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Factors Influencing Snowy Plover (*Charadrius nivosus*) Nest Survival at Great Salt Lake, Utah

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Abstract.—Reduced nest survival has been suggested as a primary cause for the decline of Snowy Plover (*Charadrius nivosus*) populations. The fates of Snowy Plover nests (n = 589) were determined from five locations at the Great Salt Lake in Utah during the 2003, 2005-2010 and 2012 breeding seasons. A five-stage hierarchical modeling procedure was used, and five competing models ($\Delta AIC_c < 2$) that best described variation in nest survival were identified. These competing models included the influences of study site and year with a quadratic time trend and covariates quantifying nest age, temperature, precipitation, distance to water control structures (dikes), and nesting substrate (barren mudflat, vegetation patches, or conspicuous objects). Among unsuccessful nests (45.6%; n = 277), the most common cause of failure was predation (72.9%), followed by weather and abandonment (10.5% and 10.1%, respectively). Daily nest survival rates ranged from 0.89 to 0.97 and varied annually and across sites. Nests located on barren flats had lower daily nest survival than those located in vegetated patches or near conspicuous objects. Proximity to dikes influenced nest survival as nests within 100 m had lower daily survival rates than nests further than 100 m from dikes. The population of Snowy Plovers on the Great Salt Lake contributes substantially to an overall imperiled North American population. Managers should consider measures to reduce the attractiveness of dikes as nesting habitat to increase nest survival rates for Snowy Plover. *Received 17 June 2014, accepted 9 July 2014.*

Key words.—*Charadrius nivosus*, Great Salt Lake, nest predation, nest survival, shorebird, Snowy Plover.

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Factors that influence nest survival of shorebirds include parental condition (Davis 1975; Amat *et al.* 2001), nest initiation date (Smith and Wilson 2010), and location of the nest in relation to the surrounding landscape (Catlin *et al.* 2011; Colwell *et al.* 2011; Saalfeld *et al.* 2011; Skrade and Dinsmore 2013). Early initiation of nests can be associated with increased nest survival, although this pattern is not always consistent (Norte and Ramos 2004; Conway *et al.* 2005; Smith and Wilson 2010; Saalfeld *et al.* 2011). Intraseasonal variation in nest density, predator abundance or behavior, or the behavior of incubating adults could influence nest survival (Smith and Wilson 2010). Reduced nest survival may have profound implications on population dynamics of shorebird species.

Reduced nest survival is considered a potential factor in the decline of Snowy Plover (*Charadrius nivosus*) in North America (U.S. Fish and Wildlife Service 2007). Snowy Plovers are broadly, but intermittently distributed across North America and depend on coastal shoreline and sparsely-vegetated lake or riverine habitats for breeding and wintering, and as migration stopover areas (Page *et al.* 2009). Nest failure for Snowy Plover is often caused by mammalian and avian predation, weather (e.g., flooding, hail, and wind), trampling, and human disturbance (Page *et al.* 2009). Moreover, unlike many shorebirds that are colonial nesters (Siegel-Causey and Hunt 1981; Post and Seals 1993), Snowy Plover nest in loose conspecific aggregations (Page *et al.* 1985; Warriner *et al.* 1986; Paton 1995) where reduced nest survival can be associated with high nest density due to density-dependent predation in coastal populations (Page *et al.* 1983).

The Great Salt Lake hosts approximately 23% of Snowy Plovers breeding in North America (Thomas *et al.* 2012). Changing habitat conditions at Great Salt Lake from encroachment of nonnative common reeds

(*Phragmites australis*; Kulmatiski *et al.* 2010) and reduced freshwater inflow provide conservation challenges that may impact Snowy Plovers. Previous estimates of Snowy Plover nest survival from the Great Salt Lake showed considerable annual and area-specific variation (estimates of annual nest survival ranged from 5.4 – 49.2%; Paton 1995). Despite the importance of the Great Salt Lake to interior Snowy Plover populations, no quantitative studies have investigated reproductive success since the early 1990s at this site.

