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THE INFLUENCE OF HABITAT ON NEST SURVIVAL OF SNOWY AND WILSON'S PLOVERS IN THE LOWER LAGUNA MADRE REGION OF TEXAS

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Abstract. Snowy Plovers (*Charadrius alexandrinus*) and Wilson's Plovers (*Charadrius wilsonia*) are two shorebird species that nest along the Gulf Coast of the US. We modeled the daily nest survival of both species in the lower Laguna Madre region of Texas during the 2003 and 2004 breeding seasons as a function of nest age, year, day in the season, maximum daily temperature, daily precipitation, and habitat features at three spatial scales (microhabitat, a 25-m radius of the nest, and landscape). Daily survival of Snowy Plover nests increased with nest age ($\hat{\beta}_{Age}$ = 0.03, 95% confidence limits were –0.01, 0.07, on a logit scale), but did not vary between years. Nests inland had substantially lower daily survival than nests on the coast ($\hat{\beta}_{Inland}$ = –0.18, 95% confidence limits were –1.03, 0.67, on a logit scale). The presence of a conspicuous object at the nest site increased daily nest survival. A quadratic trend occurred on the coefficient of variation (CV) for low vegetation (CV used as an index of low vegetation spatial heterogeneity) at the 25-m scale for Snowy Plover nests. Daily nest survival of Wilson's Plovers was best explained by a combination of two habitat metrics at the microhabitat scale. Less vegetation at the immediate nest site increased daily survival ($\hat{\beta}_{Veg}$ = –1.35, 95% confidence limits were –2.28, –0.42, on a logit scale) while daily nest survival was higher for nests with lower contagion at the microhabitat scale ($\hat{\beta}_{Contagion}$ = –0.87, 95% confidence limits were –1.65, –0.10, on a logit scale). We found no evidence for yearly differences or an effect of weather on the daily nest survival of either species. Our results illustrate the role that selected habitat features play in the nest survival of Snowy and Wilson's plovers and further our understanding of their nesting ecology. We anticipate that our results will assist in the identification and protection of habitats critical to breeding populations of these and other shorebird species.

Key Words: *Charadrius alexandrinus*, *C. wilsonia,* Laguna Madre, nest success, nest survival, program MARK, Snowy Plover, Texas, Wilson's Plover.

LA INFLUENCIA DEL HÁBITAT EN LA SOBEVIVENCIA DE NIDO DE CHORLO NEVADO Y CHORLO PICOGRUESO EN LA REGIÓN BAJA DE LA LAGUNA MADRE DE TEXAS

Resumen. El Chorlo Nevado (*Charadrius alexandrinus*) y el Chorlo Picogrueso (*Charadrius wilsonia*) son dos especies de ave de orilla que anidan a lo largo de la Costa del Golfo de EU. Modelamos sobrevivencia diaria de nido para ambas especies en la región baja de la Laguna Madre de Texas durante el 2003 y el 2004, estaciones de reproducción como función de la edad de nido, año, día en la estación, temperatura máxima diaria, precipitación diaria, y características de hábitat en tres escalas espaciales (microhabitat, un radio de 25-m del nido, y paisaje). La sobrevivencia diaria de nidos de Chorlo Nevado incrementó con la edad del nido ($\hat{\beta}_{edad}$ = 0.03, 95% de los límites de confidencia fueron –0.01, 0.07 en escala logit), pero no variaron entre los años. La anidación en tierra tuvo substancialmente una sobrevivencia menor que los nidos en la costa ($\hat{\beta}_{Inland}$ = –0.18, 95% de los límites de confidencia fueron –1.03, 0.67 en escala logit). La presencia de un objeto visible en el sitio del nido incrementó la sobrevivencia diaria del nido. Una tendencia cuadrática ocurrió en el coeficiente de variación (CV) para la vegetación baja (CV utilizado como un índice de heterogeneidad especial de baja vegetación) a la escala de 25-m para nidos de Chorlo Nevado. La sobrevivencia de nido diaria de Chorlo Picogrueso fue mejor explicada por una combinación de dos métricas de hábitat a la escala de microhabitat. Menor vegetación en la parte inmediata del nido incrementó la sobrevivencia diaria ($\hat{\beta}_{Veg}$ = –1.35, 95% de límites de confidencia fueron –2.28, –0.42 en escala logit), mientras que la sobrevivencia diaria de nido fue más alta para los nidos con menor contagio a la escala de microhábitat ($\hat{\beta}_{Contagion}$ = –0.87, 95% de límites de confidencia fueron –1.65, –0.10 en escala logit). No encontramos evidencia para diferencias anuales, o algún efecto del clima en la sobrevivencia diaria de nido para ninguna de las especies. Nuestros resultados ilustran el papel que juegan ciertas características del hábitat en la sobrevivencia de nido de Chorlos Nevado y Picogrueso, y mejora nuestro entendimiento de su ecología de anidación. Anticipamos que nuestros resultados ayudarán a la identificación y protección de hábitats críticos para poblaciones reproductoras de estas y otras especies de aves costeras.

The study of nest survival is an important and frequently used tool in investigations of breeding bird population dynamics. Several recently developed analytical approaches (Rotella et al. 2004) enable researchers to go beyond the traditional Mayfield method (Mayfield 1961) and model nest survival as a function of a wide range of factors of interest. Such detailed studies of nest survival have the potential not only to provide estimates of nest-survival probabilities, but also to examine the possible influence of various biological factors on these survival probabilities. Elucidating these biological factors and how they relate to avian reproduction is critical for taking the appropriate management or conservation actions in an attempt to improve nest survival of a declining species.

Snowy Plovers (*Charadrius alexandrinus*) and Wilson's Plovers (*Charadrius wilsonia*) are two shorebirds that depend on coastal habitats along the Gulf Coast of the U.S. for breeding, wintering, and migration stopover areas. The amount and quality of coastal habitat available to these and other shorebirds continues to decline as human activity and development in these coastal areas increase. This anthropogenic pressure is undoubtedly having a negative impact on shorebird populations, particularly those that rely on coastal areas for breeding (Gore and Chase 1989, Page et al. 1995, Corbat and Bergstrom 2000).

