research paper *Wader Study* 127(2): 130–140. doi:10.18194/ws.00199

Habitat restoration improves Western Snowy Plover nest survival

Katelyn M. Raby* & Mark A. Colwell

Wildlife Department, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, USA
**Corresponding author: kmr803@humboldt.edu*

Raby, K.M. & M.A. Colwell. 2020. Habitat restoration improves Western Snowy Plover nest survival. *Wader Study* 127(2): 130–140.

Productivity measures, such as nest survival rates, are often used to indirectly assess habitat quality and guide management practices for conservation of threatened and endangered species. The Western Snowy Plover *Charadrius nivosus nivosus* is listed as threatened due to three limiting factors: human disturbance, increasing native and introduced predator populations, and the loss and degradation of habitat. We examined the relative influence of these three limiting factors on nest survival, using 14 years of data (n = 610 nests) at eight sites in Humboldt County, California, USA. Survival varied by year and site, and increased with nest age and as the breeding season progressed. Habitat restoration had the greatest influence on nest survival. Both natural (tidal overwash) and human-implemented restoration had a positive effect on nest survival, whereas unrestored areas had a negative effect. Naturally restored areas had a stronger effect (higher and less variable survival estimates) on nest survival than human-restored areas. Human and predator activity were not strong predictors of nest survival. Consequently, we recommend that managers focus on conserving, maintaining, and creating restoration areas to enhance Snowy Plover nest survival.

Keywords

Charadrius nivosus
habitat quality
productivity
conservation
predation
human disturbance
shorebirds
waders
threatened

INTRODUCTION

The study and documentation of vital rates of threatened and endangered species is imperative to understanding the factors limiting their population size and growth (Colwell 2010). For avian species, nest survival is often used as a measure of productivity, which, in turn, is used in combination with other vital rates (e.g., juvenile and adult survival) to model population growth and viability (Jones & Geupel 2007). Although research suggests adult survival has the greatest influence on shorebird population growth, productivity is generally the focus of adaptive management efforts to increase shorebird populations because it is difficult to enhance survival of adults (Colwell 2010, Dinsmore *et al.* 2010, Mullin *et al.* 2010, Cruz-López *et al.* 2017). Demographic measures like productivity are also used to indirectly measure habitat quality, such as by quantifying variation in nest survival (Johnson 2007), and can be used by managers to assess the efficacy of management actions.

The U.S. Fish & Wildlife Service listed the Pacific Coast population of the Western Snowy Plover *Charadrius nivosus nivosus* (hereafter Snowy Plover) as threatened in 1993 after a documented decline in both population size and occupied breeding sites (Page & Stenzel 1981, Page *et al.* 1991). The recovery plan identified three main factors limiting the coastal population of Snowy Plovers: the loss and degradation of habitat (owing primarily to invasive plants and urban development), increasing predator populations (resulting in high levels of egg and chick loss), and human disturbance (USFWS 2007).

Loss and degradation of Snowy Plover breeding habitat is largely associated with the rapid expansion of the non-native European Beach Grass *Ammophila arenaria* (USFWS 2007), which creates steep and densely vegetated foredunes and backdunes (Buell *et al.* 1995) and potentially provides cover for predators (USFWS 2007). Plovers prefer to court and nest in relatively flat, open, sparsely vegetated habitats, which probably enables early detection of predators (Page *et al.* 2009, Muir & Colwell 2010, Leja 2015). Habitat restoration creates suitable Snowy Plover breeding habitat by using heavy equipment to recontour (flatten) the foredune and by removing invasive plants (Zarnetske *et al.* 2010). Sometimes oyster shells are spread to increase crypsis, and thus survival, of eggs and chicks by creating a heterogeneous substrate (Colwell *et al.* 2011). Snowy Plovers preferentially selected restored habitats (84% of nests) in northern California (Leja 2015) and habitat management significantly increased nest survival along the Oregon coast (Dinsmore *et al.* 2014).

