

HABITAT CHARACTERISTICS AND NEST SUCCESS OF SNOWY PLOVERS ASSOCIATED WITH CALIFORNIA LEAST TERN COLONIES

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Abstract. Nest success of Snowy Plovers (*Charadrius alexandrinus*) was estimated at six sites in San Diego County, California, to determine the effects of habitat characteristics and social factors on predation risk. Egg predation was expected to be lower for plovers nesting among Least Terns (*Sterna antillarum*) because of benefits associated with nesting under the “protective umbrella” of a colonial species. Snowy Plovers nested adjacent to objects and in areas with more vegetation cover than random sites in beach and fill habitats and in areas with more debris cover in beach and salt pan habitats. Estimated nest success from 1994–1997 was 50%, and most predation was attributed to corvids, primarily Common Ravens (*Corvus corax*). Social factors, including distance to nearest Least Tern and Snowy Plover nests, predicted nest success whereas habitat characteristics did not. Nest success was greatest for plovers nesting closest to an active tern nest and nesting at intermediate distances to conspecifics. Nest success also varied among years and sites, with two sites consistently less successful over the four years. Nests within tern colonies received some mitigation of egg predation. Plover nests initiated prior to the arrival of Least Terns were less likely to hatch eggs than later nests; nevertheless, Snowy Plovers in southern California initiated nesting well before Least Terns.

Key words: *Charadrius alexandrinus*, habitat selection, Least Tern, nest success, predation, Snowy Plover, *Sterna antillarum*.

Características del Hábitat y Éxito de la Nidada de *Charadrius alexandrinus* Asociados a Colonias de *Sterna antillarum*

Resumen. Para determinar los efectos de las características del hábitat y factores sociales sobre el riesgo de depredación, estimé el éxito de las nidadas de *Charadrius alexandrinus* en seis sitios del Condado de San Diego, California. Se esperaba que la depredación de huevos fuera menor para los *C. alexandrinus* que anidan junto a *Sterna antillarum* debido a los beneficios de anidar bajo un “paraguas protector” de una especie colonial. En playas y hábitats rellenados, *C. alexandrinus* anidó con mayor frecuencia en lugares adyacentes a objetos y en áreas con mayor cobertura de vegetación que en sitios aleatorios y en áreas con mayor cobertura de desechos vegetales en playas y salinas. El éxito estimado de las nidadas entre 1994–1997 fue de 50%, y la mayor tasa de depredación fue atribuida a córvidos, principalmente a la especie *Corvus corax*. Factores sociales como distancia al nido más cercano de *S. antillarum* y *C. alexandrinus* predijeron el éxito de la nidada, mientras que las características del hábitat no lo hicieron. El éxito de la nidada fue mayor para los individuos de *C. alexandrinus* que nidificaron más cerca de un nido activo de *S. antillarum* y que nidificaron a distancias intermedias de conspecificos. El éxito de la nidada también varió entre años y sitios. Dos sitios presentaron consistentemente un menor éxito durante los cuatro años de estudio. Los nidos ubicados dentro de la colonia presentaron una leve disminución en la depredación de huevos. Los huevos de nidos de *C. alexandrinus* iniciados antes de la llegada de *S. antillarum* tuvieron una menor probabilidad de eclosión que huevos de nidos más tardíos. Sin embargo, *C. alexandrinus* comenzó a nidificar bastante antes que *S. antillarum* en California del Sur.

INTRODUCTION

Nest site selection and dispersion in shorebirds has been linked to their ability to minimize egg

predation (Tinbergen et al. 1967, Gochfeld 1984, Larsen and Moldsvor 1992). Shorebirds are vulnerable to predators because they are ground-nesters, and they may mitigate density-dependent nest predation by spacing out their nests (Page et al. 1983). Many species of shorebirds depend more on subterfuge and camouflage than aggressive antipredator behaviors; therefore, nesting under the “protective umbrella” of some

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colonial species may reduce predation rates (Burger 1987, Larsen and Moldsvor 1992). Advantages of nesting within a colony include higher detection rates of predators, the ability to deter predators, and "saturation effects" (Siegel-Causey and Hunt 1981, Götmark and Andersson 1984, Post and Seals 1993, Emslie et al. 1995). In addition, some species recognize and respond to interspecific alarm calls so that nesting among other species can give early warning of approaching predators (Nuechterlein 1981, Powell and Cuthbert 1993).