In North America, Snowy Plovers breed along the Gulf Coast, the Pacific Coast, and in the Great Basin and southern Great Plains. The North American populations of Snowy Plovers are listed as highly imperiled (Prioritization Category 5) by the United States Shorebird Conservation Plan (Brown et al. 2001). The USDI Fish and Wildlife Service listed the Pacific Coast population of the Snowy Plover as threatened in 1993 (United States Department of the Interior 1993); Gulf Coast and interior populations are not listed. Primary threats to the species along the Pacific and Gulf coasts are habitat degradation and increased recreational use of beaches (Page et al. 1995).

The nesting ecology of Snowy Plovers along the Pacific Coast and inland in the Great Basin and Great Plains has been well studied (Boyd 1972, Wilson-Jacobs and Meslow 1984, Page et al. 1995, Paton 1995), but less information is available for the birds that nest along the western Gulf Coast of the U.S. (Rupert 1997). Snowy Plovers nest on barren to sparsely vegetated sand and alkaline flats of coastal areas, and inland along river channels and shorelines of saline lakes (Page et al. 1995). Nests are often located near clumps of vegetation or conspicuous objects such as debris, rocks, or large shells, on small elevated areas, or on an area of high shell or pebble concentration relative to the surrounding area (Boyd 1972, Purdue 1976, Hill 1985, Page et al. 1985, Stern et al. 1990, Paton 1995). Clutch size is typically three eggs, with the average length of incubation ranging from 25–28 d (Page et al. 1995). Several studies have estimated apparent nest success for Snowy Plovers, ranging from 13% on the Oregon coast (Wilson-Jacobs and Meslow 1984) to 87% along the California coast (Wehtje and Baron 1993). Page et al. (1995) calculated an average apparent nest success of 53% based on 17 studies in North America. Rupert (1997) reported apparent nest success for Snowy Plovers in the lower Laguna Madre region of Texas at 23% and 25% during two nesting seasons.

Wilson's Plovers occur only in the Americas and are uncommon breeders along the southern Atlantic, southern Pacific and Gulf coasts. They are listed as a species of high concern (Prioritization Category 4) by the United States Shorebird Conservation Plan (Brown et al. 2001). The primary threats to the species in the United States are habitat destruction as a result of coastal development and increased recreational use of beaches (Corbat and Bergstrom 2000).

Wilson's Plovers have been less well studied than Snowy Plovers, and relatively little is known about many aspects of the species' ecology. Bergstrom (1982, 1988) and Corbat (1990) provide information on the breeding biology of this species in Texas and Georgia, respectively. Wilson's Plovers nest on sparsely to moderately vegetated sand and mud flats in saline areas, including the front and back sides of primary dune lines and the edges of coastal bays and lagoons (Corbat and Bergstrom 2000). Corbat (1990) reported nest initiation to begin in mid-April in Georgia, and Bergstrom (1988) the first week in April in Texas, although nesting may begin as early as late March in this region (Hood 2006). Clutch size is typically three eggs, and the incubation period is estimated at 25 d (Tomkins 1965, Bergstrom 1988, Corbat 1990). Previous estimates of apparent nest success for Wilson's Plovers were 25% and 54% at two sites in Texas (Bergstrom 1988), and ranged from 11–55% for sites in Georgia (Corbat 1990).

For many shorebird species, including Snowy and Wilson's plovers, features of the nest site (e.g., the presence of a conspicuous object or the amount of vegetation near the nest cup) are often theorized to influence nest survival (Bergstrom 1982, Wilson-Jacobs and Meslow 1984, Page et al. 1985, Corbat 1990). The scale of interest is often the immediate nest site, and few investigations have examined the influence of habitat at larger scales (Knetter et al.

2002). In some cases, plover nesting success and nest-site selection have been correlated with the presence or absence of such features (Wilson-Jacobs and Meslow 1984). More often, habitat features are recorded and simply compared between successful and unsuccessful nests. In these cases, the hypothesized relationship between these habitat characteristics and the survival of the nest remains conjecture because the relationship is not quantified.

Given this context, the objective of our study was to estimate nest survival of Snowy and Wilson's plovers as a function of several external biological variables, and to test hypotheses concerning the effect of selected habitat features on nest survival. Biological variables of interest included temporal variation within year, nest age, temperature, precipitation, and habitat features measured at three spatial scales: (1) microhabitat-nest site (0.5-m radius buffer around nest), (2) macrohabitat (25-m radius buffer), and (3) landscape (800-m radius buffer). We illustrate the use of program MARK for modeling avian nest survival as a function of these variables, and the study results have important implications for the management of both species.

METHODS

STUDY AREA

The study area comprised the lower Laguna Madre region of southern Texas within portions of Cameron, Willacy, and Hidalgo counties. The area primarily included USDI Fish and Wildlife Service tracts within the Lower Rio Grande Valley National Wildlife Refuge complex, as well as some public and private lands. Study sites covered roughly 415 km^2 and included Laguna Atascosa National Wildlife Refuge, La Sal del Rey, East Lake, Brazos Island, Boca Chica-South Bay area, and South Padre Island (Fig. 1). La Sal del Rey and East Lake are hypersaline lakes located about 70 km inland which are used as breeding sites by Snowy Plovers. Birds use lake shorelines, areas surrounding salt evaporation ponds, and man-made limestone gravel, or caliche causeways for nesting. The shorelines are relatively bare but contain sparse patches of vegetation. The area immediately surrounding and slightly elevated from the shoreline is composed of a strip of grasses, shrubs, and succulents ranging from 5–30 m wide, leading into thorn-scrub woodland dominated by mesquite (*Prosopis* sp.).

The remaining study areas were the shorelines and associated flats of coastal bays (Laguna Madre and South Bay), and barrier island flats of Brazos Island and South Padre Island. In the barrier island habitats, both Snowy and Wilson's plovers nested in the area between the vegetated flats and the bayshore (the bay side of the island). A vegetated barrier flat extends from the fore dunes (or back dunes, if present) toward the tidal flats, and ranges in width from a few meters to a few kilometers before the vegetation becomes sparse and the barrier flats begin. Birds nested on these barrier flats, which typically contain tidal flats, high sand flats, algal flats, washover flats with channels, and/or active back-island dunes (Britton and Morton 1989). The flats surrounding South Bay closely resembled the habitat on the barrier islands. Mean annual precipitation near the center of the study area was approximately 71 cm for both coastal and inland sites (National Climatic Data Center 2003, 2004).

