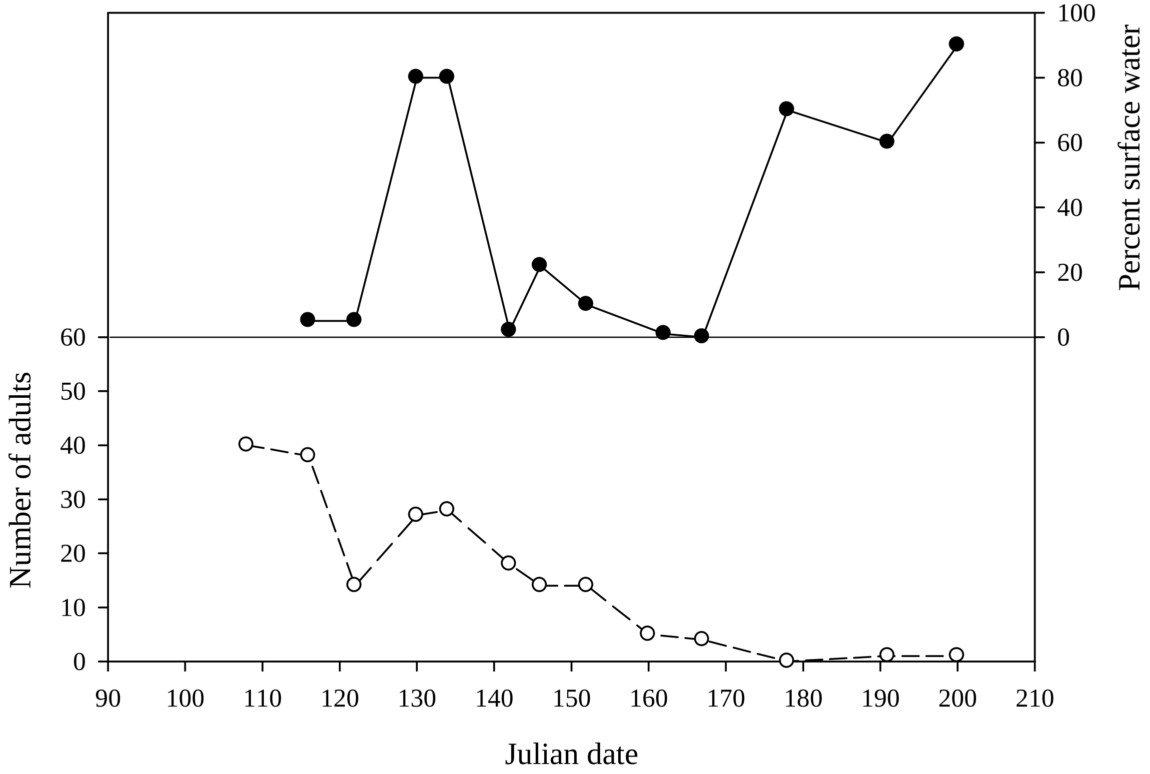

Figure 6.6. Total number (i.e., banded and unbanded) of adult Snowy Plovers observed during surveys in relation to percent surface water availability on lake A within the Southern High Plains of Texas, USA, 2008.

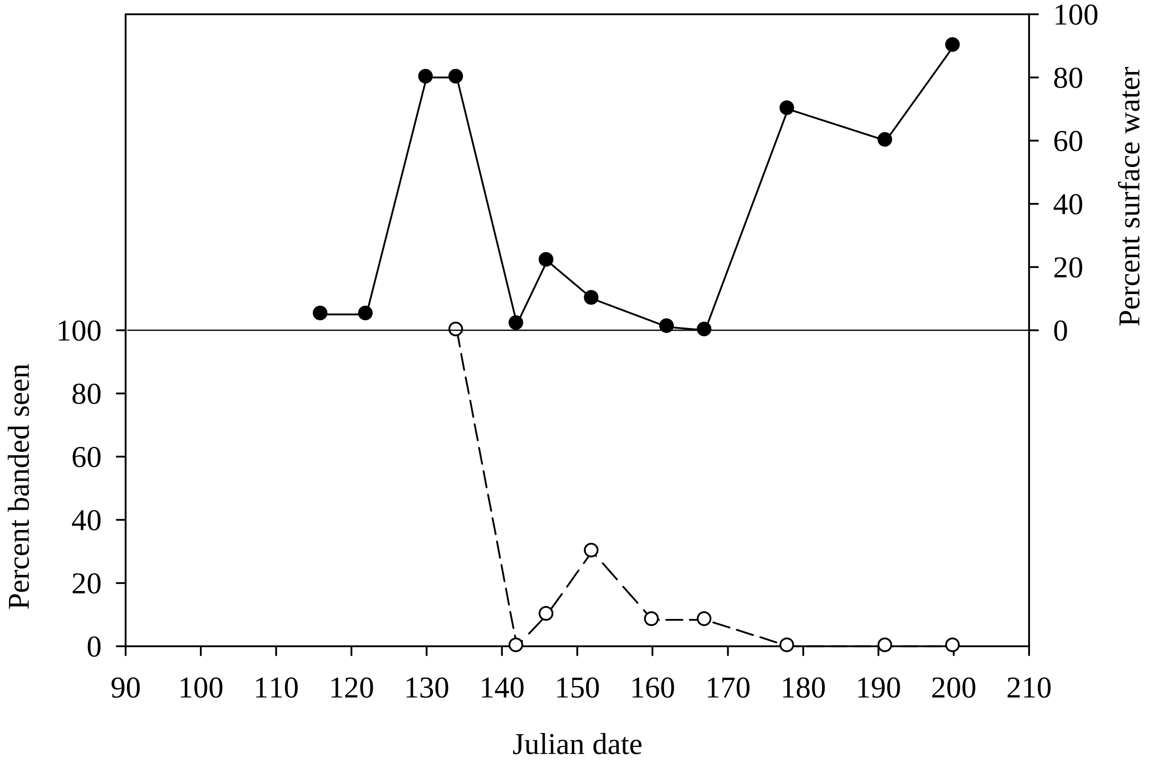

Figure 6.7. Percentage of banded adult Snowy Plovers (i.e., number of banded individuals observed divided by total number of banded individuals in the population at time of survey execution [number of birds banded on a given lake at time of survey execution + number of adults banded in previous year that were resighted at least once on a given lake during the breeding season]) observed during surveys in relation to percent surface water availability on lake A within the Southern High Plains of Texas, USA, 2008.