Snowy Plovers (*Charadrius alexandrinus*) often nest in loose conspecific aggregations (Page et al. 1985, Warriner et al. 1986, Paton 1995). Nest predation can significantly reduce annual reproductive success of Snowy Plovers. For example, experiments at Mono Lake, California, using imitation plover nests, showed reduced survival where nest densities were high (Page et al. 1983). Page et al. (1983) also found that eggs in closely spaced Snowy Plover nests were less likely to hatch than in dispersed nests. They postulated that clumped Snowy Plover nests were more vulnerable to gulls and corvids because these predators intensified their nest searches and returned to forage after a first nest was found.

In southern California, Snowy Plovers typically nest in association with California Least Terns (*Sterna antillarum browni*). Least Terns defend nests and chicks with alarm calls and flight, and by diving at and defecating on intruders (Thompson et al. 1997). Although California Least Terns are federally listed as endangered, the regional population has grown more than fourfold since 1978, whereas the Snowy Plover population has declined significantly (Powell 1998). The Pacific Coast population of Western Snowy Plovers (*C. a. nivosus*) was listed as threatened in 1993 (Federal Register 1993). Factors contributing to Snowy Plover population declines in this region have not been identified. Do Snowy Plovers benefit from sharing the same breeding areas as Least Terns in southern California or are increasing populations of Least Terns detrimental to Snowy Plover nest success? I hypothesized that Snowy Plovers nesting among Least Terns would have greater nest success than those nesting without the benefits of association with a colonial species. In addition, I describe habitat characteristics of Snowy Plover nests in coastal southern Califor-

nia and examine their influence on nest success. I also evaluated whether physical or social attributes of nest sites influence predation rates on clutches of eggs.

METHODS

STUDY AREAS

The study was conducted from 1994–1997 at six major Western Snowy Plover breeding areas within San Diego County, California (32°30'N, 117°15'W): Marine Corps Base Camp Pendleton, Batiquitos Lagoon, Naval Amphibious Base Coronado, Silver Strand State Beach, Sweetwater Marsh National Wildlife Refuge, and Tijuana Slough National Wildlife Refuge. Most sites consisted of stretches of sandy beach with low dunes supporting plants such as bur-sage (*Ambrosia chamissonis*), sand verbena (*Abronia umbellata*), and sea rocket (*Cakile maritima*). There were no areas containing invasive grasses such as Marram grass (*Ammophila arenaria*), which have been a major cause of plover habitat loss along northern California beaches (Page and Stenzel 1981). Some plover nests were located on salt pan with large patches of pickleweed (*Salicornia virginica*) and dredged-fill habitats with non-native or weedy plants, especially filaree (*Erodium* sp.), Indian sweet-clover (*Melilotus indicus*), sea rocket, and beach primrose (*Camissonia cheiranthifolia*). California Least Terns nested in various densities at all of the areas used by Snowy Plovers except Silver Strand State Beach (Fig. 1).

NESTING HABITAT

Snowy Plover nests were found by forming a search image and systematically walking through all potential breeding habitat from 1 May through 30 August 1994, and 15 March through 30 August 1995–1997. Fewer nests were located in 1994 because nest searches began later that year. Each nest was marked with a small wooden stake placed 1 m to the west of the nest. Least Tern monitors assisted in locating and monitoring Snowy Plover nests at some sites. Nests found with one egg were assumed to have been initiated that day, and initiation dates were calculated for nests found with a full clutch by counting backward from date of hatch (assuming a 7-day laying period and a 21-day incubation period, Warriner et al. 1986). After 1996, egg flotation (Westerskov 1950) was used to estimate hatch dates for nests found with three