LOCATING AND MONITORING NESTS

We conducted field work from 8 March to 15 July 2003 and from 14 March to 14 July 2004. Nests were located by systematically driving a vehicle (truck or all-terrain vehicle) through suitable breeding habitat and periodically stopping to scan for plovers. We were careful to remain on makeshift roads or existing tire paths to minimize disturbance to the birds and their nesting areas. When we located an adult bird, we watched it return to its nest to pinpoint the exact location of the nest. In smaller areas or areas unsuitable for vehicles, we searched for nests on foot.

Upon locating a nest, we recorded its position with a hand-held global positioning system (GPS) unit (Magellan SporTrak Pro) and identified it with a small numbered wooden craft stick approximately 1–3 m from the nest. A circle with a 0.5-m radius (constructed of semirigid PVC pipe) was then centered over the nest and the area was photographed using a 2.1 megapixel digital camera. These photos were later used in microhabitat data interpretation.

We checked nests every 3–7 d until the eggs hatched or the nest failed. We considered a nest successful if ≥1 egg hatched. We assumed an incubation period of 26 d for Snowy Plovers (Boyd 1972, Page et al. 1983, Hill 1985, Warriner et al. 1986) which is also the mean incubation length for Snowy Plovers nesting in Florida (Gore and Chase 1989), an area of similar latitude. We assumed an incubation period of 25 d for Wilson's Plovers (Tomkins 1965, Bergstrom 1988, Corbat 1990). Sustained incubation does not begin in either species until the last egg in a clutch is laid (Bergstrom 1988, Page et al. 1995), so we estimated daily nest survival from the beginning of sustained incubation. We

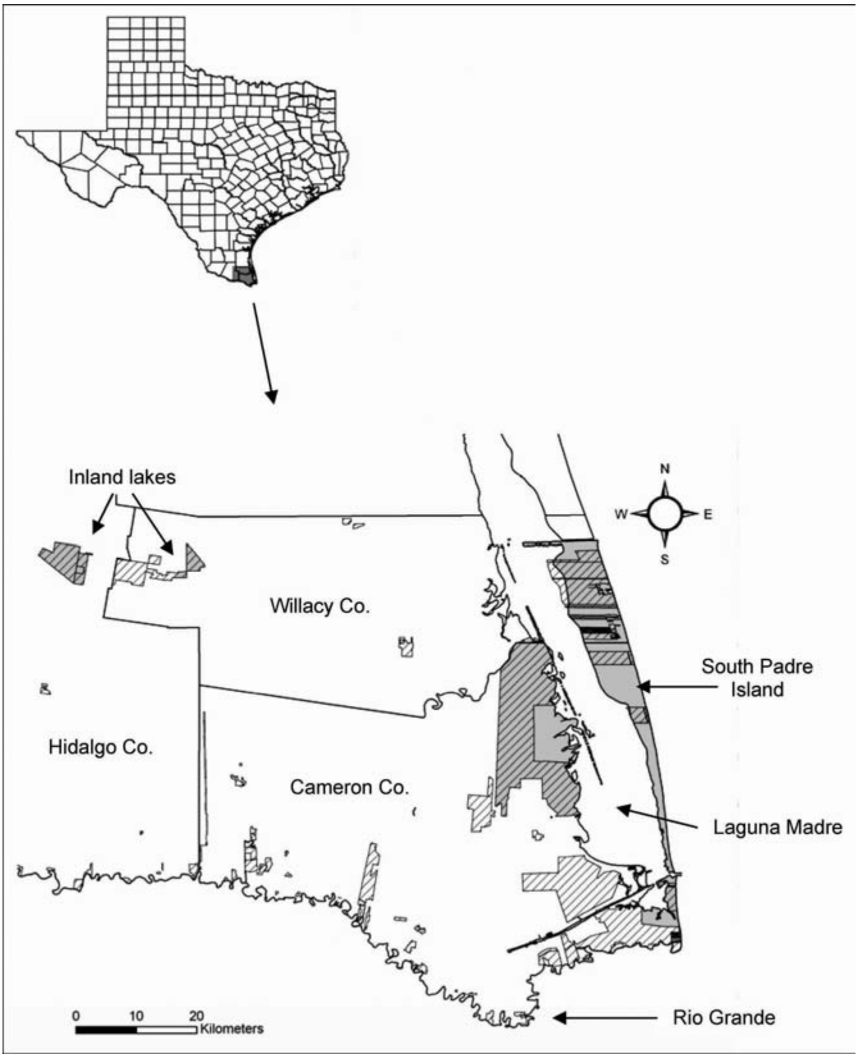

FIGURE 1. Map of Snowy and Wilson's plover study areas in the lower Laguna Madre region of Texas, 2003–2004. Study areas are shown in gray, USDI Fish and Wildlife Service properties are designated by hatch marks.

determined nest age for each species using egg flotation (Hood 2006). Using this float information we could correctly age most nests to within 1–2 d. For the small number of nests that failed between the day they were found and the day they were next checked, we assigned them the mean age of their incubation stage when they were found (Dinsmore et al. 2002). We determined nest fate using eggshell evidence (Mabee 1997) and hatch date using egg flotation or by finding young in or near the nest.

MICROHABITAT SCALE DATA

Photographs of the 0.5-m radius buffer area around each nest were digitized using ArcView GIS (version 3.2), and areas within each circle were placed into one of three classes: vegetation, bare ground, and objects or debris. We classified conspicuous objects and debris as any shell or rock larger than the nest cup, any nonliving woody debris, or any other non-natural item such as pieces of glass, plastic, and metal. The digitized images were then analyzed using FRAGSTATS (McGarigal and Marks 1995) to obtain metrics describing the proportions and distribution of these three classes within each buffered area. Metrics of interest were: percent vegetation (%vegM), presence or absence of a conspicuous object or debris (objectM), and contagion index. Contagion is a metric calculated in FRAGSTATS that describes the extent to which patch types are clumped within a landscape.

MACROHABITAT/25-M RADIUS DATA

We used line-intercept sampling (Canfield 1941) to measure various aspects of vegetation, substrate, and debris arrangement within a 25-m radius of each nest. We centered a 50-m measuring tape over the nest cup in a randomly chosen direction, and placed a second line perpendicular to the first, resulting in four 25-m transects radiating outward from the nest. By randomly placing these four transects, we collected data that were representative of a 25-m radius around the nest. These data were collected soon after the nest hatched or failed to reduce disturbance and to standardize measures between nests.