Increased efforts to monitor Snowy Plover at the Great Salt Lake over the last decade have resulted in a large data set (Cavitt 2014). This data set includes individual nest fates at several sites collected during 2003, 2005-2010 and 2012. We hypothesized that Snowy Plover would demonstrate differences in nest survival among sites and across years due to differences in predator abundance, resource quality and availability, fluctuating water levels, and human influence. Our objectives were to use this data set to: 1) estimate annual nest survival for Snowy Plover at the Great Salt Lake; 2) test hypotheses about spatial and temporal variation in nest survival in relation to local landscape features; and 3) determine probable causes of nest failure.

METHODS

Study Area

The Great Salt Lake is a large, hypersaline lake in north-central Utah (Fig. 1). It is a closed-basin system influenced by freshwater inputs that fluctuate seasonally. Small changes in the water-surface elevation result in large changes in the surface area of the lake due to its location on a shallow playa. At a water-surface elevation of 1,280 m, the lake has a surface area of about 4,300 km^2 and an average depth of 4.45 m (Baskin 2005). The Southern Pacific Railroad Causeway divides the lake into two distinct areas with unique ecological characteristics. The north arm of the Great Salt Lake is characterized by high salinity (> 25%) due to little freshwater inflow and is rarely used by waterfowl or shorebirds (Aldrich and Paul 2002). The south arm has lower salinity (average 13%) and receives most of the freshwater inflow from several rivers and streams (Loving *et al.* 2002).

Additionally, the Great Salt Lake is bordered by approximately 1,900 km^2 of freshwater and brackish wetlands, primarily on the east side of the lake (Aldrich and Paul 2002). Vegetation in Snowy Plover nesting areas was characterized by pickleweed (*Salicornia europeaerubra*), iodinebush (*Allenrolfea occidentalis*), and salt grass (*Distichlis spicata*) (Flowers 1934). Data were collected at five sites: the Great Salt Lake Shorelands Preserve, Bear River Migratory Bird Refuge, Ogden Bay Waterfowl Management Area, Farmington Bay Waterfowl Management Area, and Saltair along the eastern and southern edges of the Great Salt Lake (Fig. 1).

Nest Surveys

We conducted nest surveys at least once per week at each site during the breeding season (early April-mid August; Paton 1995) in 2003, 2005-2010 and 2012 to locate new nests and determine the status of extant nests. We located nests by systematically searching potential sites and by observing parental behavior. Once located, we recorded the spatial coordinates of each nest with a handheld GPS unit. We also recorded nest substrate type by noting the location of the nest cup in either vegetation, barren flats, or on or next to conspicuous objects (e.g., debris, cattle dung, gravel mound, etc.). We then floated eggs to estimate incubation stage and initiation date assuming an egg-laying period of 4 days and a 27-day incubation period (Paton 1995; Page *et al.* 2009). We estimated daily survival rate from the beginning of incubation, which we assumed to begin after the last egg had been laid (Page *et al.* 2009). Nests were defined as successful if at least one young survived to leave the nest or when eggs disappeared near the expected date of hatching and additional evidence supported that fate (Mabee 1997; Mabee and Estelle 2000; Mabee *et al.* 2006). A failed nest was classified as depredated if all eggs disappeared prior to the expected date of nest-leaving or there was evidence of depredation (yolk or large egg fragments).