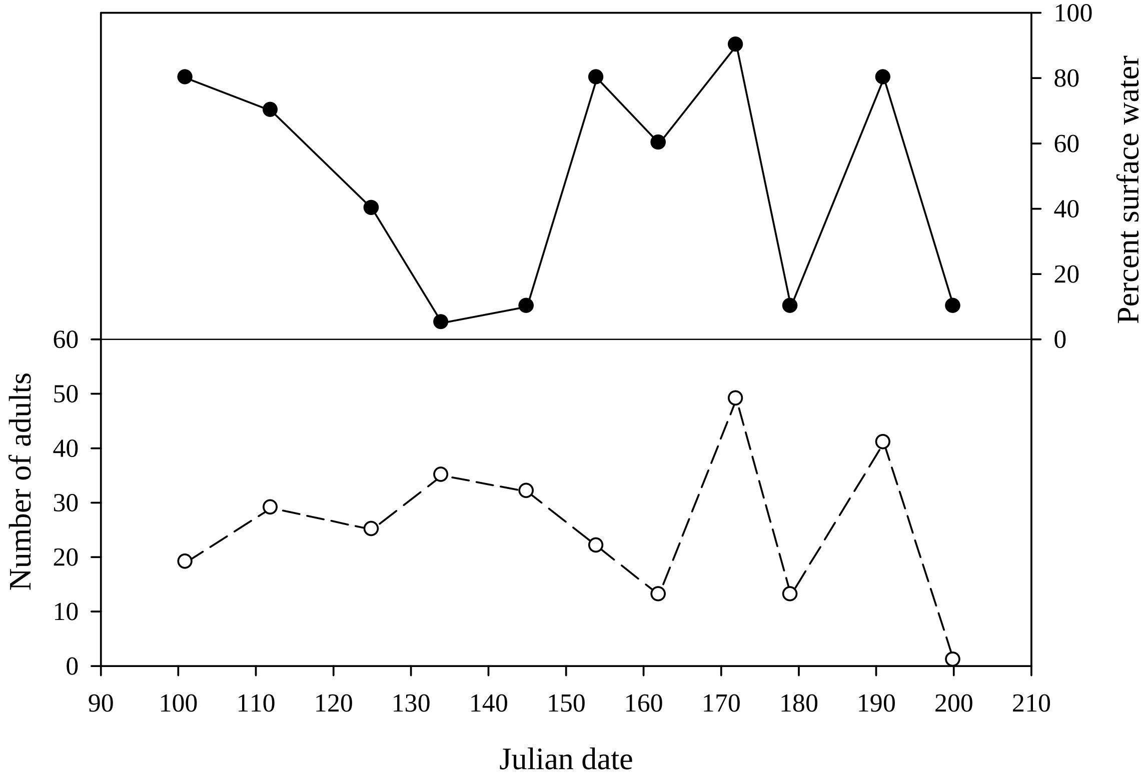

Figure 6.8. Total number (i.e., banded and unbanded) of adult Snowy Plovers observed during surveys in relation to percent surface water availability on lake A within the Southern High Plains of Texas, USA, 2009.

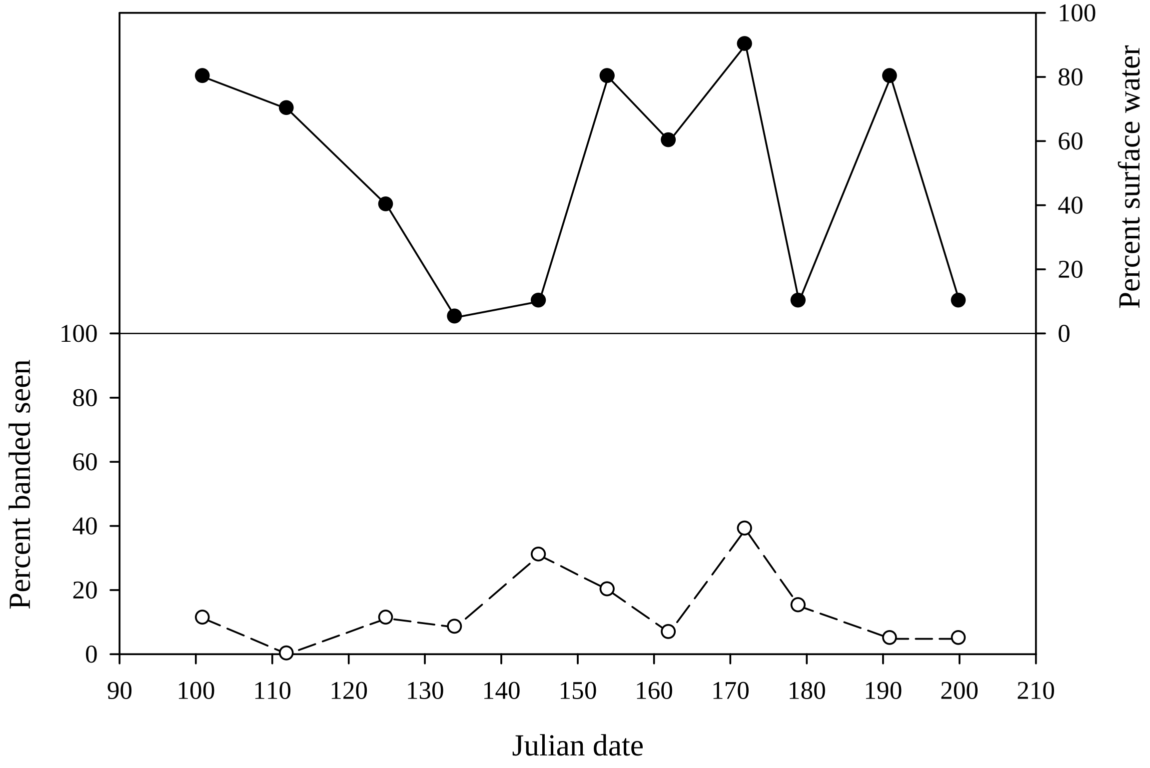

Figure 6.9. Percentage of banded adult Snowy Plovers (i.e., number of banded individuals observed divided by total number of banded individuals in the population at time of survey execution [number of birds banded on a given lake at time of survey execution + number of adults banded in previous year that were resighted at least once on a given lake during the breeding season]) observed during surveys in relation to percent surface water availability on lake A within the Southern High Plains of Texas, USA, 2009.

