Snowy Plover Nest Site Selection, Spatial Patterning, and Temperatures in the Southern High Plains of Texas

David Saalfeld

Warren C. Conway
Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State Universtiy, Nacogdoches, Texas 75962, wconway@sfasu.edu

William P. Johnson

David A. Haukos

The Journal of Wildlife Management 76(8):1703–1711; 2012; DOI: 10.1002/jwmg.404

Habitat Relations

Snowy Plover Nest Site Selection, Spatial Patterning, and Temperatures in the Southern High Plains of Texas

SARAH T. SAALFELD,[1,2] *Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, P.O. Box 6109 SFA Station, Nacogdoches, TX 75962-6109, USA*

WARREN C. CONWAY, *Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, P.O. Box 6109 SFA Station, Nacogdoches, TX 75962-6109, USA*

DAVID A. HAUKOS,[3] *U.S. Fish and Wildlife Service, Department of Natural Resources Management, Texas Tech University, Lubbock, TX 79409-2125, USA*

WILLIAM P. JOHNSON,[4] *Texas Parks and Wildlife Department, P.O. Box 659, Canyon, TX 79015, USA*

ABSTRACT Snowy plover (*Charadrius nivosus*) populations have declined throughout their range, in part because of habitat degradation and poor nest success, making information regarding regionally specific nest site selection and spatial patterns important when considering habitat conservation and management guidelines. We determined nest site selection characteristics ($n = 180$) and examined spatial patterns ($n = 215$) of snowy plover nests in saline lakes in the Southern High Plains (SHP) of Texas. At 104 nests, we examined the influence of substrate type on nest temperatures and heat mitigation. Snowy plover nests were more likely to be found near an object, on pebble substrate, and with fewer plants than random sites. High use areas were generally located in areas with pebble substrate and on human-made or natural islands, berms, and peninsulas. Overall, nests placed on pebble substrate had lower temperatures during the day than nests placed on sand substrates. Nest placement on pebble substrate may be valuable to nesting snowy plovers, providing thermal advantages to incubating adults and depressing potentially high nest predation rates. Management guidelines for this region should emphasize the importance of addressing key elements of snowy plover nesting habitat including the presence of pebble substrate and reducing vegetation encroachment.

KEY WORDS *Charadrius nivosus*, logistic regression, nesting, nest site selection, nest temperature, saline lake, snowy plover, Southern High Plains of Texas, surface water.

Western snowy plovers (*Charadrius nivosus nivosus*) are ground nesting shorebirds that breed along the Pacific and Gulf coasts of North America, and at discrete inland locations throughout the Great Plains, west to California and north to Saskatchewan (Page et al. 2009). Currently, western snowy plovers are listed as threatened by the United States Fish and Wildlife Service along the Pacific Coast (U.S. Fish and Wildlife Service 1993) and as endangered, threatened, or a species of special concern by several states, including Washington, Oregon, California, Mississippi, Florida, and Kansas (see Page et al. 2009). The decline of western snowy plovers has been attributed in part to poor nest success and habitat degradation on breeding grounds (U.S. Fish and Wildlife Service 1993, Page et al. 2009). Nesting locations vary throughout their range and include coastal beaches, salt pans, river gravel and sand bars, salt flats, dredge spoil deposits, and edges of salt evaporation ponds and alkaline or saline lakes, reservoirs, and ponds (Page et al. 2009). Throughout North America, conservation guidelines typically focus on nesting habitat management, including creation and restoration of nesting habitat, substrate modification, and vegetation control (Mabee and Estelle 2000). However, threats, population trends, and management guidelines for nesting snowy plovers are only coarsely defined for interior nesting areas. As habitat varies among nesting locations, determining regionally specific nest site selection and spatial patterns is important when developing management guidelines for nesting snowy plovers.

Because most snowy plover nest failures are a result of predation (Page et al. 2009, Saalfeld et al. 2011), we would expect nest site characteristics to mitigate risks associated

Received: 2 May 2011; Accepted: 2 March 2012
Published: 15 May 2012

Additional supporting information may be found in the online version of this article.

[1]*E-mail: saalfeldst@gmail.com*

[2]*Present address: Manomet Center for Conservation Sciences, U.S. Fish and Wildlife Service, 1011 East Tudor Road, MS 201, Anchorage, AK 99503, USA.*

[3]*Present address: U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University, 205 Leasure Hall, Manhattan, KS 66506, USA.*

[4]*Present address: U.S. Fish and Wildlife Service, National Wildlife Refuge System, Division of Biological Sciences, P.O. Box 60906, West Texas A&M University, Canyon, TX 79016, USA.*

with this pressure. Snowy plovers can reduce risks of predation to themselves and nests by adjusting adjacency to objects (Page et al. 1985), spacing patterns (Page et al. 1983), distance to upland areas (Koenen et al. 1996), substrate type (Page et al. 1985; Colwell et al. 2005, 2011), and adjacency to vegetation (Amat and Masero 2004*b*). Whereas certain objects (e.g., driftwood, vegetation, rocks, etc.) can provide concealment from predators (Page et al. 1985, Flemming et al. 1992), some types of objects (e.g., debris lines or plants) may negatively affect nest success. For example, predators might associate these objects (e.g., debris lines) with nests or use these structures as travel corridors (Grover and Knopf 1982, Page et al. 1985, Winton et al. 2000). Additionally, large or tall objects (e.g., plants) might reduce the ability of incubating adults to detect predators (Götmark et al. 1995, Amat and Masero 2004*b*, Mayer et al. 2009).

Predator avoidance can also elicit variable responses in nest spacing. For species that cannot defend themselves or their nests, the most evolutionarily favorable strategies include the use of camouflage to prevent nest detection and spacing nests 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 (Göransson et al. 1975, Andersson and Wiklund 1978, Wiklund and Andersson 1980, Götmark and Andersson 1984). Snowy plovers exhibit multiple responses depending on predator type and approach, including crouching and running away from nests, as well as more conspicuous responses such as calling, flying, and distraction displays that often attract other snowy plovers (Page et al. 2009). Because of the plasticity of responses in snowy plovers, local predator communities may be more influential on nest spacing patterns. For example, most avian nest predators (e.g., ravens [*Corvus* spp.] and gulls [*Larus* spp.]) have greater success when nests are clustered and colony size is large, because of ease of finding clustered nests from the air, reliability of prey for an extended time, and an aggregation of avian predators at prey sites (Tinbergen et al. 1967, Page et al. 1983). Compared to avian predators, mammalian predators (e.g., coyotes [*Canis latrans*]) have more success preying upon solitary nests, as solitary nests are less detectable and mammals often locate nests by scent or happenstance (Page et al. 1983). Therefore, populations of the same species may exhibit variable nest spacing patterns depending on local predator communities (Rippin Armstrong and Nol 1993).