Data Analysis

To evaluate hypotheses concerning variation in nest survival based on site, climate, location of nest, and timing of nest initiation, we used model selection and the nest survival model within Program MARK (White and Burnham 1999; Dinsmore *et al.* 2002; Table 1). We standardized the earliest date a nest was found, 26 April, as day 1 of the nesting season for all sites in each year. Encounter histories for Program MARK nest survival analysis require input of the day a nest was found, the day it was last observed active, the day it was last checked, and nest fate. We included covariates for: 1) the age of the nest when found based on estimated initiation date; 2) nesting substrate (vegetation, barren mudflat, or conspicuous objects); 3) the amount of precipitation on each day of the nesting season; 4) the maximum temperature on each day of the nesting season; 5) whether the nest was within 100 m of a dike; 6) the average number of times the nest was checked per week; and 7) whether there were any attempts to capture adults to be banded during incubation. Our choice of analysis for distance of a nest from a dike was based on an expectation of a threshold-type relationship where distance had a significant influence on nest survival across

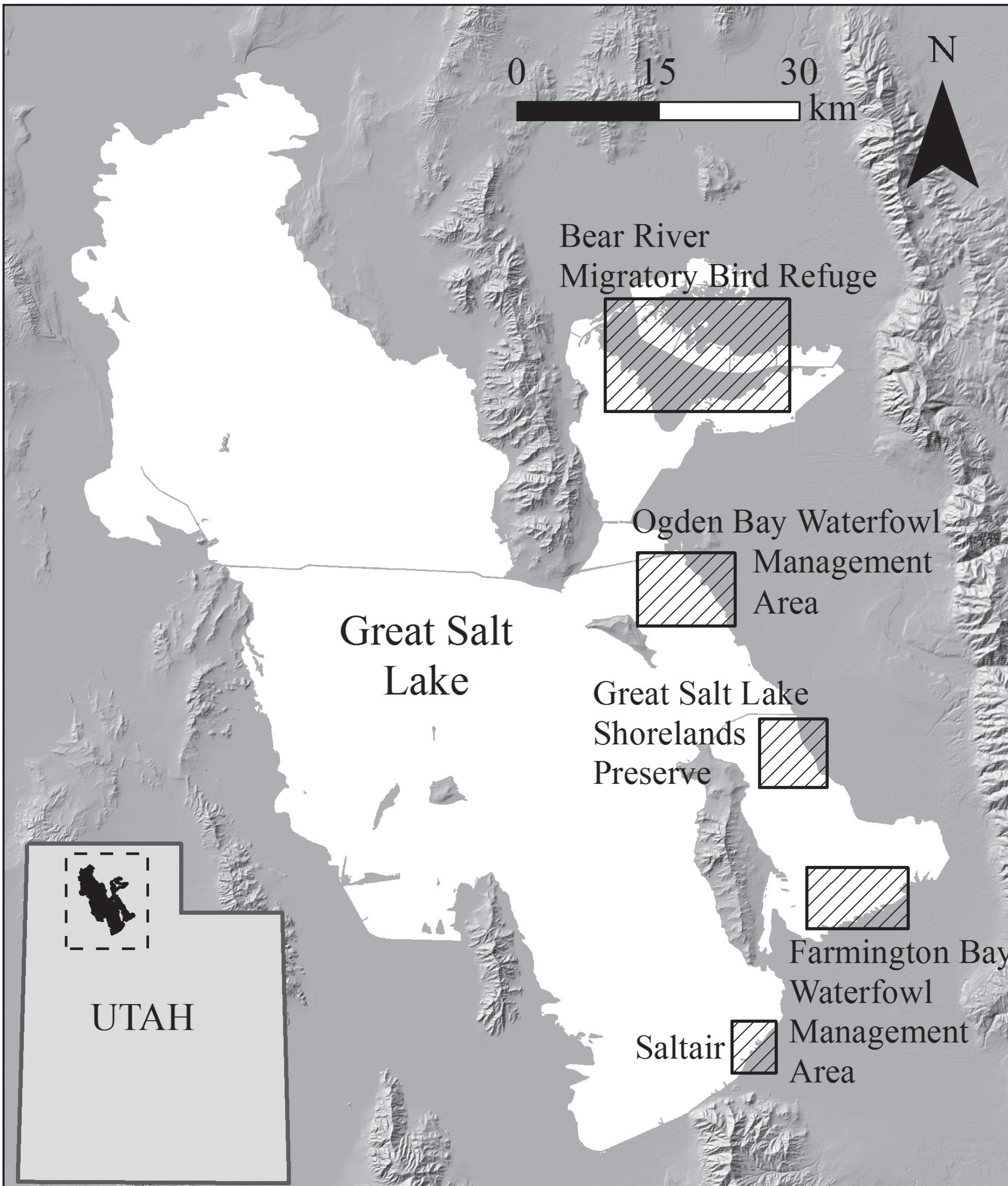

Figure 1. Study areas at Great Salt Lake, Utah (2003, 2005-2010 and 2012), where factors associated with nest survival of Snowy Plover were investigated.

some, but not all distances. Assuming a constant linear relationship across all observed distances may give inaccurate results when threshold-type responses are present (Zuur *et al.* 2010). We selected a threshold distance of 100 m from dikes by plotting apparent survival and distance to dikes and noting where the upward trend leveled off.

We evaluated relative model support using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Akaike 1998; Burnham and Anderson 2002). We used a five-stage hierarchical modeling procedure following Sexson and Farley (2012) for estimating Snowy Plover nest survival. To identify the model with the greatest support within each stage, we included every additive combination of covariates of the same type (Table 1). The most supported model or multiple competing models ($\Delta AIC_c < 2$) from each stage were advanced to the next stage of model building. In stage 1, we built models to assess the relationship between daily survival rate and Julian date including linear (T) and quadratic