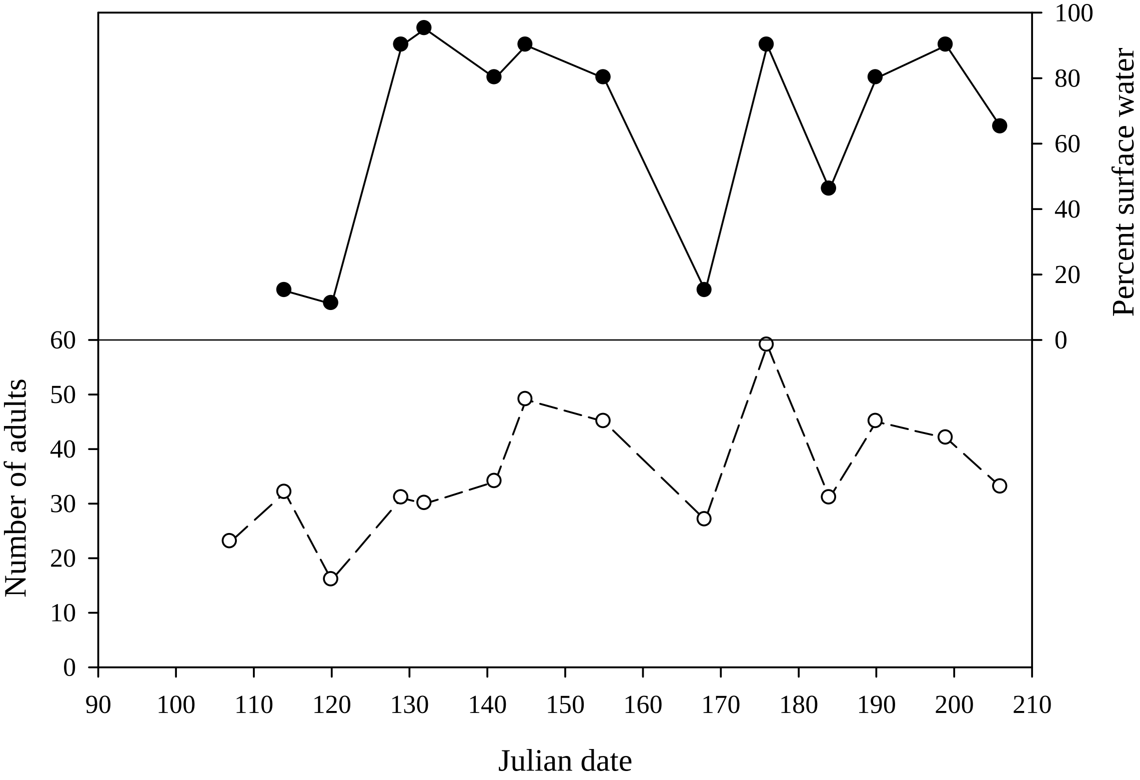

Figure 6.10. Total number (i.e., banded and unbanded) of adult Snowy Plovers observed during surveys in relation to percent surface water availability on lake B within the Southern High Plains of Texas, USA, 2008.

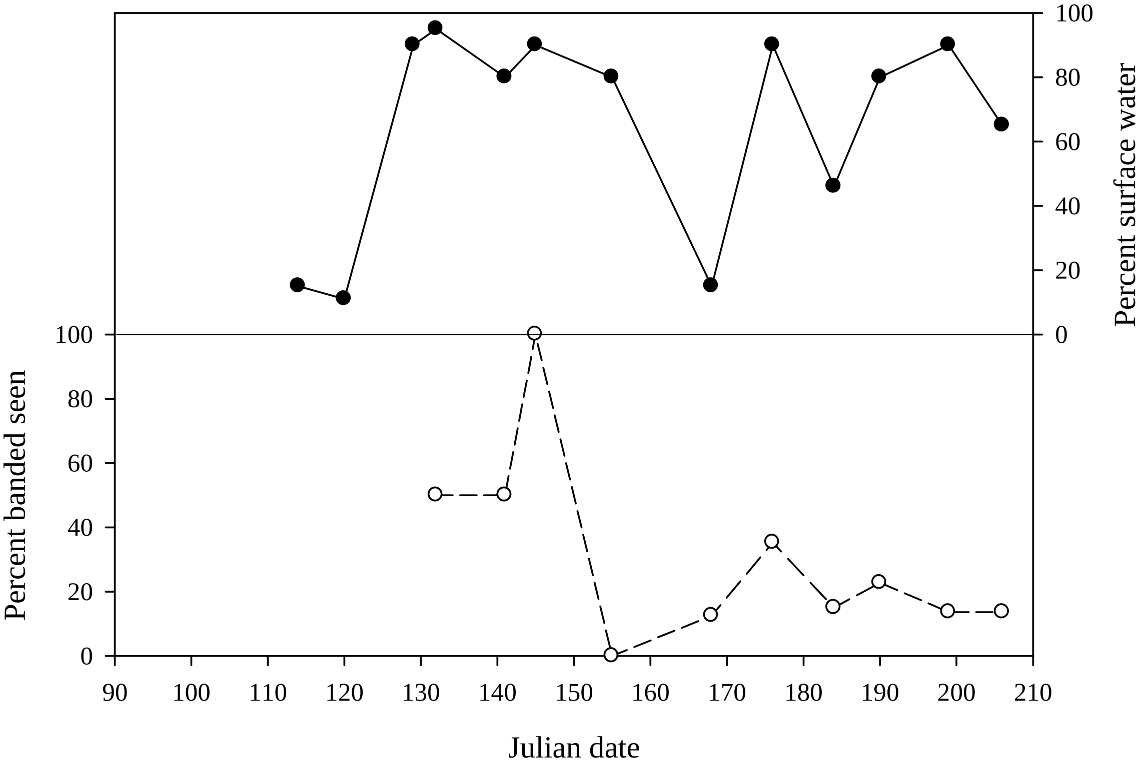

Figure 6.11. Percentage of banded adult Snowy Plovers (i.e., number of banded individuals observed divided by total number of banded individuals in the population at time of survey execution [number of birds banded on a given lake at time of survey execution + number of adults banded in previous year that were resighted at least once on a given lake during the breeding season]) observed during surveys in relation to percent surface water availability on lake B within the Southern High Plains of Texas, USA, 2008.