Continuous measurements were taken along each line, and the distance covered by each of the following variables was measured: (1) high (>30 cm, %highveg25) and low (<30 cm, %lowveg25) vegetation, (2) heterogeneity in low vegetation patch size (both linear and quadratic trends), indexed by the coefficient of variation for low vegetation (lowvegCV25) (Roth 1976), (3) bare ground (bare25), (4) substrate mixed with shells or gravel (shell/gravel25), (5) debris (debris25), and (6) roads (road25) and vehicle tracks (tracks25) as indicators of disturbance. We defined roads as well-established, regularly traveled pathways, and tracks as any marks left behind when a vehicle left the established roads and traveled over the sand flats. Roads were recorded as either present or absent within 25-m of a nest, and the number of vehicle tracks intersecting the measuring tape was recorded as an additional measure of disturbance.

LANDSCAPE-SCALE DATA

Using GPS coordinates collected for each nest, we placed nests onto a Landsat Enhanced Thematic Mapper 7 satellite image of the south Texas area from March 2003 (path 26, row 42). We buffered each nest by a radius of approximately 800 m (resulting in a circle 2 km^2 in area) using ESRI ArcMap (version 8.3). Using the supervised classification procedure in ERDAS IMAGINE (version 8.7) we classified areas as vegetation, water, or bare ground. We used high-resolution aerial photography (2004 1:24,000 Digital Ortho Quarter-Quads) as reference data to assess classification accuracy. Average overall classification accuracy was 67.0% for bare ground, 85.7% for vegetation, and 83.7% for water.

We then ran each classified and buffered nest area through FRAGSTATS to obtain metrics describing the landscape composition and configuration within 800 m of each nest. Metrics of interest were: percent bare ground (%bareL), percent vegetation (%vegL), total edge of water (total edge waterL), percent water (%waterL), and contagion index (contagionL). At the landscape scale, contagion index describes whether the landscape around the nest is composed of a few large patches or many smaller patches.

ADDITIONAL SOURCES OF VARIATION

In addition to the above habitat covariates specific to each nest, we examined the influence of five additional variables that were not related to habitat. These were: year, temporal variation within years (evaluated using a constant daily nest-survival model as well as linear (T) and quadratic (TT) trends), nest age (age), location (site), and maximum daily temperature, and daily precipitation. We monitored Snowy Plover nests at two very different locations—coastal areas and two inland lakes. We included location as a covariate because we believed differences in size and in densities of nesting birds between coastal and inland locations would result in differential nest survival. Wilson's Plovers were not present at the two inland lakes, so models for this species did not include a location effect. We obtained all weather data from the National Oceanic and Atmospheric Administration (National Climatic Data Center 2003, 2004). We used data from the Raymondville, Texas, weather station for inland Snowy Plover nests and averaged data from the South Padre Island and Brownsville, Texas, weather stations for all nests along the coast.

MODELING APPROACH

We used the nest-survival model in program MARK (White and Burnham 1999) to model the daily survival rates of Snowy and Wilson's plover nests. We standardized 19 March as day one of the nesting season for Snowy Plovers, and 31 March as day one for Wilson's Plovers. For Snowy Plovers, year and location were combined and modeled as groups, resulting in four groups (lakes and coast in both years). For Wilson's Plovers, only two groups were used, one for each year, because Wilson's Plovers did not nest at East Lake or La Sal del Rey. Snowy Plover nests were monitored from 19 March to 9 July (113 d) and Wilson's Plover nests from 31 March to 15 July (107 d) in both years.

We selected the best approximating model for inference in a three-stage, hierarchical modeling process using AIC$_c$ model selection

(Burnham and Anderson 2002). Our approach was the same for both Snowy and Wilson's plovers, but each species was analyzed separately. In the first stage, we evaluated possible sources of temporal variation in daily nest survival rates within years by constructing models with constant daily nest survival (analogous to a Mayfield estimate), a logit-linear time trend, and a logit-quadratic time trend. To the model that best described temporal variation within year, we added the other non-habitat, or main effects, singly. These included year, location (Snowy Plovers only), nest age, maximum daily temperature, and daily precipitation. If more than one of these effects emerged as competing models ($\Delta AIC_c \leq 2.0$), we combined those effects into an additive model to test the hypothesis that two (or more) variables together performed better than they had separately. To the best model from stage two we added each habitat covariate from the three spatial scales singly. For each species, we also included a model that combined the best performing covariate from each spatial scale into one additive model. We hypothesized that features from different spatial scales working in concert might be more important in explaining variation in nest survival than one feature at any single scale. We also developed three models for each species that reflected specific a priori hypotheses representing combinations of two covariates at each spatial scale that we thought might influence daily nest survival rates.

Snowy Plover

1. An additive model combining the presence or absence of an object and percent vegetation present at the microhabitat scale. We hypothesized that the presence of an object near the nest cup would have a positive effect on nest survival, and increasing amounts of vegetation would have a negative effect on nest survival.
2. An additive model combining the amount of shell or gravel and a quadratic trend on the heterogeneity index for low vegetation at the 25-m buffer scale. We hypothesized that a large amount of shell or gravel and a moderate level of heterogeneity would both have a positive effect on nest survival.
3. An additive model combining percent bare ground and percent water at the landscape scale. We hypothesized that nest survival would be positively influenced by large amounts of bare ground and large amounts of water at the landscape scale.

Wilson's Plover

1. An additive model combining percent vegetation and contagion index at the microhabitat scale. We hypothesized that smaller amounts of vegetation and low contagion values would result in higher daily nest survival rates, as this species seemed to prefer areas in which the vegetation present occurred in small patches and was spread out in a diffused manner.
2. An additive model combining percent low vegetation and the heterogeneity index for low vegetation at the 25-m buffer scale. As with the microhabitat scale, we hypothesized that low to moderate amounts of vegetation occurring in variably-sized patches (moderate coefficient of variation) would result in higher nest survival. If the amount of vegetation present around the nest is too great or it occurs in very large patches, the ability of the incubating adult to scan for predators and to quickly escape from the nest may be hindered.
3. An additive model combining percent water and percent bare ground at the landscape level. We hypothesized that larger amounts of bare ground and water at the landscape scale would result in higher daily nest survival.