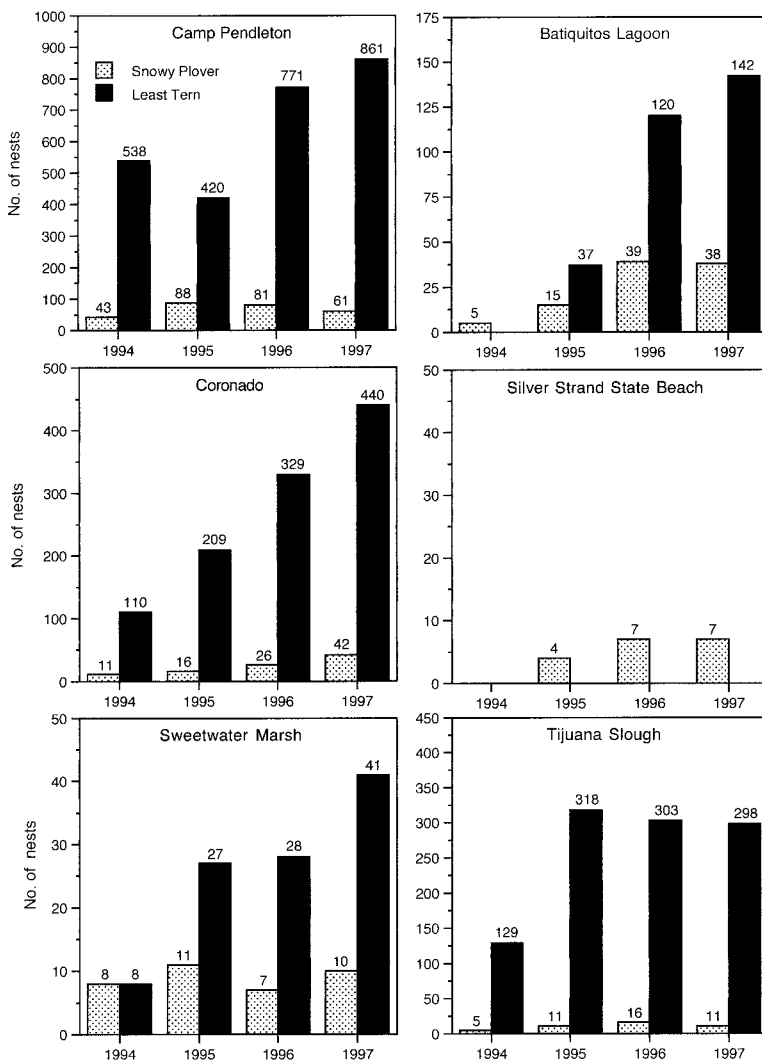


FIGURE 1. Number of Snowy Plover and California Least Tern nests found at six study sites within San Diego County, California, 1994–1997. Note differences among y-axis scales. Data on numbers of Least Tern nests from California Department of Fish and Game, Bird and Mammal Conservation Program, Sacramento, California, unpubl. reports.

eggs, using modifications for Snowy Plovers developed by Point Reyes Bird Observatory (G. Page, unpubl. data). Nests found with a full clutch that were lost before hatching were assigned an initiation month using information from egg flotation and knowledge of incubation periods. Plover nests were checked from 1–7 times per week until eggs hatched or the nest failed. Eggs were considered abandoned if they were cold, no adults were observed in the area, or there were no plover footprints around the

nest. Abandonment was verified by repositioning the egg and checking for movement later. Nests lost before they were expected to hatch were examined for evidence of predation (tracks or other sign, broken eggshells, or punctured eggs) or hatching (observations of the adults nearby with chicks, intense distraction displays, or clean eggshell caps with loose and clean membranes in or near the nest; Maybee 1997). Nest success was estimated using the Mayfield method (Mayfield 1961) and is reported with

95% confidence limits. I then estimated the total number of nests by dividing the number of successful nests (in which ≥ 1 egg hatched) by the Mayfield estimate of nest success (Johnson and Shaffer 1990). Percent of nests we did not find was estimated by dividing the number of found nests by the number of estimated total nests and subtracting from 100.