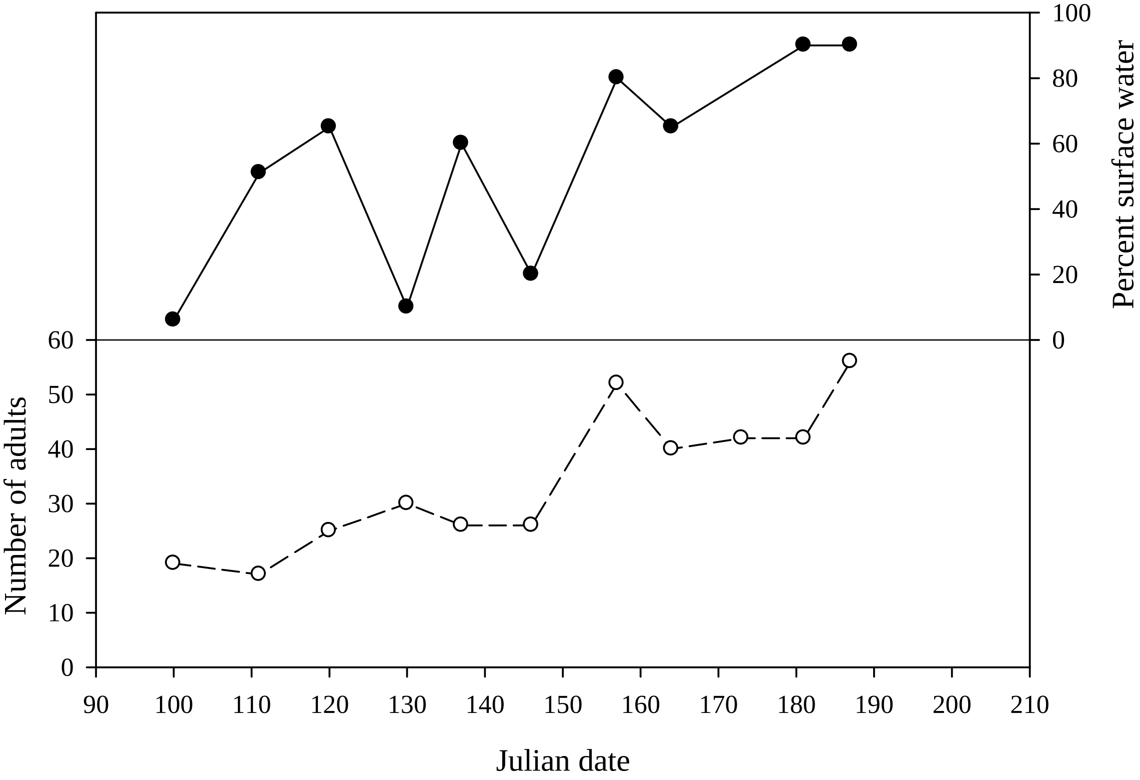

Figure 6.12. Total number (i.e., banded and unbanded) of adult Snowy Plovers observed during surveys in relation to percent surface water availability on lake B within the Southern High Plains of Texas, USA, 2009.

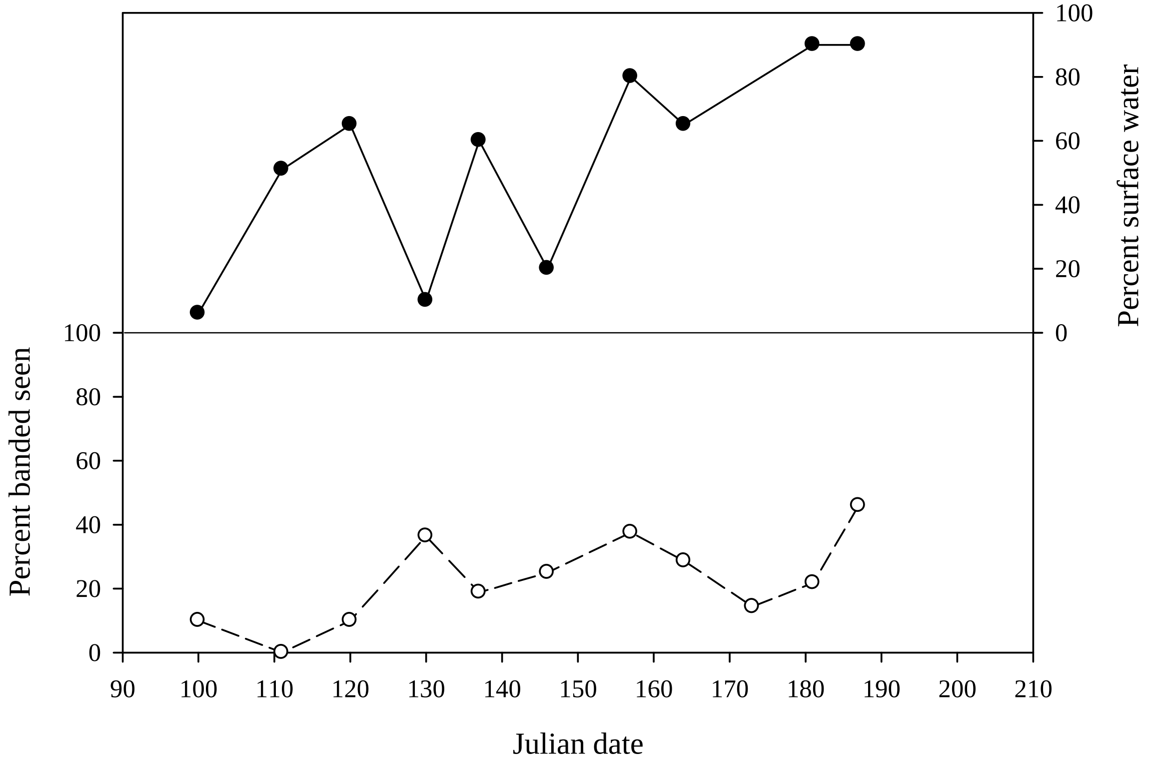

Figure 6.13. Percentage of banded adult Snowy Plovers (i.e., number of banded individuals observed divided by total number of banded individuals in the population at time of survey execution [number of birds banded on a given lake at time of survey execution + number of adults banded in previous year that were resighted at least once on a given lake during the breeding season]) observed during surveys in relation to percent surface water availability on lake B within the Southern High Plains of Texas, USA, 2009.