In addition to minimizing predation, nest sites often provide an appropriate microclimate for incubation (Amat and Masero 2004*b*). Nesting snowy plovers in the Southern High Plains (SHP) of Texas are exposed to high ambient temperatures in a thermally stressful nesting environment (Saalfeld 2010). In this region, nests often reach temperatures outside thermally moderate zones (i.e., 31–40° C), and adults must attend nests constantly to avoid eggs reaching lethal temperatures (Purdue 1976*b*). Several adaptive behaviors have developed to allow incubating parents, eggs, and chicks to cope with extremely high temperatures including biparental incubation, shading nests, belly soaking, standing in water, panting, and gular fluttering (Maclean 1975; Kainady and Al-Dabbagh 1976; Purdue 1976*a*, *b*; Amat and Masero 2004*a*). These behaviors are physiologically costly (i.e., increased energy expenditure; Hinsley and Ferns 1994) and conspicuous, potentially increasing predation risks for adults and nests. Therefore, thermally favorable nest sites (e.g., shaded nests) are often selected to alleviate heat stress. However, selection of such sites might reduce the ability of incubating adults to detect predators (Götmark et al. 1995, Amat and Masero 2004*b*, Mayer et al. 2009). As an alternative, selecting nest sites with specific substrate characteristics may simultaneously improve crypsis and alleviate heat stress (Page et al. 1985, Mayer et al. 2009). Nests on heterogeneous substrates are more camouflaged and experience lower predation rates than nests located on more homogeneous substrates or in vegetated areas (Bowman and Harris 1980; Page et al. 1985; Colwell et al. 2005, 2011), and pebble substrates generally have lower temperatures than sand substrates (Page et al. 1985, Mayer et al. 2009). Selection of pebble substrate for nest placement may allow snowy plovers to simultaneously alleviate heat stress and minimize predation.

A large proportion of the interior population of snowy plovers nest within and migrate through saline lakes within the SHP of Texas (Conway 2001, Conway et al. 2005*a*). However, habitat quality of saline lakes has declined, making many of them unsuitable for migrating (Andrei et al. 2008) and nesting shorebirds. Saline lakes within this semi-arid region are discharge wetlands containing springs fed by the Ogallala aquifer (Brune 2002), but having an overall saline water chemistry (Osterkamp and Wood 1987). Historically, many springs provided reliable freshwater during the avian breeding season (Brune 2002). However, declining spring flow because of decreasing water table levels of the aquifer has occurred since the 1950s (Brune 2002), resulting in shortened hydroperiods, reduced water area, 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. 2005*a*). Freshwater springs not only provide reliable and necessary surface water during the breeding season (Conway et al. 2005*b*), but also reduce vegetation encroachment on saline lakes. Land use practices surrounding saline lakes have important implications for structuring saline lake habitat. For example, removing vegetation in upland areas surrounding saline lakes for agricultural production, mining, and development increases wind and water erosion rates during locally severe weather events. Therefore, to develop regional management and conservation guidelines for inland populations of snowy plovers, managers must determine relationships between habitat characteristics and current nest site selection patterns as they may relate to current land use practices. The objectives of our study were to 1) determine habitat characteristics influencing the probability of snowy plover nest placement; 2) examine spatial patterns of snowy plover nests in relation to substrate type and proximity to conspecific nests; and 3) evaluate the effectiveness of substrate type for heat mitigation in the SHP of Texas.

STUDY AREA

The SHP is an approximately 80,000 km^2 region in the western Texas panhandle, south to Midland, Texas, and into New Mexico (see Fig. 1; Osterkamp and Wood 1987). This region contains approximately 40 saline lakes (Reeves and Temple 1986) where snowy plovers nest (Conway et al. 2005*a*). In 2008 and 2009, we conducted our study at 3 saline lakes (lakes A, B, and C) that historically have consistent surface water throughout the nesting season and contain the majority of regional nesting snowy plovers (Conway et al. 2005*a*). Lakes A, B, and C were located within close proximity to one another (<40 km) and ranged in size from approximately 270 to 600 ha. Each study site lake contained 2–6 fresh to slightly saline springs distributed along lake margins (Brune 2002). The primary land use surrounding study site lakes was pasture and grassland with some held in the United States Department of Agriculture Conservation Reserve Program. Other land uses in surrounding areas included row-crop agriculture production (mostly cotton [*Gossypium* spp.]), mineral excavation (e.g., caliche), and development (mostly small home and ranch developments).

Weather conditions were similar between 2008 and 2009, with April–July temperatures in the city of Tahoka (Lynn County, Texas), the closest city to all 3 study site lakes (<40 km), ranging from 1.1 to 39.4° C in 2008 and −2.8 to 40° C in 2009. Cumulative rainfall in the city of Tahoka in April–July 2008 and 2009 was 19.7 cm and 19.1 cm, respectively, with the greatest amount of precipitation occurring in May in 2008 (11.3 cm) and in July in 2009 (8.8 cm). Drought conditions were present in both years of this study, with cumulative rainfall in the city of Tahoka from January to 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, accessed 25 Feb 2010; station ID # 418818; Tahoka, Texas).