We evaluated the strength of evidence for model variables included in our research hypotheses using the approach of Burnham and Anderson (2002). To illustrate the effects of the most important explanatory variables, we also predicted their influence on nest survival using the best model and reasonable ranges of a particular variable while keeping other variables constant.

RESULTS

We monitored 105 Snowy Plover nests and 94 Wilson's Plover nests during this 2-yr study with average apparent nest success being 55% and 69% for Snowy Plovers and Wilson's Plovers, respectively.

SNOWY PLOVER NEST SURVIVAL

We averaged five competing models with $\Delta AICc \leq 2.0$ across all candidate models to obtain estimates of any covariate effects and of daily nest survival rates (Table 1). The daily survival of Snowy Plover nests varied temporally and was a function of both location and nest age. A negative linear time trend was found in survival ($\hat{\beta}_T = -0.016$, SE = 0.006, 95% CI = 0.027, –0.005 on

TABLE 1. MODEL SELECTION RESULTS FOR THE NEST SURVIVAL OF SNOWY PLOVERS IN THE LOWER LAGUNA MADRE REGION OF TEXAS, USA, 2003–2004.

Model[a]	AIC_c[b]	ΔAIC_c	w_i[c]	K[d]	Deviance
S_T + age + site + objectM + low vegCV^{2}25 +% waterL	257.01	0.00	0.14	8	240.86
S_T + age + site + low vegCV^{2}25	258.48	1.47	0.07	6	246.39
S_T + age + site + % high veg25	258.53	1.52	0.07	5	248.47
S_T + age + site + objectM	258.62	1.61	0.06	5	248.56
S_T + age + site	258.97	1.96	0.05	4	250.93
S_T + age + site + % shell/gravel25	259.02	2.01	0.05	5	248.95
S_T + age + site + objectM + % vegM	259.10	2.09	0.05	6	247.01
S_T + site	259.11	2.10	0.05	3	253.08
S_T + age + site + % waterL	259.49	2.48	0.04	5	249.43
S_T + age + site + % vegM	259.50	2.49	0.04	5	249.44
S_T + age + site + low vegCV25	259.87	2.85	0.03	5	249.80
S_T + age + site + tracks25	260.11	3.10	0.03	5	250.05
S_T + age + site + debris25	260.17	3.16	0.03	5	250.10
S_T + age + site + low vegCV^{2}25 + % shell/gravel25	260.22	3.21	0.03	7	246.10
S_T + age + site + % bareL	260.30	3.28	0.03	5	250.23
S_T + age + site + road25	260.33	3.32	0.03	5	250.26
S_T + age + site + contagionL	260.56	3.55	0.02	5	250.49
S_T + age + site + % bare25	260.91	3.89	0.02	5	250.84
S_T + age + site + % vegL	260.93	3.92	0.02	5	250.86
S_T + age	260.95	3.94	0.02	3	254.92
S_T + age + site + contagionM	260.99	3.98	0.02	5	250.92
S_T + age + site + % lowveg25	260.99	3.98	0.02	5	250.93
S_T + age + site + total edge waterL	260.99	3.98	0.02	5	250.93
S_T + age + site + % bareL + % waterL	261.34	4.33	0.02	6	249.25
S_T + year	261.35	4.33	0.02	3	255.32
S_T	262.04	5.03	0.01	2	258.03
S_{TT}	262.76	5.75	0.01	3	256.74
S_T + temp	263.09	6.08	0.01	3	257.07
S_T + precip	263.20	6.19	0.01	3	257.18

[a] Models are ranked by ascending ΔAIC_c.
[b] Akaike's information criteria adjusted for small sample size.
[c] AIC model weight.
[d] Number of parameters.

a logit scale), indicating that daily nest survival rates decline slightly over the nesting season. The best overall model included age effects; the coefficient on age was positive but small ($\hat{\beta}_{age}$ = 0.03, SE = 0.02 on a logit scale) and its confidence interval contained zero, indicating the possibility of a weak effect of nest age on daily nest survival rates. Snowy Plover nests at the inland lakes had lower daily survival than those at coastal sites (Fig. 2).

The best approximating model contained habitat covariates at each of the three spatial scales measured. Nests that contained an object or debris at the immediate nest site had higher daily survival than those that did not. The estimate for the additive effect of an object within 0.5 m of the nest was $\hat{\beta}_{objectM}$ = 0.62 (SE = 0.30, 95% CI = 0.03, 1.21) on a logit scale. To illustrate the effects of nest age, location, and the presence or absence of an object, we plotted predicted daily survival rates using the logistic-regression equation with selected values of each variable. For nests early (nest age = 1) and late (nest age = 26) in incubation, we plotted daily survival of nests at the inland lakes (site = 1) and at coastal sites (site = 0) for nests with (object = 1) and without (object = 0) an object or debris within 0.5 m of the nest (Fig. 2).

The best approximating model also included a quadratic trend on the coefficient of variation (CV) for low vegetation at the 25-m radius scale. Daily nest survival decreased with increasing variability in low vegetation patch size, but then increased slightly at very high levels of vegetation patch size heterogeneity. This effect also appeared as the only habitat covariate in the second best model (ΔAIC_c = 1.47; w_i = 0.07), providing further support for the influence of this factor on daily nest survival. Using the logistic-regression equation from the best approximating model, we plotted daily survival of nests with selected low vegetation CV values. We held nest age and site constant (nest age = 1, site = 0, or coast) and varied the low vegetation CV value to predict daily nest survival rates at three levels of spatial heterogeneity of low vegetation within 25 m of the nest cup. The values 0, 200, and 400 that we chose for low vegetation