Table 1. Covariates hypothesized to influence Snowy Plover nest survival at Great Salt Lake, Utah (2003, 2005-2010 and 2012). We present mean ± SE or percentages; *n* = 589.

Stage	Abbreviated covariate	Description	Mean
2	Age	Age of nest when found based on estimated initiation date	10.50 ± 0.30
3	Prcp	Cumulative amount of precipitation on each day of the nesting season (mm)	1.10 ± 0.13
3	T_{max}	Maximum temperature on each day of the nesting season (°C)	30.27 ± 0.23
	Substrate:		
4	Obj	Nest located on or next to object	20.4%
4	Mudf	Nest located on barren flat	39.4%
4	Veg	Nest located in vegetation	40.2%
4	Dike	Nest located within 100 m of dike	28.5%
5	Trap	Attempted trapping at nest any time during incubation	31.4%
5	AvgC	Average number of times nest was checked per week	2.96 ± 0.13

relationships (TT). We also assessed annual and spatial (site) variation in this stage. In stage 2, we added the age of the nest when found to competing models from stage 1. In stage 3, we added maximum daily temperature and precipitation to the best model from stage 2. In stage 4, we added habitat covariates (nest substrate and within 100 m of dikes) to the top two models from stage 3. In stage 5, we added covariates to assess researcher effects including trapping attempts and the mean number of days each nest was visited per week. In the event of model-selection uncertainty, we generated model-averaged estimates of nest survival (Burnham and Anderson 2002). To evaluate individual covariates, we looked for overlap in confidence intervals around real parameters and whether or not 95% CI around β estimates overlapped zero. We calculated annual estimates of nest success by exponentiation of daily survival rate to 27, consistent with a 27-day incubation period (Paton 1995; Page *et al.* 2009).

RESULTS

We found a total of 608 nests during 2003, 2005-2010 and 2012 (Table 2). A 110-day nesting season was estimated from 26 April to 13 August (day first nest was discovered to day last nest was active). The earliest nest initiation was on 17 April, and the latest on 13 July. We used valid encounter histories, consisting of at least 1 exposure day for 589 nests (Table 2). We could not construct encounter histories for 19 nests (3.1%) because they were found after they had failed or hatched. The most common cause of nest failure was predation (72.9%), followed by weather and abandonment (10.5% and 10.1%, respectively). Other minor causes of nest failure (6.5%) included trampling by cattle, vehicles and humans; unhatched nests; and unknown failure (Table 2).