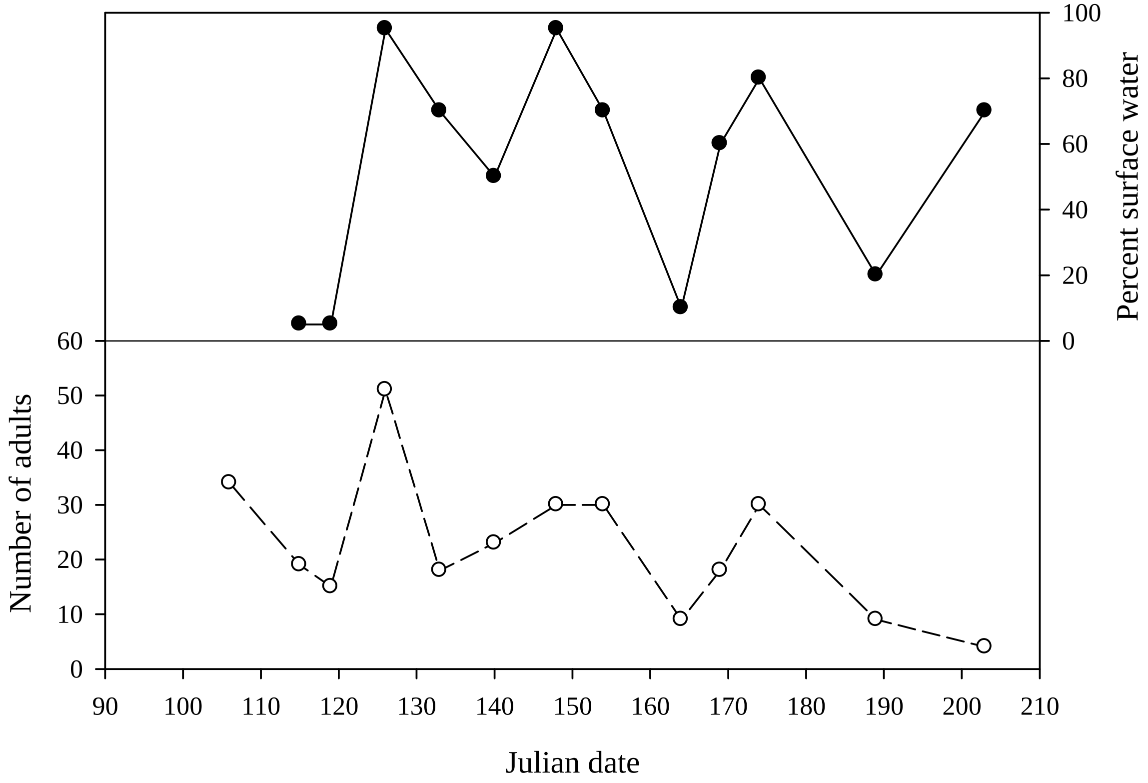

Figure 6.14. Total number (i.e., banded and unbanded) of adult Snowy Plovers observed during surveys in relation to percent surface water availability on lake C within the Southern High Plains of Texas, USA, 2008.

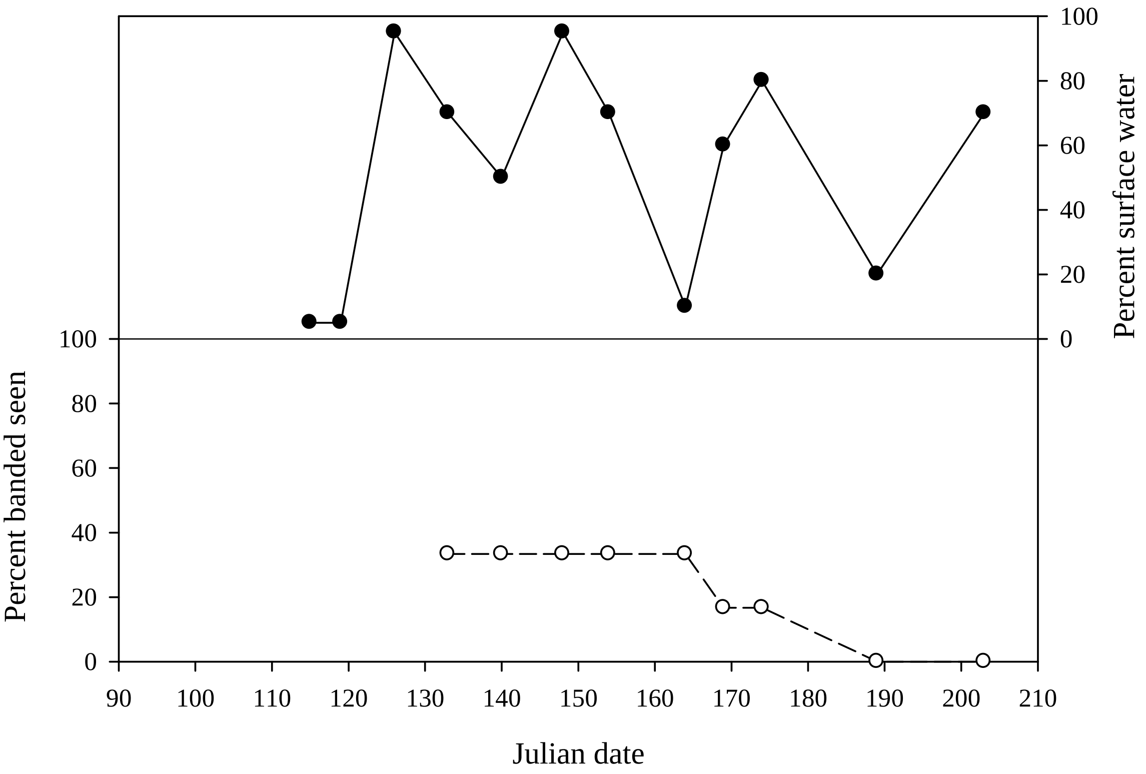

Figure 6.15. Percentage of banded adult Snowy Plovers (i.e., number of banded individuals observed divided by total number of banded individuals in the population at time of survey execution [number of birds banded on a given lake at time of survey execution + number of adults banded in previous year that were resighted at least once on a given lake during the breeding season]) observed during surveys in relation to percent surface water availability on lake C within the Southern High Plains of Texas, USA, 2008.