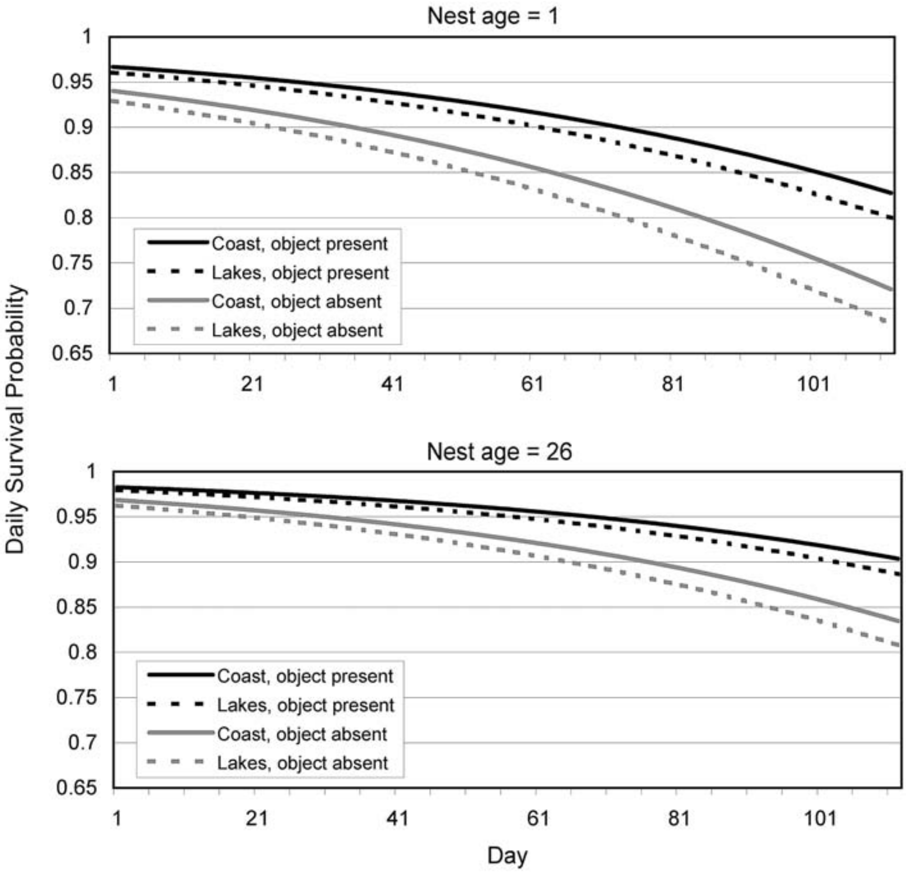

FIGURE 2. The effects of nest age (1- and 26-d-old nests), location (coast versus inland lakes), and the presence of an object within 0.5 m of the nest on the daily survival rates of Snowy Plover nests in south Texas, 2003–2004. Day one corresponds to 19 March, and day 112 corresponds to 9 July.

CV reflect the actual range of values observed in the field (range 0–385). Daily nest survival rates are lowest at medium levels of spatial heterogeneity of low vegetation, and highest at both low and high levels of heterogeneity (Fig. 3).

The landscape-level habitat covariate in the best approximating model was the percentage of water contained within 800 m of a nest. This effect was negative ($\hat{\beta}_{\mathrm{waterL}}$ = –0.02, SE = 0.01, 95% CI = –0.04, 0.01 on a logit scale), suggesting that daily nest-survival rates decreased as the proportion of water in the surrounding landscape increased. This effect is likely confounded by location, however, as nests at the inland lakes were surrounded by more water (mean = 35%, range = 7–56%) than those at coastal sites (mean = 10%, range = 0–36%) but also had lower nest survival than at coastal sites.

The remaining five competing models were three single-scale habitat models containing the same three effects present in the top model, a model with no habitat effects, and a single-scale habitat model including the amount of high vegetation present at the 25-m radius scale. The latter model ranked third, and the effect of high vegetation was negative ($\hat{\beta}_{\mathrm{high\ veg25}}$ = –0.08, SE = 0.05, 95% CI = –0.17, 0.02 on a logit scale), suggesting that daily nest survival is lower for nests with large amounts of high vegetation within 25 m. No statistical support was found for year effects or for the influence of daily precipitation or maximum daily temperature on Snowy Plover nest survival.

We used the logistic-regression equation from the best model to predict period survival (the probability of a nest surviving the 26-d incubation period) for Snowy Plovers at both the inland lakes and coastal nesting sites. We incorporated age and time effects, and held the effects of habitat covariates constant by multiplying the coefficients of each habitat covariate by the mean value of that covariate.

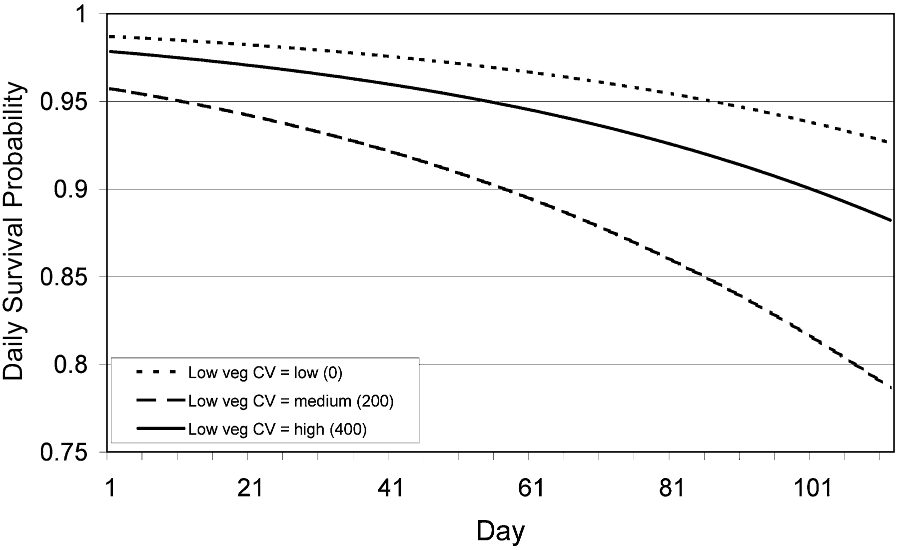

FIGURE 3. The effect of selected values of low vegetation heterogeneity (indexed by low vegetation CV) on the daily survival rates of Snowy Plover nests in south Texas, 2003–2004. Day one corresponds to 19 March, and day 112 corresponds to 9 July.

The covariate object was a categorical variable, however, and so we held its effect constant at 1, or present. The probability of a nest at each location surviving the entire 26-d incubation period (following initiation on day *x* of the nesting season) is illustrated in Fig. 4.