Data on habitat characteristics of nest sites were collected from 1994–1996. Each nest was characterized as being in one of three habitat types: beach, salt pan, or fill. I noted whether nests were placed next to an object (plant, debris, or none; Page et al. 1985). A 1-m² quadrat was centered on each nest and the percent cover of live plants and debris (nonliving matter, including sticks, rocks, dead plants, kelp, and debris) were visually estimated after nests failed or hatched to minimize nest abandonment. Mean plant height was calculated by the average of the height of the three tallest plants within each quarter of the quadrat. Percent cover and mean plant height were also recorded for a paired 1-m² quadrat placed at a random distance and compass bearing within 50 m of each nest and within the same habitat. In 1994–1997, distances (m) were estimated from each Snowy Plover nest to its nearest neighboring plover and Least Tern nest. Distances were estimated only for those plover and tern nests that were active at the time the focus nest was initiated. At some sites such as Camp Pendleton and Batiquitos Lagoon, nesting areas had marked grids at specific distances (30 or 50 m). Internest distances were thus estimated using a combination of grids, pacing, and measuring with a meter tape.

STATISTICAL ANALYSES

I compared habitat characteristics (percent cover, plant height) of Snowy Plover nests and paired random non-nest quadrats using paired *t*-tests. I then used two-way ANOVA to compare percent cover of vegetation, plant height, percent cover of debris, and distance to water with year and habitat type as factors and nest quadrats as observations. When there was no interaction between year and habitat I used the Tukey-Kramer ($\alpha = 0.05$) method to compare habitats (Sokal and Rohlf 1981). Values are reported as means \pm SE.

I used logistic regressions to model probability of nest success based on habitat characteristics, time of nest initiation, and proximity to oth-

er Snowy Plover and Least Tern nests, with stepwise selection and backward elimination used to choose the best set of predictors. The dependent variable, nest success, was a binomial response in all models, and I used Hosmer and Lemeshow (1989) goodness-of-fit tests to select the final model. I was interested in the effects of habitat and social factors on predation risk and therefore did not include nests that were flooded, abandoned, or run-over by vehicles in my analyses.

The following variables were used as potential predictors of nest success: year, site, distance to nearest tern nest, distance to nearest plover nest, month, month², initiation before or after Least Terns initiated nests, object type, plant cover, debris cover, plant height, and distance to water. Distances to nearest Least Tern nests were divided into categories based on the distances I observed terns responding to disturbance: 0–100 m (strong response), 101–500 m (variable response), and >500 m (no response or no terns in the area). I also categorized distances to nearest Snowy Plover nests into 5 classes: <50 m (very close), 51–100 m (close), 101–200 m (middle), 201–500 m (far), and >500 m (no neighbor). I found a linear effect of distance from Least Tern nest and a quadratic effect of distance to nearest Snowy Plover nest; therefore, I included (distance to nearest plover)². Based on previous research on Snowy Plovers, I expected that nest success would be lowest in the middle part of nest initiation (Page et al. 1983). Thus, I added month and month² into the models to describe potential effects of season.

I ran an initial model that did not include data from 1997 because only distance data (to tern and plover nests) were taken that year. None of the habitat variables (habitat, object type, plant cover, plant height, debris cover, distance to water) entered the initial model. I then added 1997 data and again habitat variables did not enter the model. I conducted a final test to ensure that habitat variables (for years 1994–1996) were still not significant by forcing the predicting variables of the final model into a new model, while making the habitat variables available as well. The final model indicated that the habitat variables were not significant in the presence of the predictors of the final model ($\chi^2_8 = 8.2$, $P = 0.4$). Finally, I used correlation analysis to determine whether Snowy Plover nest success was related to Least Tern colony size.

TABLE 1. Habitat characteristics (mean \pm SE) of Snowy Plover nests and paired random non-nest quadrats (n) within three habitat types in southern California, 1994–1996.

Habitat variable	Beach (159)		Salt pan (95)		Fill (73)	
	Nest	Random	Nest	Random	Nest	Random
Plant cover (%)	8.3 \pm 0.9	5.6 \pm 1.6*	12.6 \pm 2.2	19.3 \pm 3.5	7.7 \pm 1.6	4.8 \pm 1.1*
Debris cover (%)	9.8 \pm 1.2	4.6 \pm 0.9**	11.4 \pm 1.9	2.5 \pm 0.8**	1.3 \pm 0.4	1.0 \pm 0.5
Plant height (cm)	50.3 \pm 3.0	32.6 \pm 2.8**	53.2 \pm 8.4	66.9 \pm 11.9	31.4 \pm 5.9	19.8 \pm 4.2

* $P < 0.05$; ** $P < 0.01$ determined by paired t -tests.