Mean daily survival rate was highest at Farmington Bay Waterfowl Management Area (0.98; 95% CI = 0.96 – 0.98; *n* = 83), followed by Bear River Migratory Bird Refuge (0.97; 95% CI = 0.94 – 0.98; *n* = 47), Ogden Bay Waterfowl Management Area (0.97; 95% CI = 0.96 – 0.98; *n* = 105) and Great Salt Lake Shorelands Preserve (0.96; 95% CI = 0.95 – 0.97; *n* = 229; Fig. 2). Saltair had the lowest daily survival rate (0.92; 95% CI = 0.90 – 0.93; *n* = 125; Fig. 2). Overall daily survival rate for all years and sites was 0.96 (95% CI = 0.95 – 0.96). Nest survival over the entire incubation period for Snowy Plovers at the Great Salt Lake ranged from 0.05 – 0.46 ($\bar{x}$ = 0.32) with considerable annual variation (Table 2).

We developed 36 candidate models through a five-stage hierarchical modeling procedure (see Table 3 for top models resulting from stages 1 through 4 and all models in stage 5). Stage 5 of model building produced five models with $\Delta AIC_c < 2$. Each of these models included the interactive effect of group (study site, year, and quadratic date trend) and nest age. The most parsimonious model included 44 parameters (w_i = 0.25), including the interactive effect of study site, year, and quadratic date trend, as well as nest age (β = 0.03 ± 0.01, 95% CI = 0.01 – 0.06), daily maximum temperatures (β = 0.04 ± 0.02, 95% CI = < 0.01 – 0.07), nesting substrate (Fig. 3A; objects: β = 0.12 ± 0.27, 95% CI = -0.41 – 0.65; vegetation: β = 0.33 ± 0.31, 95% CI = -0.28 – 0.93; mudflat: β = -1.11 ± 0.30, 95% CI = -1.70 – -0.53), and within 100 m of dikes (Fig. 3B; β = -1.10 ± 0.21, 95%

Table 2. Number of Snowy Plover nests found at Great Salt Lake, Utah (2003, 2005-2010 and 2012), during each year, nest fates, number and percent of total nests with a valid encounter history, daily survival rate (DSR) calculated using the means of all covariates in the top model (95% CI), and estimates of annual nest survival (daily survival rate by exponentiation to the 27-day incubation period; 95% CI).

	2003	2005	2006	2007	2008	2009	2010	2012	Total (*n*)
Nests found	52	43	45	42	143	102	138	43	608
Nests included	52	38	39	39	141	102	135	43	589
Successful	34	18	25	14	82	43	80	21	317
Unsuccessful	18	18	15	27	60	59	58	22	277
Predation	11	15	8	20	45	44	41	18	72.9% (202)
Weather	0	0	5	2	6	10	6	0	10.5% (29)
Trampled	0	1	0	0	1	0	3	1	2.2% (6)
Abandoned	3	2	2	5	2	4	7	3	10.1% (28)
Unhatched	0	0	0	0	2	0	1	0	1.1% (3)
Unknown	4	0	0	0	4	1	0	0	3.2% (9)
Unknown	0	7	5	1	1	0	0	0	14
DSR	0.97 (0.96, 0.98)	0.94 (0.91, 0.96)	0.96 (0.94, 0.98)	0.89 (0.84, 0.93)	0.97 (0.96, 0.98)	0.95 (0.93, 0.96)	0.97 (0.96, 0.98)	0.95 (0.93, 0.97)	0.96 (0.95, 0.97)
27-day survival	0.46 (0.30, 0.61)	0.19 (0.08, 0.33)	0.34 (0.18, 0.52)	0.05 (0.01, 0.13)	0.39 (0.30, 0.48)	0.22 (0.14, 0.31)	0.43 (0.33, 0.52)	0.25 (0.12, 0.40)	0.32 (0.28, 0.36)