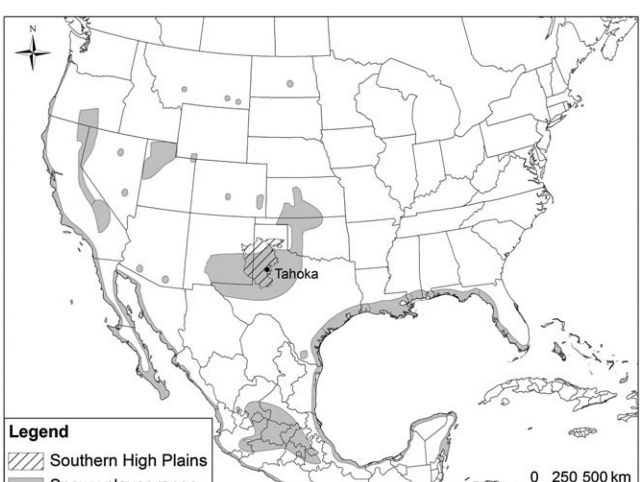

Figure 1. Distribution of snowy plovers in relation to the Southern High Plains. Snowy plover distribution maps obtained from NatureServe (Ridgely et al. 2007).

METHODS

Nest Surveys

To locate nests, we conducted surveys at least once per week at each lake between early April and mid-August in each year, with search effort remaining consistent within and among lakes. We located nests by observing adult snowy plovers incubating nests, flushing from or returning to nests, and searching appropriate habitat (Conway et al. 2005*a*). To compare nest sites with habitat available, we generated an equal number of random sites per year and study site using Hawth's Analysis Tools in ArcGIS 9.2 (Beyer 2004). We restricted random sites to sparsely vegetated areas (i.e., away from highly vegetated freshwater springs) between uplands and the average high water mark digitized from 2004 National Agriculture Imagery Program (NAIP) digital orthophoto quarter-quadrangle aerial photographs (Texas Water Development Board 2004).

Nest Habitat Measurements

After we determined nest fate (i.e., hatching or failure) for a companion study, we recorded the following habitat characteristics at nest and random sites: primary nest substrate (i.e., sand or pebble) and presence or absence of an object within 15 cm of nest or random site. We centered a 30-cm diameter hoop on each nest and random site, and took 2 photographs with a digital camera. Using photographs, we counted all rocks (i.e., >8 cm diameter), pebbles (i.e., <8 cm diameter; includes gypsum), plant stems, and other objects (i.e., woody debris, cow feces, feather and bone, clumps of soil, and human-made objects) within 15 cm of the nest or random site. Nesting snowy plovers often bring additional objects (e.g., pebbles) into the nest scrape (Page et al. 2009), increasing pebble density within the nest as incubation progresses. As we wanted to determine habitat selection patterns of snowy plovers during nest initiation, prior to the inclusion of additional objects in the nest, we did not count objects located within the nest scrape. We could not determine the original location of objects brought into the nest, some objects may have been present within 15 cm and used for initial nest site selection; however, we are unsure how often this occurred. To remain consistent with nest sites, we placed a circle the same size as an average nest scrape (i.e., 10.4-cm diameter) in the center of the hoop at random sites and did not count objects within.

We obtained Global Positioning System (GPS) locations for each nest using a Trimble GeoXH GPS unit (Trimble Navigation Ltd, Sunnyvale, CA). We calculated distance to nearest upland using Euclidian distance to nearest upland edge. We digitized upland boundaries using 2004 NAIP digital orthophoto quarter-quadrangle (DOQQ) aerial photographs (Texas Water Development Board 2004).

Nest Temperature Determination

We placed Thermochron iButtons (Model DS1922L; Maxim Integrated Products, Inc., Sunnyvale, CA) within a subset of nests upon discovery. We attempted to place temperature probes in as many nests as possible, distributing them among and within lakes and laying dates throughout the nesting season. To estimate ambient substrate temperatures and determine the effects of incubation, we placed an equal number of iButtons at control sites <2 m from nests with similar microhabitat (e.g., substrate type, vegetative cover, etc.). Similar to Schneider and McWilliams (2007), we attached iButtons to galvanized nails with Velcro to deter removal by adults. We placed all iButtons just beneath (<2 cm) the substrate in the nest (adjacent to or underneath eggs) or control location to minimize negative effects (i.e., predator detection, heat conductance, or disturbance to incubating birds) of iButtons being visible on the surface. We programmed iButtons to record temperatures at ≤1-hour intervals; however, to remain consistent among nests, we included only 1-hour intervals in analyses.

Data Analysis

Nest site selection.—We used logistic regression to identify habitat variables that were most likely to predict snowy plover nest site selection (PROC LOGISTIC; SAS Institute, Cary, NC). We developed a set of 24 candidate models, a priori, consisting of biologically relevant combinations of habitat variables including presence or absence of an object within 15 cm of the nest or random site (coded: presence = 1, absence = 0), substrate type (coded: pebble = 1, sand = 0), distance to upland, and number of pebbles or rocks, number of plants, and total number of objects within 15 cm of the nest or random site. We did not include correlated ($P \leq 0.05$; Pearson correlation; PROC CORR; SAS Institute) variables in the same model. We used Akaike's Information Criterion corrected for small sample size (AIC_c) to compare candidate models (a model was considered plausible when $\Delta AIC_c < 2$; Burnham and Anderson 2002). We present parameter estimates, standard errors, confidence intervals, and odds ratios from plausible models. We determined parameter likelihoods using model averaging (sum of model weights for models that included a given parameter; Burnham and Anderson 2004). We used the Hosmer and Lemeshow goodness-of-fit statistic to test for goodness-of-fit of the most supported model (PROC LOGISTIC). We estimated accuracy of plausible models 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.

Nest spatial patterning.—For each nest, we determined the distance to the nearest active (i.e., day first egg was laid to day hatched or failed) nest using Hawth's Analysis Tools (Beyer 2004). To locate areas of high use, we constructed kernel density estimates in ArcGIS 9.2 (Environmental Systems Research Institute, Inc., Redlands, CA) using a consistent output cell size (6 m × 6 m) and search radius (50 m) for each lake and year separately. We used kernel densities to visually assess high use areas in relation to nest substrates.

Nest temperatures.—To include only nest temperatures during which parental incubation occurred, we truncated temperature data. For nests that failed, we truncated to 0700 hours the morning we last observed the nest active, and for nests that hatched, we truncated to 0700 hours the morning nests hatched. Additionally, we classified temperature data as day (0700–2059 hours) or night (2100–0659 hours). We calculated the effect of incubation and adult attendance on nest temperatures by subtracting paired control temperatures from nest temperatures, hereafter referred to as incubation value. Within months, we examined 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 between substrate type (i.e., pebble or sand) 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). As we did not detect variation in the above metrics between years ($P > 0.05$), we did not include year as a covariate in our analysis.