WILSON'S PLOVER NEST SURVIVAL

The nest survival of Wilson's Plovers was a function of both the amount and spatial structure of vegetation present at the microhabitat scale (Table 2). The model best describing temporal variation within the nesting season was the constant nest-survival model. Although the addition of several habitat covariates substantially improved the constant-survival model, only one model had $\Delta AIC_c \leq 2.0$ and it included the effects of percent vegetation and contagion at the microhabitat scale. Nests with less vegetation within a 0.5-m radius had higher survival than those with greater amounts. From the best overall model (w_i = 0.82), the coefficient on the effect of vegetation at the microhabitat scale was $\hat{\beta}_{\%\ vegM} = -1.35$ (SE = 0.47, 95% CI = –2.28, –0.42) on a logit scale. To demonstrate this effect, we used the logistic-regression equation from the best approximating model to predict daily nest survival at three different values of percent vegetation (10, 40, and 70%, chosen to reflect the range we observed in our study). When holding the effect of contagion constant, the predicted survival of a Wilson's Plover nest containing 10% vegetation within 0.5 m of the nest was 0.97 and this decreased to 0.50 at 40% vegetation and 0.03 at 70% vegetation.

Daily nest survival was higher for Wilson's Plover nests with low contagion at the microhabitat level. From the best model, the slope estimate for contagion at the microhabitat level was negative ($\hat{\beta}_{contagionM} = -0.87$, SE = 0.39, 95% CI = –1.65, –0.10 on a logit scale). To demonstrate this effect, we used the same approach as with vegetation (above), this time varying only the contagion values (50, 75, and 100%, again chosen to reflect the range we observed in our study) and keeping percent vegetation constant at the mean observed value. Predicted daily nest survival of a Wilson's Plover nest with 50% contagion at the microhabitat scale was 0.998 and this decreased to 0.987 at 75% and 0.930 at 100%.

No statistical support existed for year or age effects or for the influence of daily precipitation or maximum daily temperature on Wilson's Plover nest survival. We used the logistic-regression equation from the best model to compute the best estimate of nest survival for this species. We held the effects of habitat covariates constant by multiplying the coefficients of each habitat covariate by the mean value of that covariate. The predicted probability of a Wilson's Plover nest surviving the 25-d incubation period was 0.58, regardless of the date of nest initiation.

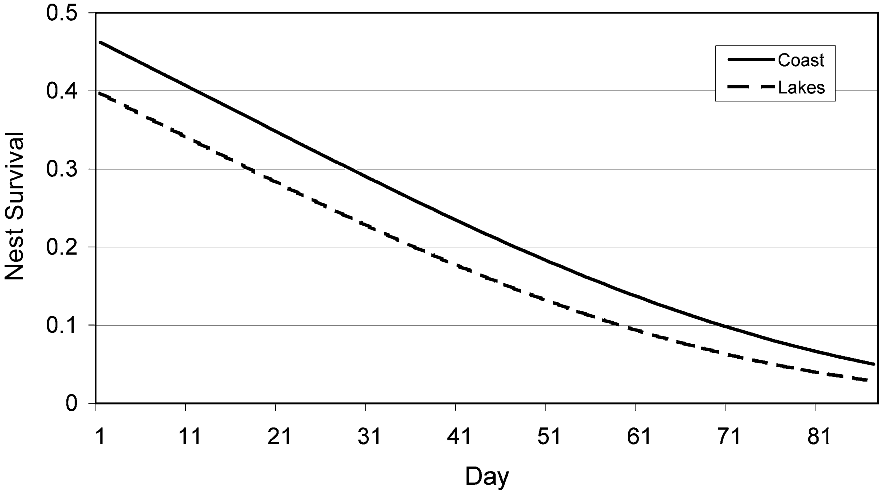

FIGURE 4. Predicted nest survival (the probability that a nest initiated on day *x* of the season survives the 26-d incubation period) for Snowy Plovers nesting at inland and coastal sites in south Texas, 2003–2004. Day one corresponds to 19 March, and day 87 corresponds to 13 June.

TABLE 2. MODEL SELECTION RESULTS FOR THE NEST SURVIVAL OF WILSON'S PLOVERS IN THE LOWER LAGUNA MADRE REGION OF TEXAS, USA, 2003–2004.

Model[a]	$\mathrm{AIC_c}$[b]	$\Delta\mathrm{AIC_c}$	w_i[c]	K[d]	Deviance
$S_{\%\ \mathrm{vegM} + \mathrm{contagionM}}$	202.18	0.00	0.82	3	196.16
$S_{\%\ \mathrm{vegM}}$	206.21	4.03	0.11	2	202.20
$S_{\%\ \mathrm{vegM} + \%\ \mathrm{high\ veg25} + \%\ \mathrm{vegL}}$	210.15	7.97	0.02	4	202.12
$S_{\%\ \mathrm{vegL}}$	212.25	10.07	0.01	2	208.24

[a] Models are ranked by ascending $\Delta\mathrm{AIC_c}$.
[b] Akaike's information criteria adjusted for small sample size.
[c] AIC model weight.
[d] Number of parameters.

DISCUSSION

SNOWY PLOVER

In the lower Laguna Madre region, Snowy Plover daily nest survival was influenced by location, the daily age of the nest, nest-initiation date, and habitat features at each of three spatial scales. At the inland lakes, nest survival over the 26-d incubation period ranged from 40% for a nest initiated on day one of the nesting season to 3% for a nest initiated on day 87 of the season (Fig. 4). Period survival at coastal sites ranged from 46% for nests initiated on day 1–5% for nests initiated on day 87 (Fig. 4). This supports our hypothesis that nest survival of Snowy Plovers was lower at the inland lake sites than at coastal sites. This location effect is likely due to differences in size and habitat structure between the two areas, and how these features affect the vulnerability of a nest to predation. During this study, the primary predator of nests of both Snowy and Wilson's plovers appeared to be the coyote (*Canis latrans*), based on observations of tracks leading directly to depredated nests. A potential mammalian predator might more easily locate plover nests while walking the narrow shoreline of a lake than while traversing the expansive sand and mud flats of a large barrier island or other coastal site. This arrangement of nesting habitat at the lakes also results in higher nest densities than in the coastal areas, which may also increase predation risk (Page et al. 1983).

The temporal trend reported in this study suggests a slight decline in daily nest survival during the nesting season. This trend may be the result of older, more experienced adults returning to the breeding grounds first. These individuals might be more likely to have successful nests because they are more experienced breeders or because they arrive early and occupy the best nesting sites (Nisbet et al. 1978). Other reasons for a decrease in nest survival during a season include a decrease in body condition of nesting adults as the season progresses (especially if females put significant energy into multiple re-nesting attempts) or a change in predator feeding preferences or behavior as a result of the birth and development of their young (Klett and Johnson 1982).