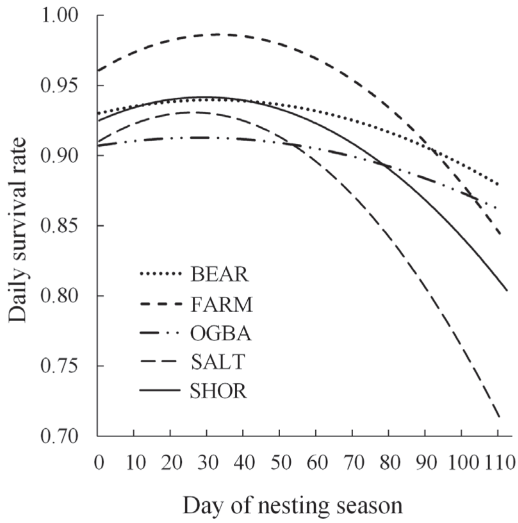

Figure 2. Daily survival rate of Snowy Plover nests at five sites over the 110-day nesting season at Great Salt Lake, Utah (2003, 2005-2010 and 2012). Daily survival rate was calculated using the mean of all covariates in the top model. Day 1 corresponds to 26 April, and day 110 corresponds to 13 August. BEAR-Bear River Migratory Bird Refuge, FARM-Farmington Bay Waterfowl Management Area, OGBA-Ogden Bay Waterfowl Management Area, SALT-Saltair, SHOR-Great Salt Lake Shorelands Preserve.

CI = -1.51 – -0.70) (Table 4). Among the competing models, 95% confidence intervals for β estimates associated with number of nest visits and/or attempted trapping overlapped zero. A quadratic date trend best described daily survival rate for all years suggesting that nest survival was highest mid-season (Fig. 2).

DISCUSSION

Nest survival estimates for Snowy Plovers were highly variable at the Great Salt Lake and ranged from 0.05 – 0.46 ($\bar{x}$ = 0.32) with considerable site and yearly variation. Estimates of Snowy Plover nest survival at Great Salt Lake have remained consistent since the early 1990s (0.05 – 0.49 (Paton 1995) and 0.46 (Edwards 2009)). Our nest survival estimates were similar to interior populations of Snowy Plover in the Southern High Plains of Texas (0.07 – 0.33; Saalfeld *et al.* 2011), Kansas (0.11 – 0.29; Sexson and Farley 2012) and Oklahoma (0.37 – 0.58; Winton *et al.* 2000). Coastal populations of Snowy Plover have experienced variable nest survival depending on the region, including low rates of success in northern California (0.05 – 0.08; Hardy and Colwell 2012) and Oregon (0.13; Wilson-Jacobs and Meslow 1984). Our estimates have a lower limit than estimates from southern California (0.36 – 0.77; Powell *et al.* 2002), and were lower than those reported in Puerto Rico (0.61 – 0.73; Lee 1989). Annual variation in shorebird nest survival is common and could be a result of fluctuating water levels, differences in predator abundance, and resource quality and availability (Colwell 2010).

In many shorebird species, predation is the greatest cause of nest failure (Nguyen *et al.* 2003; Conway *et al.* 2005; Smith *et al.* 2007) and is hypothesized to be a limiting factor in many *Charadriidae* populations (Johnson and Oring 2002). Predation accounted for the majority of Snowy Plover nest failures at our study sites (Table 2). Predation has remained the primary cause of nest failure since the early 1990s at Great Salt Lake (86%; Paton 1995). In Kansas, Snowy Plover nest failures were primarily attributed to flooding (43%), and predation

Table 3. Supported models for Snowy Plover nest survival at the Great Salt Lake, Utah (2003, 2005-2010 and 2012), showing model structure, change in Akaike's Information Criterion adjusted for small sample sizes (ΔAIC_c), model weight (w_i), model likelihood, number of parameters (K) and model deviance. See Table 1 for definitions of covariates; TT = Julian date quadratic relationship.