RESULTS

HABITAT CHARACTERISTICS

Snowy Plovers nested in association with Least Tern colonies that ranged in size from 8–861 nests, and the proportion of plover to tern nests varied among sites and years (Fig. 1). Populations of nesting Least Terns increased at four of the six sites over the four years (Fig. 1). Snowy Plovers nested in beach habitat (54%), salt pan (22%), and fill (24%) habitats. There was more plant cover around nests in salt pan (16 \pm 3%) than in beach (8 \pm 1%) or fill (8 \pm 2%) habitats ($F_{2, 313} = 7.0$, $P < 0.01$). Likewise, plant height was taller around salt pan nests (54.3 \pm 8.7 cm) than fill (31.8 \pm 6.1 cm; $F_{2, 313} = 3.6$, $P = 0.03$). There was very little debris cover around nests in fill (2 \pm 0.4%) compared to beach (10 \pm 1%) and salt pan (12 \pm 2%) habitats ($F_{2, 313} = 11.8$, $P < 0.01$). In summary, salt pan nests were surrounded by taller, denser vegetation than beach habitats, and nests on fill had the least amount of cover by either vegetation or debris.

Distances of nests to water also varied among habitat types ($F_{2, 264} = 8.1$, $P < 0.01$). Nests located on beaches were significantly closer to water (53.5 \pm 2.4 m) than those on fill (87.9 \pm 9.4 m; critical difference = 20.6, $P = 0.05$), with nests on salt pan at intermediate distances (71.6 \pm 9.3 m). Within habitats, nest quadrats had more plant and debris cover than random non-nest quadrats in beaches, more plant cover in fill, and more debris cover in salt pans (Table 1). Mean plant height was taller around nests than non-nest quadrats in beach habitats. Most Snowy Plover nests were placed near an object; 33% near debris and 41% next to live vegetation. The average distance of Snowy Plover nests to neighboring conspecifics (within 500 m) was 113 \pm 86 m. For Snowy Plovers nesting within Least Tern colonies, the average distance to an active tern nest was 68 \pm 87 m (range = 1–450 m).

REPRODUCTIVE SUCCESS

I estimated that I found between 83% (in 1994) and 93% (in 1995) of Snowy Plover nests during the four-year period. Least Terns did not initiate nesting until 45–56 days after Snowy Plovers; 43% of plover nests were initiated before Least Terns began nesting. Most Snowy Plover nests were initiated in April (27%), May (32%), and June (30%) with the earliest nest initiated on 10 March 1995, and the latest nest on 24 July 1995. Success for nests initiated before Least Terns nested was 54% ($n = 182$, 95% CI = 46–62%), whereas success for nests initiated after tern nests was 86% ($n = 237$, 95% CI = 80–91%).

Estimated Snowy Plover nest success was 50% (95% confidence interval = 46–55%) for the four years pooled. Nest success was 51% (39–66%) in 1994, 64% (56–74%) in 1995, 46% (39–55%) in 1996, and 43% (36–53%) in 1997. Of the eggs that did not hatch, predation was the most likely cause (Fig. 2). A less conservative estimate of predation rates includes nests lost to unknown causes. This estimate includes nests that disappeared before their estimated hatch date for which there was no direct evidence of depredation. With nests lost to unknown causes assumed depredated, the percentage of nests lost to predators ranged from 14% in 1995 to 35% in 1996. Predators or their sign were observed at 58 failed nests: Common Ravens (*Corvus corax*) at 50, American Crows (*C. brachyrhynchos*) at six, and striped skunks (*Mephitis mephitis*) at two.