RESULTS

Nest Site Selection

We located 215 snowy plover nests and associated random sites, 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). We obtained complete habitat data from 180 nests (34 from lake A, 105 from lake B, and 41 from lake C); rain events altered habitat conditions prior to measurements at 35 nests, which we excluded from analysis. Nearly all nests (97% at lake A, 95% at lake B, and 98% at lake C) were located within 15 cm of an object (i.e., pebble, rock, plant, woody debris, bone, feather, cow feces, coyote feces, clump of soil, and human-made object). Additionally, more nests had pebble substrate and objects (e.g., rocks, pebbles, etc.) and fewer plants than random sites (Table 1).

Among 24 candidate models, 2 models were highly supported ($\Delta AIC_c < 2$; Table 2). The odds ratios from the top

Table 1. Percentage of snowy plover nests or random sites that contained substrate type and objects within 15 cm of the nest or random site on saline lakes within the Southern High Plains of Texas, USA, 2008–2009.

	% of total	
	Nest (n = 180)	**Random (n = 215)**
Substrate type		
Sand	43.3	91.2
Pebble	56.7	8.8
Objects		
Pebble or rock	83.3	38.6
Pebble	83.3	38.6
Rock	41.7	1.9
Plant	11.1	19.1
Other	70.6	41.9
Woody debris	57.8	35.3
Cow feces	4.4	0.0
Feather and bone	23.9	4.7
Clump of soil	6.1	10.2
Human-made object	3.9	0.5
Any object	96.1	52.1

Table 2. Logistic regression models for habitat variables predicting snowy plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008–2009.

Model	K^a	AIC_c	ΔAIC_c^b	w_i^c
Object + substrate + no. plants	4	380.44	0.00	0.44
Object + substrate + no. plants + total no. objects	5	381.72	1.27	0.23
Object + substrate + dist. upland	4	383.05	2.61	0.12
Object + substrate	3	383.81	3.37	0.08
Object + substrate + no. pebbles/rocks	4	384.06	3.62	0.07
Object + substrate + total no. objects	4	384.83	4.38	0.05
Object + no. plants + total no. objects	4	407.34	26.89	0.00
Object + no. pebbles/rocks	3	418.28	37.83	0.00
Object + total no. objects	3	419.00	38.55	0.00
Object + no. plants	3	420.27	39.82	0.00
Object + dist. upland	3	432.15	51.70	0.00
Substrate	2	436.56	56.11	0.00
Substrate + no. pebbles/rocks	3	436.97	56.52	0.00
Object	2	438.08	57.63	0.00
Substrate + dist. upland	3	438.31	57.87	0.00
Substrate + total no. objects	3	438.51	58.06	0.00
Substrate + no. plants	3	438.52	58.07	0.00
Substrate + no. plants + total no. objects	4	440.50	60.05	0.00
No. plants + total no. objects	3	482.92	102.47	0.00
Total no. objects	2	483.77	103.33	0.00
No. pebbles/rocks	2	490.15	109.71	0.00
Dist. upland	2	513.49	133.05	0.00
No. plants	2	542.86	162.42	0.00
Intercept	1	546.49	166.05	0.00

[a] No. of parameters.
[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.

model predicted that a location with an object within 15 cm was 14 times more likely to be selected for nest placement than a location without an object. Similarly, a location on pebble substrate was 6 times more likely to be selected for nest placement than a location on sand substrate. However, selection of a location for nest placement was less likely (odds ratio = 0.98) with each additional plant within 15 cm (Table 3). In the second model, the odds ratio (1.0) predicted that total number of objects within 15 cm did not have an effect on the likelihood of selection. Additionally, 95% confidence intervals overlapped zero, suggesting total number of objects within 15 cm of a nest or random site was an uninformative and insignificant parameter to snowy plover nest site selection. For all other parameters, 95% confidence intervals did not overlap zero, suggesting a significant effect of presence of an object, substrate type, and number of plants within 15 cm of a nest on nest site selection. Parameter likelihoods also indicated that presence of an object (likelihood = 1.0), substrate type (likelihood = 1.0), and number of plants within 15 cm of a nest or random site (likelihood = 0.68) were the most influential variables included in the models receiving the most support. However, total number of objects within 15 cm of a nest or random site was a less influential variable (likelihood = 0.28). The logistic regression model correctly predicted nest and random sites based on presence of an object, substrate type, and number of plants within 15 cm of a nest or random site with 75.9% accuracy. Adding total number of objects within 15 cm of a nest or random site to the most likely model did not increase overall accuracy (75.9%). The Hosmer–Lemeshow goodness-of-fit statistic suggested that the most likely model fit the data ($P = 0.73$).

Table 3. Parameter estimates (β), standard error, lower and upper 95% confidence intervals, and odds ratios of habitat variables included in logistic regression models predicting the location of snowy plover nests on saline lakes within the Southern High Plains of Texas, USA, 2008–2009.

Parameter	β	SE	Lower	Upper	Odds ratio
Top-ranked model					
Intercept	−2.759	0.394	−3.532	−1.987	
Object	2.672	0.427	1.835	3.509	14.47
Substrate	1.846	0.307	1.245	2.447	6.33
No. plants	−0.025	0.012	−0.048	−0.002	0.98
Second-ranked model					
Intercept	−2.721	0.394	−3.492	−1.949	
Object	2.687	0.428	1.848	3.525	14.69
Substrate	2.118	0.447	1.242	2.994	8.31
No. plants	−0.025	0.012	−0.047	−0.002	0.98
Total no. objects	−0.001	0.001	−0.003	0.001	1.00

Nest Spatial Patterning

Most (57%) snowy plover nests were located within 100 m of the nearest active nest ($\bar{x} = 144.1$ m; range = 5.6–1,810.9 m; $n = 215$; Fig. 2). In general, kernel density estimates for all lakes and years showed high use areas corresponded with areas of pebble substrate and natural or human-made islands, berms, and peninsulas (see Fig. 3 for lake B; for lakes A and C see Figs. S1 and S2, available online at www.onlinelibrary.wiley.com).