Model	ΔAIC_c	w_i	Model Likelihood	K	Model Deviance
S(Year*TT*Site+Age+T_{max}+Substrate+Dike)	0	0.25	1.00	44	1,497.45
S(Year*TT*Site+Age+Prcp+Substrate+Dike)	0.21	0.22	0.90	44	1,497.66
S(Year*TT*Site+Age+T_{max}+Substrate+Dike+AvgC)	0.69	0.18	0.71	45	1,496.12
S(Year*TT*Site+Age+Prcp+Substrate+Dike+AvgC)	0.81	0.17	0.67	45	1,496.24
S(Year*TT*Site+Age+T_{max}+Substrate+Dike+Trap)	1.82	0.10	0.40	45	1,497.25
S(Year*TT*Site+Age+Prcp+Substrate+Dike+Trap)	2.06	0.09	0.36	45	1,497.49

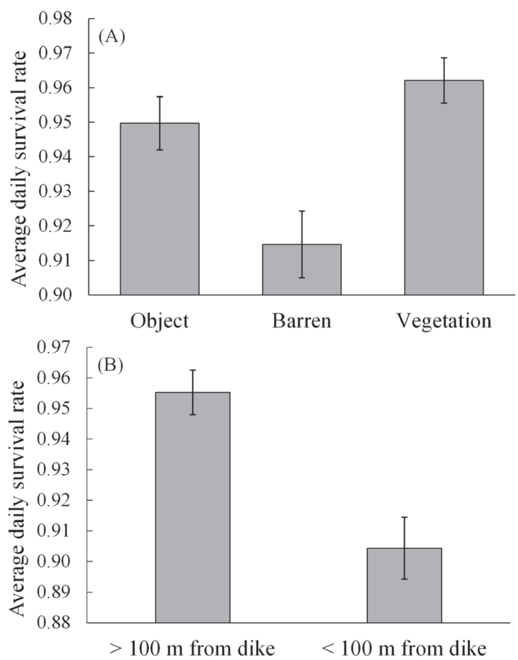

Figure 3. Daily survival rates for Snowy Plover nests found at the Great Salt Lake, Utah (2003, 2005-2010 and 2012), in response to changes in habitat covariates with 95% confidence intervals. Daily survival rate was calculated using the mean of all other covariates in the top model. Average daily survival rates and 95% confidence intervals across the 110-day nesting season are reported for nesting substrate at all sites and all years (A), and for nests located > 100 m from dike and < 100 m from dike at all sites and all years (B).

had much lower values (15%; Sexson and Farley 2012). In the Southern High Plains of Texas, predation accounted for 40% of nest

Table 4. Model-averaged parameters and descriptive statistics of covariates included in the top models of daily survival of Snowy Plover nests at the Great Salt Lake, Utah (2003, 2005-2010 and 2012). Lower and upper 95% CI derived by Program MARK. Covariates with confidence intervals not overlapping 0 flagged with an *. Covariate names match those from Table 1.

Covariate	Weight (%)	β	CI
Age*	100	0.04	0.02 – 0.07
Dike*	100	-1.13	-1.53 – -0.72
T_{max}*	52	0.04	0.02 – 0.10
Prcp*	48	-0.04	-0.08 – -0.01
AvgC	34	0.13	-0.09 – 0.35
Trap	19	-0.07	-0.37 – 0.23
Substrate:			
Veg	100	0.33	-0.28 – 0.93
Mudf*	100	-1.11	-1.70 – -0.53
Obj	100	0.12	-0.41 – 0.65

failures and weather accounted for 36% of nest failures (Saalfeld *et al.* 2011). Extreme weather events (e.g., hail storms and flooding) do not occur as frequently in northern Utah as in the Great Plains, resulting in fewer nests being destroyed by weather. Although we did not quantify predator abundances, the main predators observed included California Gulls (*Larus californicus*), Common Raven (*Corvus corax*), raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*) and coyote (*Canis latrans*). We observed predation events by California Gulls, Common Ravens and coyotes during the study period. Populations of many of these predators are large at Great Salt Lake. For example, Great Salt Lake has the largest colonies of California Gulls within the interior west (Cavitt *et al.* 2014).