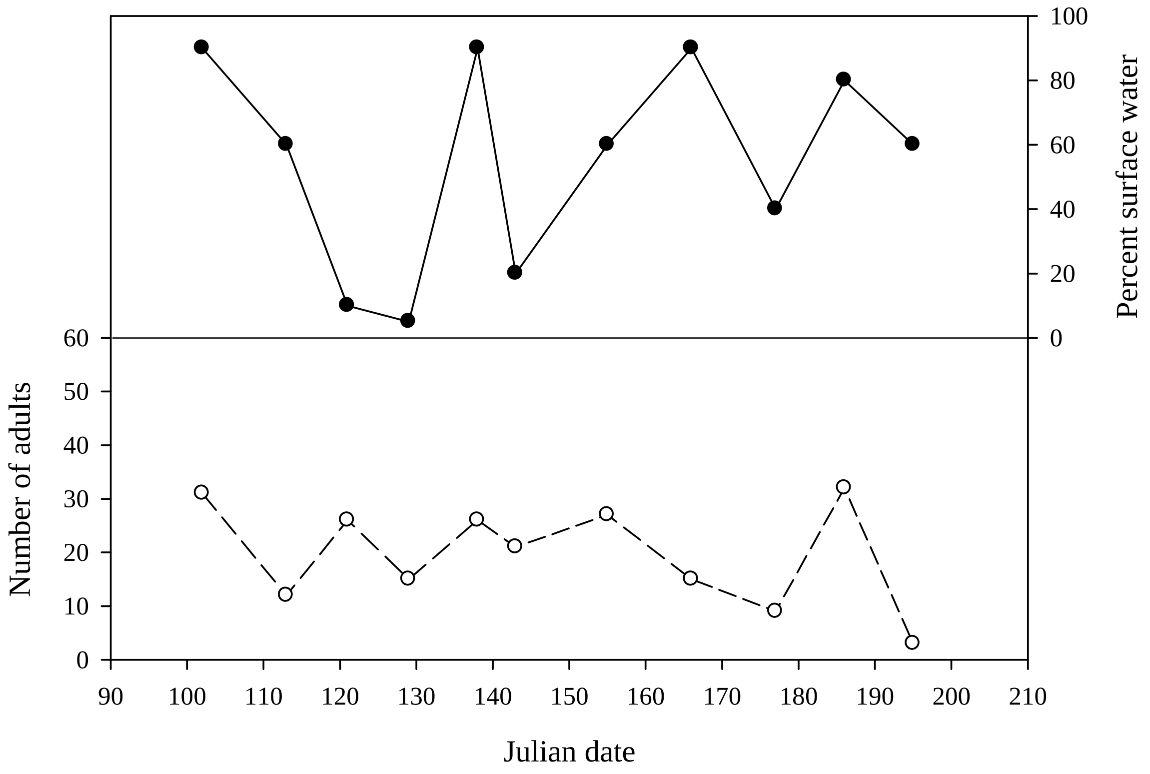

Figure 6.16. Total number (i.e., banded and unbanded) of adult Snowy Plovers observed during surveys in relation to percent surface water availability on lake C within the Southern High Plains of Texas, USA, 2009.

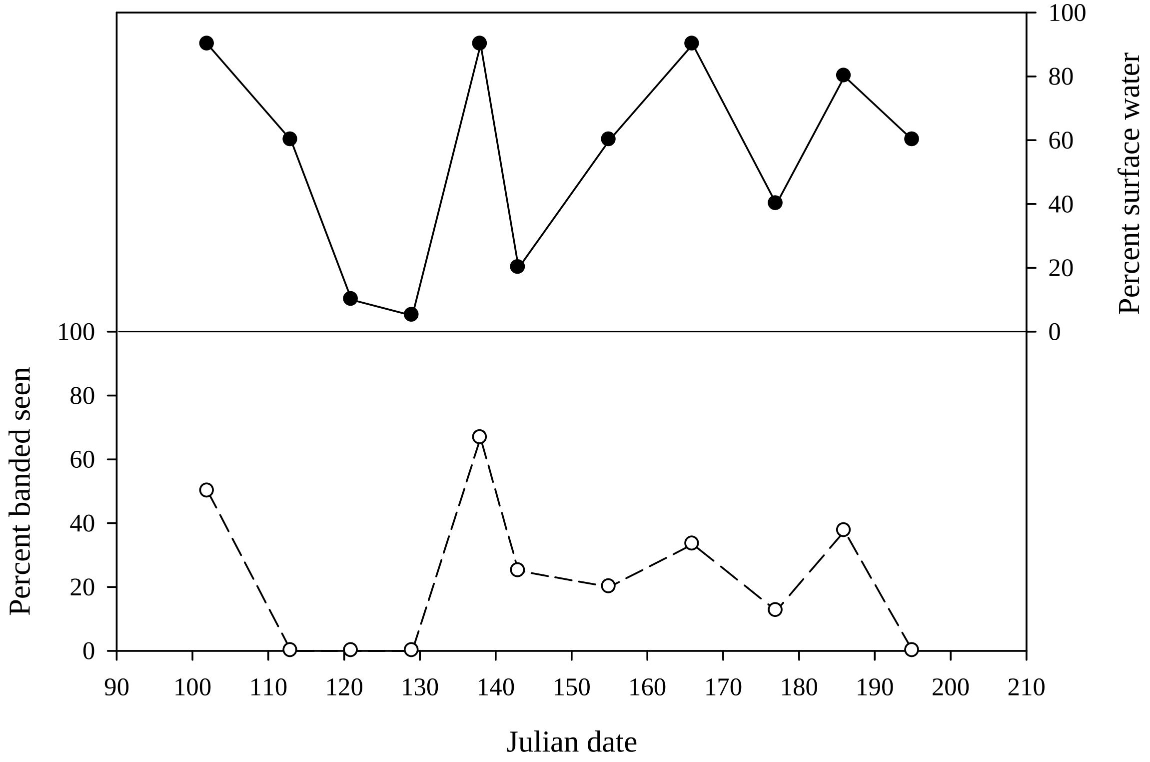

Figure 6.17. Percentage of banded adult Snowy Plovers (i.e., number of banded individuals observed divided by total number of banded individuals in the population at time of survey execution [number of birds banded on a given lake at time of survey execution + number of adults banded in previous year that were resighted at least once on a given lake during the breeding season]) observed during surveys in relation to percent surface water availability on lake C within the Southern High Plains of Texas, USA, 2009.