Nest Temperatures

We placed iButtons in 104 nests and control sites (20 in 2008 and 84 in 2009; 22 in lake A, 65 in lake B, and 17 in lake C) between 12 June and 26 July 2008, and 1 May and 5 August

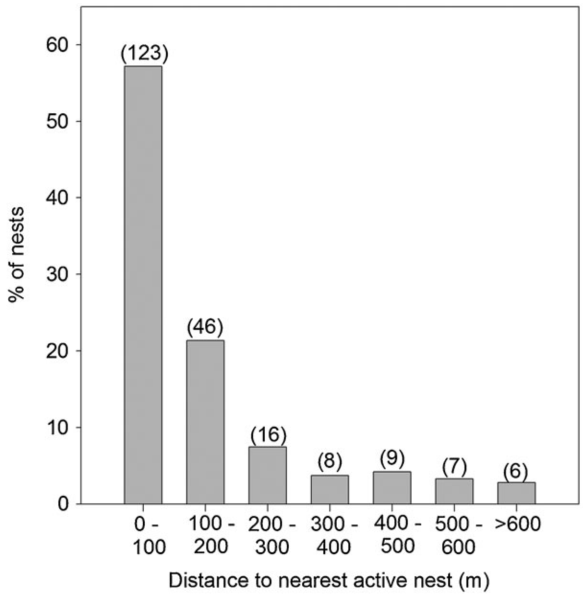

Figure 2. Percentage of snowy plover nests ($n = 215$) in relation to distance to nearest active nest on saline lakes within the Southern High Plains of Texas, USA, 2008–2009. Numbers above bars correspond to sample sizes of nests within distance categories.

2009, and recorded 15,312 hours of temperature data over 142 days. Nest temperatures ranged from 12.2° C to 47.2° C (12.2–47.2° C during day, 12.7–39.2° C during night), and control temperatures ranged from 6.7° C to 54.0° C (6.7–54.0° C during day and 7.2–38.6° C during night). In general, nest and control temperatures (both day and night) were greater on sand than pebble substrate, with significant differences between sand and pebble substrates observed for day and night nest temperatures in July and day and night control temperatures in June and July (Fig. 4). During the day, nests were kept cooler than controls, with a greater temperature difference between paired nests and controls occurring on sand substrate, but only significant in June. Conversely, during night, nests were kept warmer than controls, with a greater temperature difference between paired nests and controls occurring on pebble substrate, but only significant for June (Fig. 5).

DISCUSSION

Similar to previous studies (see Page et al. 2009), almost all (96%) snowy plover nests were adjacent to an object. In our study, presence of an object, substrate type, and number of plants within 15 cm of a nest were the key habitat variables 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 in the SHP of Texas may gain protection against extreme weather (e.g., wind, hail, and rain; Flemming et al. 1992, Norte and Ramos 2004), concealment from predators (Page et al. 1985, Flemming et al. 1992), and perhaps enhanced visual cues to incubating adults for nest relocation (Grover and Grover 1982). However, like

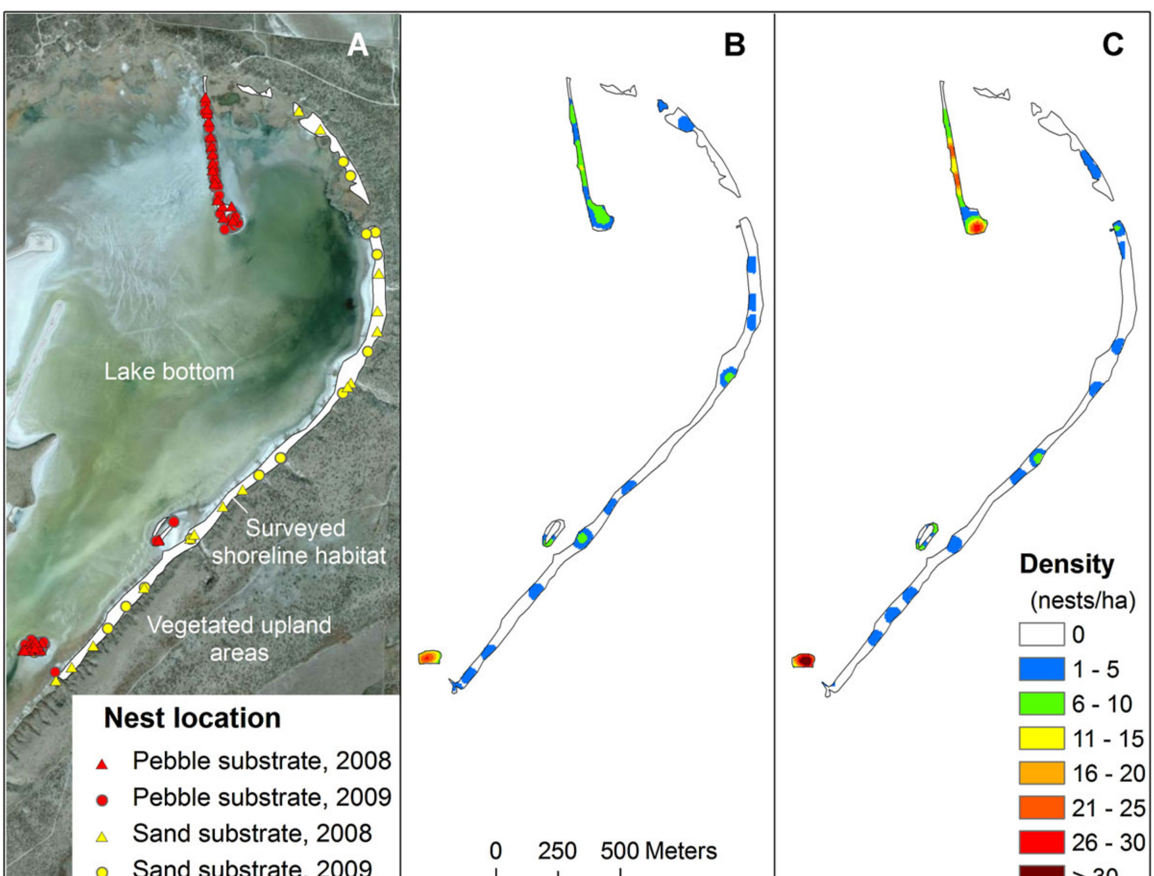

Figure 3. Snowy plover nest locations, 2008–2009 (A), and kernel density estimates on lake B within the Southern High Plains of Texas, USA, 2008 (B) and 2009 (C).