The probability of success for all years reached a maximum at close (51–100 m) and middle (101–200 m) distances to Snowy Plover nests, and was lowest at far distances (distance to plover: Wald $\chi^2_1 = 10.5$, $P < 0.01$, [distance to plover]²: Wald $\chi^2_1 = 12.3$, $P < 0.01$; Fig 3A). In addition, probability of success decreased as distances to Least Tern nests increased (Wald $\chi^2_1 = 13.1$, $P < 0.01$; Fig 3B). I found no relation-

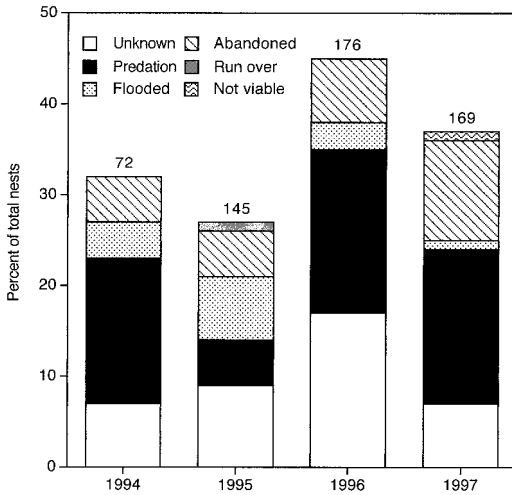


FIGURE 2. Causes of nest failure for Snowy Plover nests in San Diego County, California, 1994–1997. Sample sizes appear above each bar.

ship between Least Tern colony size and Snowy Plover nest success ($r^2 = 0.02$). Finally, nest success varied among sites and years. Probability of nest success over all sites was higher in 1995 (Wald $\chi^2_1 = 12.6$, $P < 0.01$) and 1994 (Wald $\chi^2_1 = 16.4$, $P < 0.01$) than other years. Camp Pendleton and Silver Strand State Beach had lower nest success than all other sites (Wald $\chi^2_1 = 36.1$, $P > 0.01$).

DISCUSSION

In southern California, Snowy Plovers selected nest sites with intermediate amounts of cover; they selected sparser cover over dense cover, yet most nests were placed adjacent to an object. However, there did not appear to be a benefit associated with the “disruptive effect” of an object next to the nest (Page et al. 1985), and predation risk did not appear to be reduced by selection of a particular habitat type, amount of cover around the nest, or distance to water. Although I estimated that I found a large percentage of the total nests each year, missed nests may have failed before they were detected. If missed nests were located within a particular habitat type or had some common characteristic the models may be biased.

Social factors such as distance to nearest conspecific or Least Tern nest influenced predation risk. In Connecticut, Brunton (1999) found that an intermediate colony size (approximately 150 nests) was optimal for Least Tern nesting suc-

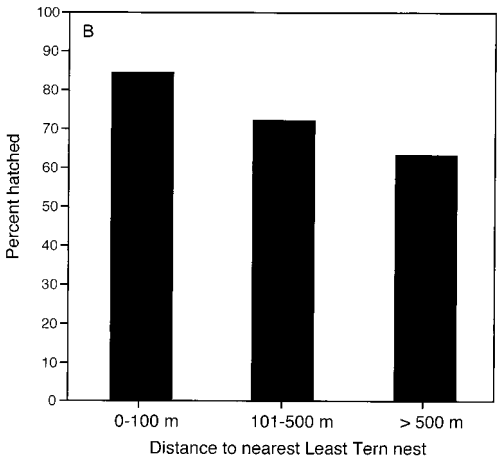
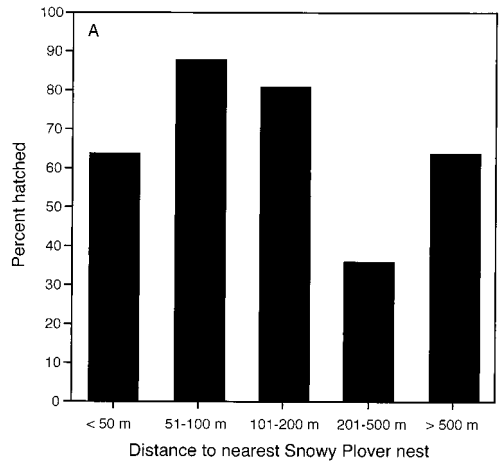


FIGURE 3. Predicted nest success for Snowy Plover nests in relation to distance from (A) closest conspecific nest and (B) closest Least Tern nest.