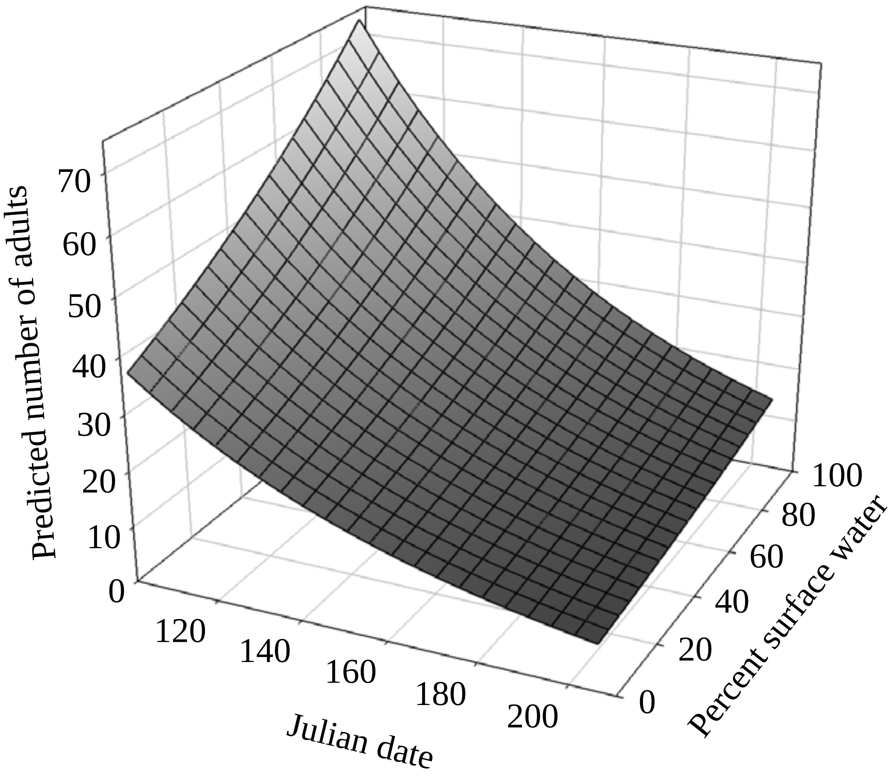

Figure 6.18. The effects of percent surface water and Julian date from model = Julian*lake + % water on predicted number of adult Snowy Plovers observed during weekly surveys on lake A within the Southern High Plains of Texas, USA, 2008 – 2009.

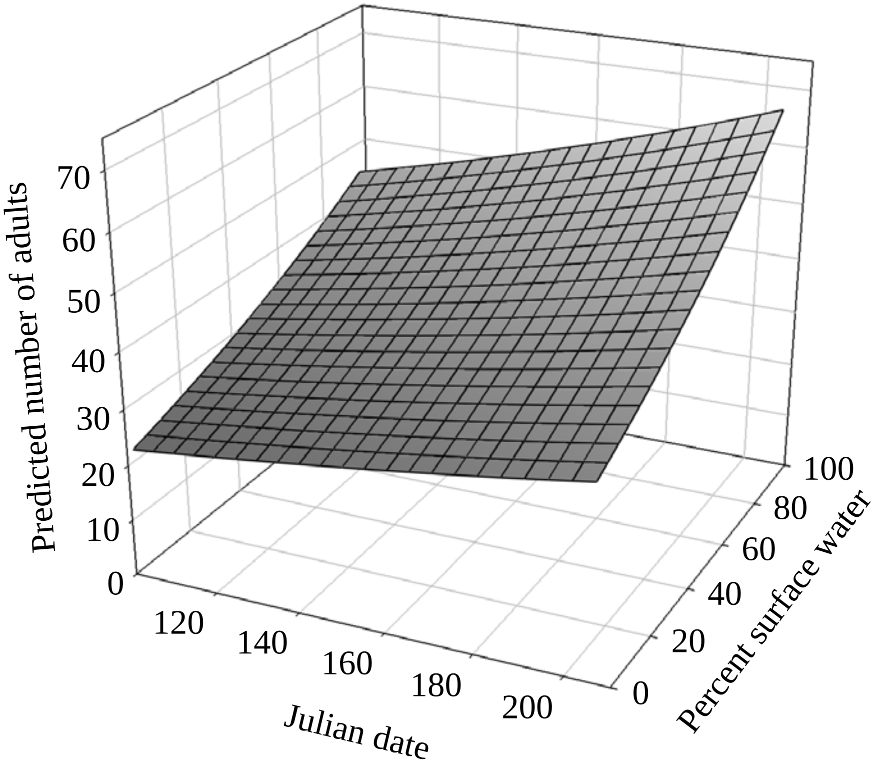

Figure 6.19. The effects of percent surface water and Julian date from model = Julian*lake + % water on predicted number of adult Snowy Plovers observed during weekly surveys on lake B within the Southern High Plains of Texas, USA, 2008 – 2009.

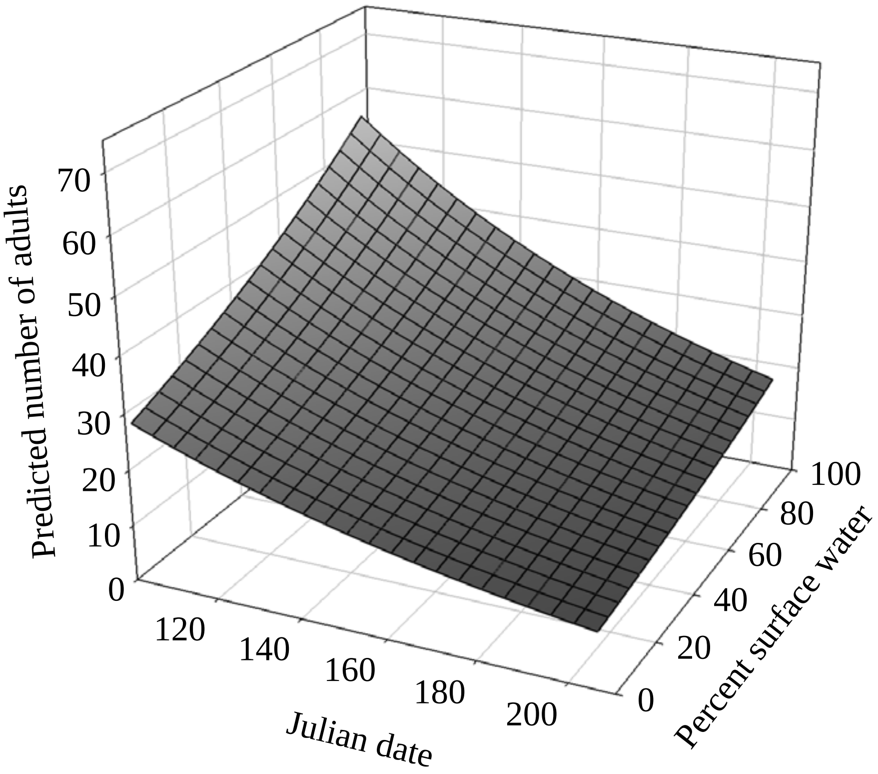

Figure 6.20. The effects of percent surface water and Julian date from model = Julian*lake + % water on predicted number of adult Snowy Plovers observed during weekly surveys on lake C within the Southern High Plains of Texas, USA, 2008 – 2009.