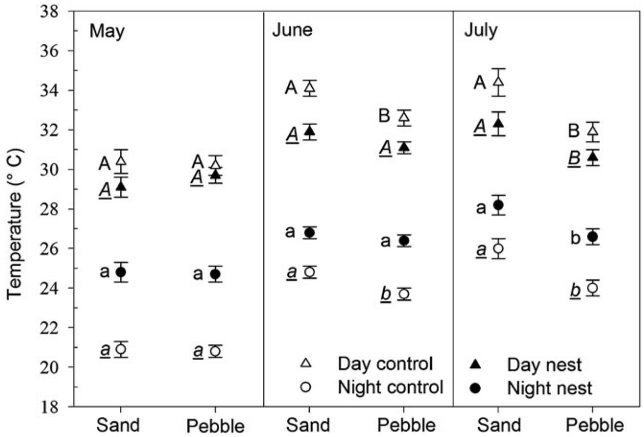

Figure 4. Least squares estimates and standard errors of snowy plover day and night nest and control temperatures by substrate type and month on saline lakes within the Southern High Plains of Texas, USA, 2008–2009. Estimates with same letters (of the same case and font) within a month are not different ($P > 0.05$; least squares cross validation).

many studies (Hill 1985, Paton 1994, Conway 2001, Powell 2001, Norte and Ramos 2004), nesting near objects did not affect nest success in the SHP of Texas (Saalfeld et al. 2011). Advantages gained by nesting near objects may only be beneficial in environments saturated with objects, so that systematically searching objects would not be cost effective for predators searching for nests (Page et al. 1985). In the SHP of Texas, nesting habitat is not saturated with objects and predators often search appropriate habitat (i.e., debris lines) for nests. Placing nests near objects may be an artifact of species-wide evolutionary selection and predation pressures or geographical selection and predation pressures (Paton 1994), and hence, have little effect on present nest success for snowy plovers nesting within the SHP of Texas (Saalfeld et al. 2011).

Given that snowy plovers select nest sites close to objects, it seems intuitive that plants would also provide advantages from disruptive effects in addition to benefits from shading

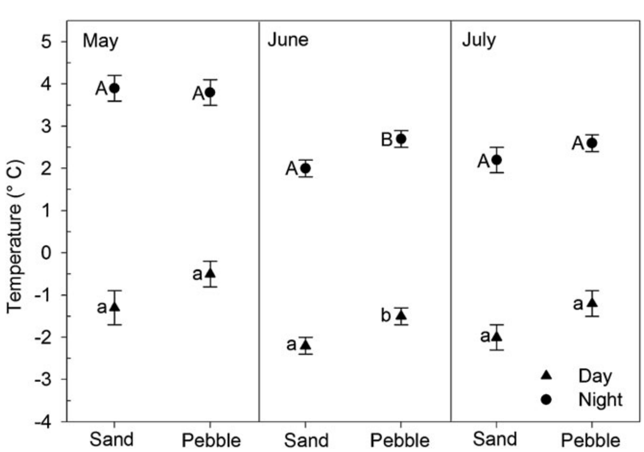

Figure 5. Least squares estimates and standard errors of snowy plover day and night incubation values (i.e., difference between paired nest and control temperature) by substrate type and month on saline lakes within the Southern High Plains of Texas, USA, 2008–2009. Estimates with same letters (of the same case) within a month are not different ($P > 0.05$; least squares cross validation).

(e.g., smaller temperature fluctuations; Amat and Masero 2004*b*). However, incubating adults may be more susceptible to predation while incubating nests near plants because of reduced detection of approaching predators (Amat and Masero 2004*b*). 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. 1996, Mabee and Estelle 2000, Hood and Dinsmore 2007), perhaps because of regional differences in predator communities and behavioral responses to predators among prey species (Mabee and Estelle 2000). In the SHP of Texas, snowy plover nest success was negatively influenced by the presence of plants near nests (Saalfeld et al. 2011). Therefore, despite the thermoregulatory advantages of placing nests near plants, snowy plovers avoid nesting locations with plants, potentially increasing their nest success.

Selection of pebble substrate type by snowy plovers may be a compromise to simultaneously improve crypsis and alleviate heat stress to incubating adults and eggs (Page et al. 1985, Mayer et al. 2009). However, substrate type did not influence nest success in the SHP of Texas (Saalfeld et al. 2011), despite heterogeneous substrates (e.g., pebble) being shown to contribute to nest 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, 2011). Nonetheless, substrate type allowed snowy plovers to alleviate heat stress during incubation, with pebble substrates up to 2.5° C cooler than sand substrates during the day. Similarly, selection of light colored pebbles with greater heat reflectance provided thermal benefits for piping plover (*Charadrius melodus*) nests, with nests remaining 2–6° C cooler than surrounding substrate (Mayer et al. 2009). These selection patterns became increasingly influential as the season progressed and ambient temperatures increased, more often reaching temperatures outside the thermal moderate range; 30% of temperature readings in May, 40% of temperature readings in June, and 36% of temperature readings in July were >40° C. Although substrate type did not influence nest success (Saalfeld et al. 2011), snowy plovers cluster nests on pebble substrate and probably gain thermoregulatory benefits during incubation.

Similar to previous studies (Powell 2001, Norte and Ramos 2004), the majority (57%) of snowy plover nests were located <100 m from the nearest active nest. Although nest success of snowy plovers generally improves when nests are placed close to conspecifics (Powell 2001), the distance to nearest nest was unrelated to success in the SHP of Texas (Saalfeld et al. 2011). Spatially separated populations of the same species may experience different predation risks when nesting communally, because of local predator community and predation pressures (Rippin Armstrong and Nol 1993). Within the SHP of Texas, snowy plovers may use a mixed-strategy for nest clustering, with some nests placed close to conspecifics, and others placed in isolation. Clustering of nests may result in decreased predation by mammalian predators (Page et al. 1983, Brunton 1997).