Our results indicate that nests further along in incubation may have higher survival; this pattern is similar to results observed in other plover species (Dinsmore et al. 2002). This relationship likely exists because these older nests have already been exposed to a risk period to which younger nests have not (Klett and Johnson 1982).

The strongest habitat effect we found for Snowy Plovers was the presence of a conspicuous object or debris within 0.5 m of the nest, which resulted in increased nest survival. Placement of nests next to conspicuous objects is a well-documented behavior in Wilson's and Snowy plovers, and may confer some advantage in survival of the nest (Bergstrom 1982, Winton et al. 2000). Our results provide quantitative evidence in support of this hypothesis. Page et al. (1985), however, found that Snowy Plover nests next to objects were more likely to fail than those under objects or in the open. They speculated that nest predators may use conspicuous objects as part of their search image, but acknowledged that this technique may benefit predators only where objects are not common. On the coastal beaches where the majority of nests in our study were located, debris and objects such as large shells are probably too numerous to be used in locating nests.

Beyond the immediate nest site, it is likely that the spatial structure and composition of the vegetation and other features also play a role in nest survival. The amount of high vegetation within 25 m of the nest received weak support as a predictor of daily nest survival, and Snowy Plover nest survival decreased with increasing amounts of high vegetation within 25 m of the nest. Although Snowy Plovers typically locate their nests in areas devoid of vegetation, some type of vegetation is usually located in the larger surrounding area, probably for use as a foraging area or brood-rearing habitat (Rupert 1997). This vegetation is usually <30 cm (considered high vegetation in this study) in height, however, probably because higher vegetation may conceal mammalian predators and reduce an incubating adult's ability to scan for potential predators.

When low vegetation is present within 25 m of the nest site, the structure of that vegetation may also influence nest survival. Nest survival was highest at very low levels of variation in low vegetation patch size, and generally decreased with increasing variation. At very high levels of heterogeneity, however, nest survival increased slightly. Heterogeneity in vegetation patch size translates into areas containing both very large and very small patches of vegetation. Most Snowy Plover nests in this study were not located within 25 m of vegetation, and it was these nest sites devoid of vegetation that were responsible for most of the values of low vegetation CV equal to or near zero. Those nests that were located near vegetation were typically on an area of sand or mud flat adjacent to an expanse of vegetated barrier flat. Vegetation present in these areas typically occurred along a gradient moving from very sparse on the margin of the sand flat to dense within the vegetated barrier flat, resulting in a very heterogeneous vegetation profile. Our results suggest that Snowy Plover nests located on bare sand flats or near the transition zone between vegetated and sand flats have higher nest survival than those in other vegetated areas. Nesting in or adjacent to open areas may offer incubating adults easier escape routes from the nest upon the approach of a predator. A Snowy Plover's low, crouched run and accompanying distraction display probably functions less efficiently if the incubating bird is forced to flee into vegetation where it may not be seen or which may impede its escape if the predator decides to pursue the adult.

The amount of water at a landscape scale was present in the top model, although we suspect that this effect was confounded with location. Nests at inland lakes all contained a large amount of water at the landscape scale ($\overline{x}$ = 35%, range = 7–56%) because they were all located around the edge of a lake. These nests also had lower daily survival rates than those along the coast. Nests in coastal areas contained, on average, much lower proportions of water ($\overline{x}$ = 10%, range = 0–36%). Because obvious differences in nest survival occurred in these two locations, we do not believe the amount of water present on a landscape level to be a true habitat effect, but rather a redundant effect of location.

WILSON'S PLOVER

Wilson's Plover daily nest survival in the lower Laguna Madre region was a function of the amount of vegetation present and the spatial distribution of the features around the nest, both at the microhabitat scale. Nest survival was higher when the vegetation at the immediate nest site was present in relatively small amounts. Greater amounts of vegetation can restrict the line of sight for an incubating bird scanning for predators, may impede rapid escape from the nest with the approach of a predator, and may also provide cover for potential predators.

Our results also showed strong evidence of the effect of contagion at the microhabitat level on nest survival of Wilson's Plovers. This metric describes the extent to which patch types are aggregated, or clumped within a landscape—in this case within a 0.5-m buffer area around the nest. High contagion values reflect the presence of a few large patches and low values indicate many small patches. Three patch types were measured for each nest (bare ground, vegetation, and object/debris), but the majority of nests (N = 58, 62% of total) did not contain an object or debris. For nests that did contain objects or debris, these features comprised only a small portion (usually only one patch) of the overall landscape. Taking this into consideration, the contagion metric essentially refers to the structure or clumpiness of vegetation and bare ground components at the nest site. Nest survival was higher for lower values of contagion, or for nests at which vegetation patches were spread out in a diffuse manner rather than present in large clumps. This supports our hypothesis that although Wilson's Plovers may place their nests in or near vegetation, the vegetation would be present in a smaller proportion than bare ground and in small diffuse patches rather than in large contiguous ones.

STUDY IMPLICATIONS

Our study has important implications for illustrating the use of contemporary nest-survival modeling approaches, and also for providing information needed for the conservation of Snowy and Wilson's plovers.

Our nest-survival modeling for Snowy and Wilson's plovers in program MARK illustrates the many advantages of this approach over traditional constant-nest-survival methods like those of Mayfield (1961). In particular, we were able to (1) rigorously test multiple models of nest survival using information-theoretic approaches, (2) fit complex models that included seasonal variation in nest survival and the effects of covariates at multiple spatial scales, and (3) use this information to predict how specific factors would be expected to influence the nest survival of these species. Ultimately, we hope our approach here provides a general example for the use of program MARK for a nest-survival analysis.

An understanding of the habitats needed for the continued survival and reproduction of a given species is a critical component of conservation planning. Our study provides the first estimates of nest survival for Snowy and Wilson's plovers in the lower Laguna Madre region of Texas as well as some important baseline information on how habitat characteristics may influence the nest survival of two plover species of conservation concern. Continued efforts to further our understanding of their habitat requirements and breeding ecology are necessary in order to develop effective methods for conservation of these and other shorebird species.

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