Table 6.1. Means ($\bar{x}$), standard errors (SE), and *F* and *P*-values resulting from analyses of variance of number of adult Snowy Plovers observed during weekly surveys by month and year on lake A within the Southern High Plains of Texas, USA, 1998 – 2009 (see Figure 6.2 for mean separation).

	1998			1999			2000			2008			2009				
	n[a]	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*F*	*P*
April	1	43.0	---	4	59.5	8.3	3	52.3	5.2	2	39.0	1.0	2	24.0	5.0	3.19	0.086
May	5	129.6	21.9	8	65.8	5.7	5	49.0	11.1	5	20.2	3.1	3	31.7	3.3	13.09	<0.001*
June	4	60.5	19.4	10	81.5	10.1	8	72.4	13.7	4	5.8	3.0	4	26.3	8.9	5.49	0.003*
July	2	19.0	2.0	8	79.4	14.5	3	85.0	13.6	2	1.0	0.0	2	22.0	21.0	3.93	0.029*
Combined[b]	12	80.9	16.7	30	73.8	5.4	19	65.1	7.2	13	15.7	3.8	11	26.5	4.3	11.57	<0.001*

[a] Number of surveys.

[b] Surveys for all months combined.

* Significant *P*-value ($P < 0.05$).

Table 6.2. Means ($\bar{x}$), standard errors (SE), and F and P-values resulting from analyses of variance of number of adult Snowy Plovers observed during weekly surveys by month and year on lake B within the Southern High Plains of Texas, USA, 1998 – 2009 (see Figure 6.3 for mean separation).

	1998			1999			2000			2008			2009				
	n[a]	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	F	P
April	---	---	---	2	38.5	2.5	4	21.3	6.4	3	23.7	4.6	3	20.3	2.4	1.94	0.201
May	3	122.0	36.1	4	29.5	6.7	4	42.3	11.7	4	36.5	4.9	3	27.3	1.3	6.22	0.005*
June	4	73.3	23.3	5	38.4	10.7	4	71.8	13.8	3	43.7	9.3	4	44.8	2.9	1.48	0.258
July	4	34.8	11.3	4	21.3	9.7	1	36.0	---	4	40.3	3.0	1	59.0	---	1.18	0.384
Combined[b]	11	72.5	16.2	15	31.5	4.7	13	44.4	7.9	14	36.4	3.1	11	34.6	4.2	4.08	0.006*

[a] Number of surveys.

[b] Surveys for all months combined.

* Significant P-value ($P < 0.05$).

Table 6.3. Means ($\bar{x}$), standard errors (SE), and F and P-values resulting from analyses of variance of number of adult Snowy Plovers observed during weekly surveys by month and year on lake C within the Southern High Plains of Texas, USA, 1998 – 2009 (see Figure 6.4 for mean separation).

	1998[a]			1999[a]			2000[a]			2008			2009				
	n[b]	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	F	P
April	---	---	---	---	---	---	---	---	---	3	22.7	5.8	2	21.5	9.5	0.01	0.917
May	---	---	---	---	---	---	---	---	---	4	31.0	7.1	4	22.0	2.6	1.41	0.280
June	---	---	---	---	---	---	---	---	---	4	22.3	5.4	3	17.0	5.3	0.46	0.529
July	---	---	---	---	---	---	---	---	---	2	6.5	2.5	2	19.0	16.0	0.60	0.521
Combined[c]	---	---	---	---	---	---	---	---	---	13	22.6	3.6	11	20.0	3.0	0.30	0.588

[a] Lake C was not used as a study site in 1998 – 2000.

[b] Number of surveys.

[c] Surveys for all months combined.

* Significant P-value ($P < 0.05$).

Table 6.4. Negative binomial regression models for variables predicting number of adult Snowy Plovers observed during weekly surveys on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009.

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
Julian*lake + % water[c]	8	0.00	0.88
Julian*lake + % water*lake	10	4.90	0.08
Julian + lake + % water	6	7.76	0.02
Julian + lake + % water + year	7	9.46	0.01
Julian*lake + year	8	9.83	0.01
Julian*lake	7	10.01	0.01
Lake + % water	5	11.08	0.00
% water*lake + Julian	8	11.42	0.00
Lake + % water + year	6	12.62	0.00
% water*year + lake	7	15.03	0.00
% water*lake	7	15.28	0.00
Julian + % water	4	15.46	0.00
% water	3	16.30	0.00
% water*lake + year	8	16.59	0.00
Lake	4	16.70	0.00
Julian + lake	5	17.33	0.00
Julian + % water + year	5	17.56	0.00
Lake*year	7	17.94	0.00
Lake + year	5	18.11	0.00
Julian*year + lake	7	18.12	0.00
% water + year	4	18.23	0.00

Table 6.4. Continued.

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
Julian + lake + year	6	18.78	0.00
Julian*year + % water	6	19.20	0.00
% water*year + Julian	6	19.71	0.00
% water*year	5	20.21	0.00
Intercept[d]	2	24.59	0.00
Year	3	26.60	0.00
Julian	3	26.62	0.00
Julian + year	4	28.72	0.00
Julian*year	5	30.20	0.00

[a] Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[b] AIC_c relative weight attributed to model.

[c] Model of additive effects of Julian date, lake, and % water and the interaction between Julian date and lake.

[d] Model of no effects.

Table 6.5. Estimates (log-link) of top-ranked negative binomial regression model for variables predicting number of adult Snowy Plovers observed during weekly surveys on saline lakes within the Southern High Plains of Texas, USA, 2008 – 2009 (coefficients for percent surface water and Julian date are based upon centered data [i.e., mean subtracted from each datum; where mean Julian date = 150.11 and mean percent surface water = 51.87]).

			95% CI	
Parameter	Estimate	SE	Lower	Upper
Lake A	2.991	0.109	2.777	3.205
Lake B	3.454	0.103	3.253	3.656
Lake C	2.950	0.107	2.741	3.159
Julian date (lake A)	-0.015	0.004	-0.024	-0.007
Julian date (lake B)	0.004	0.004	-0.003	0.011
Julian date (lake C)	-0.011	0.004	-0.019	-0.002
Percent surface water	0.007	0.002	0.004	0.011
Dispersion	0.207	0.048	0.112	0.302