However, predation by avian predators (i.e., ravens and black-crowned night herons [*Nycticorax nycticorax*]) seems to have increased in recent years (Saalfeld et al. 2011). 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 dispersed distribution.

Nest clustering may be an artifact of population density if nest site availability becomes limited as population size and density increases (Page et al. 1983). Although regional populations of snowy plovers nest on saline lakes, which are numerically limited, no evidence exists to suggest that these lakes are saturated, where clustering occurs because of limited space. 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 chicks (e.g., decreased predation risks and temperature control), these areas are often preferred. However, pebble substrate is generally limited at individual saline lakes, and nests can become clustered. Additionally, selection of human-made or natural islands, berms, and peninsulas that are farther from lake edges or upland areas may reduce nest predation rates because these areas may be inaccessible to land-based predators during times of high water.

MANAGEMENT IMPLICATIONS

The use of pebble substrates for nesting snowy plovers in the SHP of Texas provides thermoregulatory benefits during incubation. Habitat enhancement through substrate modification (i.e., restoring pebble substrate areas lost to sand deposition) could be explored as a means to maintain current nesting habitat, as well as reduce thermal stress to incubating adults. As current land use practices surrounding saline lakes (e.g., agriculture, mining, development, etc.) can affect both wind and water erosion rates, conservation guidelines for this region should focus on landowner incentives (e.g., U.S. Department of Agriculture Conservation Reserve Program) to maintain vegetation in surrounding uplands that could decrease sedimentation of saline lakes. However, as vegetation encroachment may have serious impacts to nesting snowy plovers, maintaining natural fire regimes within vegetated upland areas may reduce vegetation encroachment on saline lakes within this area. Furthermore, flooding events may decrease vegetation growth on saline lakes (Faanes 1983); however, these events depend on unpredictable weather as well as surface flow and groundwater seepage.

ACKNOWLEDGMENTS

Financial, logistical, and technical support was provided in part by the Texas Parks and Wildlife Department, Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, the Department of Natural Resources Management, Texas Tech University, and the United States Fish and Wildlife Service. Thanks to J. Neal, D. Saalfeld, M. Buckingham, R. Baker, M. McDonough, and all others who assisted with field and laboratory work. We thank B. Burt, C. Comer, and D. Scognamillo for comments and reviews on previous versions of this manuscript. Finally, we thank the landowners for allowing access to saline lakes located on their properties.

LITERATURE CITED

Amat, J. A., and J. A. Masero. 2004*a*. How Kentish plovers, *Charadrius alexandrinus*, cope with heat stress during incubation. Behavioral Ecology and Sociobiology 56:26–33.

Amat, J. A., and J. A. Masero. 2004*b*. Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. Animal Behaviour 67:293–300.

Andersson, M., and C. G. Wiklund. 1978. Clumping versus spacing out: experiments on nest predation in fieldfares (*Turdus pilaris*). Animal Behaviour 26:1207–1212.

Andrei, A. E., L. M. Smith, D. A. Haukos, and J. G. Surles. 2008. Habitat use by migrant shorebirds in saline lakes of the Southern Great Plains. Journal of Wildlife Management 72:246–253.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. <http://www.spatialecology.com/htools>. Accessed 15 Jun 2007.

Bowman, G. B., and L. D. Harris. 1980. Effect of spatial heterogeneity on ground-nest depredation. Journal of Wildlife Management 44:806–813.

Brune, G. M. 2002. Springs of Texas. Volume 1. Texas A&M University Press, College Station, USA.

Brunton, D. H. 1997. Impacts of predators: center nests are less successful than edge nests in a large nesting colony of least terns. Condor 99:372–380.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition, Springer, New York, New York, USA.

Burnham, K. P., and D. R. Anderson. 2004. Multimodal inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Colwell, M. A. 1992. Wilson's phalarope nest success is not influenced by vegetation concealment. Condor 94:767–772.

Colwell, M. A., J. J. Meyer, M. A. Hardy, S. E. McAllister, A. N. Transou, R. R. LeValley, and S. J. Dinsmore. 2011. Western snowy plovers *Charadrius alexandrinus nivosus* select nesting substrates that enhance egg crypsis and improve nest survival. Ibis 153:303–311.

Colwell, M. A., C. B. Millett, J. J. Meyer, J. N. Hall, S. J. Hurley, S. E. McAllister, A. N. Transou, and R. R. LeValley. 2005. Snowy plover reproductive success in beach and river habitats. Journal of Field Ornithology 76:373–382.

Conway, W. C. 2001. Breeding ecology of shorebirds in the playa lakes region of Texas. Dissertation, Texas Tech University, Lubbock, USA.

Conway, W. C., L. M. Smith, and J. D. Ray. 2005*a*. Shorebird breeding biology in wetlands of the playa lakes, Texas, USA. Waterbirds 28:129–138.

Conway, W. C., L. M. Smith, and J. D. Ray. 2005*b*. Shorebird habitat use and nest-site selection in the Playa Lakes Region. Journal of Wildlife Management 69:174–184.

Faanes, C. A. 1983. Aspects of the nesting ecology of least terns and piping plovers in central Nebraska. Prairie Naturalist 15:145–154.

Flemming, S. P., R. D. Chiasson, and P. J. Austin-Smith. 1992. Piping plover nest site selection in New Brunswick and Nova Scotia. Journal of Wildlife Management 56:578–583.

Göransson, G., J. Karlsson, S. G. Nilsson, and S. Ulfstrand. 1975. Predation on birds' nests in relation to antipredator aggression and nest density: an experimental study. Oikos 26:117–120.

Götmark, F., and M. Andersson. 1984. Colonial breeding reduces nest predation in the common gull (*Larus canus*). Animal Behaviour 32:485–492.

Götmark, F., D. Blomqvist, O. C. Johansson, and J. Bergkvist. 1995. Nest site selection: a trade-off between concealment and view of the surroundings? Journal of Avian Biology 26:305–312.

Grover, P. B., Jr., and M. Grover. 1982. Breeding charadriiform birds of the Great Salt Plains. Bulletin of the Oklahoma Ornitholigical Society 15:11–14.

Grover, P. B., and F. L. Knopf. 1982. Habitat requirements and breeding success of charadriiform birds nesting at Salt Plains National Wildlife Refuge, Oklahoma. Journal of Field Ornithology 53:139–148.