Mammalian predators may use dikes, footpaths, roads and similar channels as corridors into nesting areas, thereby increasing prey exposure (Kuehl and Clark 2002; Frey and Conover 2006). In our study, 28.5% of nests were located within 100 m of a dike (Table 1). Proximity to a dike was included in our top model, and Snowy Plover nests had lower probability of daily survival when located near dikes (Fig. 3B). Additionally, the proportion of failed nests from predation was 77.2% when nests were within 100 m of dikes and 68.3% when nests were further than 100 m from dikes. Snowy Plover nest survival was not affected when nests were within 20 m of roads in Kansas (Sexson and Farley 2012). At Great Salt Lake, however, dikes are the primary means of accessing wetland complexes by mammalian predators and serve as den sites for both raccoons and foxes (Frey and Conover 2006).

Nest microhabitat characteristics can potentially affect Snowy Plover nest survival by altering nest concealment (Colwell *et al.* 2011), ability to detect predators (Amat and Masero 2004), thermoregulation (Purdue 1976) and the effects of precipitation (Sexson and Farley 2012). The effect of nest microhabitat characteristics on Snowy Plover nest survival varies among studies and breeding areas. We found that nests were less successful when located on barren flats. In coastal Texas, nests were more successful when located on barren flats than in vegetated areas (Hood and Dinsmore 2007). In some areas, Snowy Plover nests near debris had lower survival rates than those in open habitats (Page *et al.* 1985; Winton *et al.* 2000), whereas in coastal Texas, Snowy Plover nests near debris had greater survival rates (Hood and Dinsmore 2007). We found that nest survival was not highly affected when nests were located in vegetated areas or near debris and other objects, similar to other studies (Hill 1985; Powell 2001; Norte and Ramos 2004; Saalfeld *et al.* 2012). In northern California, Snowy Plover nest survival had a weak relationship with habitat features (Hardy and Colwell 2012). Similarly, nest survival of Snowy Plovers in Kansas was not influenced by nest microhabitat characteristics (Sexson and Farley 2012).

Indirect effects of researcher presence may include the attraction of nest predators. Common Ravens, for example, have been observed depredating Snowy Plover nests immediately after incubating adults flush from the nest in response to a disturbance (Hardy and Colwell 2012). In our study, however, nest survival was not sensitive to researcher influence (average number of nest visits per week or trapping attempts during incubation) as these effects received very little support in our modeling effort (Table 4).

Our results indicate that nest age was positively associated with survival rates. A positive relationship between nest age and daily survival rate has been previously documented in Snowy Plovers (Dinsmore *et al.* 2002; Hood and Dinsmore 2007), and our results support this consensus. This relationship could exist if the most vulnerable nests fail early (Klett and Johnson 1982). It is also possible that incubating adults change their behavior as nests age, influencing the probability of nest survival (Smith and Wilson 2010). Additionally, some species of biparental shorebirds increase nest defense as their nest ages throughout the breeding season (Smith and Wilson 2010).

The population of Snowy Plover at the Great Salt Lake was the largest population at any site surveyed during the International Snowy Plover Survey suggesting that this population contributes substantially to an overall imperiled North American population (Thomas *et al.* 2012). Predator use of dikes as travel corridors has possible implications for the success of ground-nesting birds. Because we found that dikes can serve as an ecological trap for Snowy Plover, managers should examine ways to reduce the attractiveness of dikes to nesting shorebirds. Dikes are likely attractive because they provide a preferred substrate for nest concealment (Paton and Bachman 1996; Colwell *et al.* 2011). Fewer Snowy Plover may nest on dikes when larger sized gravel is used as a road base along with the placement of suitable microhabitat in small patches on barren flats away from dikes (Paton and Bachman 1996; Colwell *et al.* 2011).

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