cess. She found that predation by small mammals, gulls, and crows was dependent on colony size and these predators were deterred from colonies with more than 100 nests. The effectiveness of antipredator behaviors in large colonies of Least Terns may vary depending on the strategies of the predators; those that enter a colony from its edge may be driven off, but predators such as Black-crowned Night-Herons (*Nycticorax nycticorax*) that go directly to the colony center may not (Brunton 1997). Likewise, hatching success of Piping Plovers (*Charadrius melodus*) nesting in New Jersey was a function of the density of Least Tern nests within colonies where both avian and mammalian predators were present (Burger 1987). Although Mayer

and Ryan (1991) found no evidence of increased survival rates of artificial Piping Plover nests located within American Avocet (*Recurvirostra americana*) colonies, most of the predation within their study area was attributed to mammals. The alkali wetlands used in their experiment were probably more similar to salt pans than sandy beaches in terms of cover and substrate type. In addition, the avocet colonies were relatively small in comparison to the tern colonies in southern California (Mayer and Ryan 1991). In contrast to Piping Plovers on the East Coast, predation on Snowy Plover nests in southern California (this study) was attributed primarily to corvids and occurred before Least Terns began nesting. I often located plover nests early in the nesting season by following plover footprints in the sand until they concentrated around a scrape or nest. I observed ravens using the same strategy to locate nests: walking along the sand apparently following plover tracks. After Least Terns arrived, this search strategy was not effective because the sand became saturated with tracks of terns. Thus, Snowy Plovers may also benefit from a reduction in search efficiency by corvids after terns begin nesting.

Interactions among timing of nest initiation, distance to Least Tern and conspecific nests, site, and year influenced Snowy Plover nest success. For example, plovers in southern California can begin nesting by early March because they are year-round residents along the coast, although a proportion of the wintering population consists of migrants from inland sites (Warriner et al. 1986, Stenzel et al. 1994). Early in the season Snowy Plovers nested in low densities of <1 nest ha^{-1} . Regardless of the low nesting densities of Snowy Plovers, nests initiated before the arrival of Least Terns were more likely to be preyed upon by corvids. Least Terns did not return to breeding colonies until mid-April and initiated egg laying around 15 May; thus potential benefits to Snowy Plovers were not apparent for approximately two months. Because of this time lag, the relationship between terns and plovers did not fit one of the "protective umbrella" assumptions because plovers did not select tern colonies early in the nesting season (Larsen and Moldsvor 1992). Survival of Snowy Plover clutches was higher after the arrival of Least Terns, and those located within range of strong antipredator response by terns were more likely to hatch. Female Snowy Plovers often abandon

broods to be tended by males soon after hatch (Warriner et al. 1986). Therefore, there is an advantage to females to initiate nesting early because they have the opportunity to nest several times within one breeding season (Amat et al. 1999). As part of a related study, I found that 35% of females nested twice during a breeding season and 8% had three nests during 1994–1997 (Powell et al., in press). Male plovers re-nested at a lower rate (22%) because they stayed with their broods after hatching; therefore re-nesting for males was usually associated with nest loss. Thus, there was a tradeoff for both sexes between increased likelihood of losing early clutches and the chance of producing more offspring over an entire breeding season.

The population of Snowy Plovers in southern California has declined significantly since the 1970s, probably due to a combination of habitat loss, human disturbance, and increased populations of Common Ravens. Nesting habitat is limited because of heavy recreational beach use and urban development (Powell 1998). Although Least Tern habitat has been protected by law and is actively managed, only 7 of 14 tern colonies in San Diego County provided plover brood-rearing habitat and supported nesting plovers during this study. Silver Strand State Beach was the only area that supported plovers but not terns; only small numbers of plovers nested there and only prior to its heavy recreational use beginning Memorial Day. Habitat characteristics of nest and brood-rearing areas may be more important to fledging success than nest success because plover chicks depend on cryptic behavior to avoid detection by predators. In addition, I observed some plover broods moving away from Least Tern colonies; therefore any protective benefits of nesting among terns may be lost after eggs hatch. Heavy recreational beach use coincided with the peak of hatching for Snowy Plover eggs. Plover chicks were therefore more exposed to human disturbance later in the breeding season because recreational use of the beaches increased as the season progressed. Although nesting among terns may mitigate lower reproductive output of Snowy Plovers due to egg predation, its advantages with respect to chick survival remain unknown and difficult to determine.

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