Hill, L. A. 1985. Breeding ecology of interior least terns, snowy plovers, and American avocets at Salt Plains National Wildlife Refuge, Oklahoma. Thesis, Oklahoma State University, Stillwater, USA.

Hinsley, S. A., and P. N. Ferns. 1994. Time and energy budgets of breeding males and females in sandgrouse *Pterocles* species. Ibis 136:261–270.

Hood, S. L., and S. J. Dinsmore. 2007. The influence of habitat on nest survival of snowy and Wilson's plovers in the lower Laguna Madre region of Texas. Studies in Avian Biology 34:124–135.

Kainady, P. V. G., and K. Y. Al-Dabbagh. 1976. Some observations on the behaviour of incubating *Charadrius alexandrinus* on hot summer days. Bulletin of the Basrah Natural History Museum 3:121–137.

Koenen, M. T., D. M. Leslie, Jr., and M. Gregory. 1996. Habitat changes and success of artificial nests on an alkaline flat. Wilson Bulletin 108:292–301.

Lauro, B., and E. Nol. 1995. Patterns of habitat use for pied and sooty oystercatchers nesting at the Furneaux Islands, Australia. Condor 97:920–934.

Mabee, T. J., and V. B. Estelle. 2000. Nest fate and vegetation characteristics for snowy plover and killdeer in Colorado, USA. Wader Study Group Bulletin 93:67–72.

Maclean, G. L. 1975. Belly-soaking in the charadriiformes. Journal of the Bombay Natural History Society 72:74–82.

Mayer, P. M., L. M. Smith, R. G. Ford, D. C. Watterson, M. D. McCutchen, and M. R. Ryan. 2009. Nest construction by a ground-nesting bird represents a potential trade-off between egg crypticity and thermoregulation. Oecologia 159:893–901.

McCrimmon, D. A., Jr. 1980. The effects of timing of breeding, dispersion of nests, and habitat selection on nesting success of colonial waterbirds. Transactions of the Linnaean Society of New York 9:87–102.

Norte, A. C., and J. A. Ramos. 2004. Nest-site selection and breeding biology of Kentish plover *Charadrius alexandrinus* on sandy beaches of the Portuguese west coast. Ardeola 51:255–268.

Osterkamp, W. R., and W. W. Wood. 1987. Playa-lake basins on the Southern High Plains of Texas and New Mexico: Part I. Hydrologic, geomorphic, and geologic evidence for their development. Geological Society of America Bulletin 99:215–223.

Page, G. W., L. E. Stenzel, G. W. Page, J. S. Warriner, J. C. Warriner, and P. W. Paton. 2009. Snowy plover (*Charadrius alexandrinus*). Account 154. *in* A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://bna.birds.cornell.edu/bna/species/154>. Accessed 3 Oct 2010.

Page, G. W., L. E. Stenzel, and C. A. Ribic. 1985. Nest site selection and clutch predation in the snowy plover. Auk 102:347–353.

Page, G. W., L. E. Stenzel, D. W. Winkler, and C. W. Swarth. 1983. Spacing out at Mono Lake: breeding success, nest density, and predation in the snowy plover. Auk 100:13–24.

Paton, P. W. C. 1994. Breeding ecology of snowy plovers at Great Salt Lake, Utah. Dissertation, Utah State University, Logan, USA.

Powell, A. N. 2001. Habitat characteristics and nest success of snowy plovers associated with California least tern colonies. Condor 103:785–792.

Prindiville Gaines, E., and M. R. Ryan. 1988. Piping plover habitat use and reproductive success in North Dakota. Journal of Wildlife Management 52:266–273.

Purdue, J. R. 1976*a*. Adaptations of the snowy plover on the Great Salt Plains, Oklahoma. Southwestern Naturalist 21:347–357.

Purdue, J. R. 1976*b*. Thermal environment of the nest and related parental behavior in snowy plovers, *Charadrius alexandrinus*. Condor 78:180–185.

Reeves, C. C., Jr., and J. M. Temple. 1986. Permian salt dissolution, alkaline lake basins, and nuclear-waste storage, Southern High Plains, Texas and New Mexico. Geology 14:939–942.

Ridgely, R. S., T. F. Allnutt, T. Brooks, D. K. McNicol, D. W. Mehlman, B. E. Young, and J. R. Zook. 2007. Digital distribution maps of the birds of the Western Hemisphere, version 3.0. NatureServe, Arlington, Virginia, USA. <http://www.natureserve.org/getData/birdMaps.jsp>. Accessed 1 Dec 2011.

Rippin Armstrong, A., and E. Nol. 1993. Spacing behavior and reproductive ecology of the semipalmated plover at Churchill, Manitoba. Wilson Bulletin 105:455–464.

Saalfeld, S. T. 2010. Snowy plover population and breeding ecology in saline lakes of the Southern High Plains of Texas. Dissertation, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Saalfeld, S. T., W. C. Conway, D. A. Haukos, and W. P. Johnson. 2011. Nest success of snowy plovers (*Charadrius nivosus*) in the Southern High Plains of Texas. Waterbirds 34:389–399.

Schneider, E. G., and S. R. McWilliams. 2007. Using nest temperature to estimate nest attendance of piping plovers. Journal of Wildlife Management 71:1998–2006.

Texas Water Development Board. 2004. Texas Natural Resources Information System. <http://www.tnris.state.tx.us/>. Accessed 15 May 2007.

Tinbergen, N., M. Impekoven, and D. Franck. 1967. An experiment on spacing-out as a defence against predation. Behaviour 28:307–321.

U.S. Fish and Wildlife Service. 1993. Endangered and threatened wildlife and plants; determination of threatened status for the Pacific Coast population of the western snowy plover. Federal Register 58:12864–12874, Washington, D.C., USA.

Wiklund, C. G., and M. Andersson. 1980. Nest predation selects for colonial breeding among fieldfares *Turdus pilaris*. Ibis 122:363–366.

Winton, B. R., D. M. Leslie, Jr., and J. R. Rupert. 2000. Breeding ecology and management of snowy plovers in north-central Oklahoma. Journal of Field Ornithology 71:573–584.

Associate Editor: Wayne Thogmartin.