Predation can account for approximately 80% of nest loss

in avian species (Martin 1993), especially for ground-nesting shorebirds. A variety of non-native and native predators (e.g., Gray Fox *Urocyon cinereoargenteus*, Northern Harrier *Circus hudsonius*, and Striped Skunk *Mephitis mephitis*) have been documented depredating Snowy Plover eggs, but corvids (*Corvus corax* and *C. brachyrhynchos*) are consistently considered the most significant egg predators (Liebezeit & George 2002, USFWS 2007). Corvid populations have substantially increased in recent decades, likely due to their effective exploitation of urban and agricultural landscapes, leading to increased nest predation of threatened and endangered species (Luginbuhl *et al.* 2001, Kelly *et al.* 2002, Liebezeit & George 2002, Marzluff & Neatherlin 2006). Lethal and non-lethal predator control (e.g., exclosures, taste aversion, translocation) has been used in an effort to combat high levels of nest predation across the Snowy Plover's range (Liebezeit & George 2002, Colwell 2019). Several studies have shown that exclosures can increase nest survival for Snowy Plovers, but they may also increase nest abandonment and adult mortality (Hardy & Colwell 2008, Dinsmore *et al.* 2014, Pearson *et al.* 2014). There is some evidence that lethal predator control can also improve survival of unexclosed Snowy Plover nests (Dinsmore *et al.* 2014).

Over one-third of the United States human population lives in a coastal zone, and human development and coastal populations are projected to continue to increase (NOAA 2018). This rise in human activity, and thus potential disturbance, in coastal zones could have negative effects on shorebird populations (e.g., by altering behavior and local distribution; Weston 2019). Human disturbance can cause nest failure directly by the crushing of eggs (e.g., by a vehicle; Colwell *et al.* 2010), or indirectly by causing incubating adults to leave the nest, which could increase the risk of predation, sand burial, or slow embryo development (USFWS 2007, Burrell & Colwell 2012, Hardy & Colwell 2012). In contrast to adults or broods, nests are particularly vulnerable to the indirect and direct effects of human disturbance because Snowy Plovers cannot move the nest in response to changing levels of disturbance (Colwell 2010). Additionally, human activity indirectly leads to an overabundance of predators because many predators are attracted to areas of human development and refuse (Schulz & Stock 1993, USFWS 2007, Colwell 2019). Managers have employed a variety of practices, such as symbolic fencing, vehicle and dog restrictions, and public education, to reduce human disturbance to breeding plovers (Weston 2019). Vehicle restrictions and symbolic fencing to provide nesting and brooding Snowy Plovers with refuge from human activity have successfully improved various measures of productivity (e.g., Lafferty *et al.* 2006, Wilson & Colwell 2010, Eberhart-Phillips & Colwell 2014).

Few studies (e.g., Dinsmore *et al.* 2014, Hunt *et al.* 2018) have examined the influence of natural or human-restored sites on Snowy Plover productivity, despite widespread use of restoration to boost population levels of Snowy and Piping *Charadrius melodus* Plovers. In this study, we used a long-term dataset to evaluate and compare the effects of habitat restoration (human-implemented and natural) and human and predator activity on Snowy Plover nest survival.

METHODS

Study area and population

We studied a small population of Snowy Plovers in Humboldt County, California, USA during 2004–2017. This population has experienced large fluctuations in size (19–74 breeding individuals; Colwell *et al.* 2017) and has been considered a population sink in most years due to low reproductive success (Eberhart-Phillips & Colwell 2014). Snowy Plovers breed on approximately 80 km of sandy, ocean-fronting beaches (Fig. 1; Colwell *et al.* 2017). Beaches are backed by bluffs or dunes and form expansive sand spits at river mouths and lagoons (Page & Stenzel 1981). Beach vegetation varies from sparse native dune flora (e.g., sand verbena *Abronia* spp., Dune Grass *Elymus mollis*), to dense stands of introduced plants (mainly European Beach Grass, Iceplant *Carpobrotus edulis*, and Yellow Bush Lupine *Lupinus arboreus*). Debris fields of driftwood, stones, shells, trash, hydrozoans *Velella velella*, carapaces, and dried vegetation (e.g., Eelgrass *Zostera marina*) form seasonally during winter storms and high tides, especially on sand spits (Colwell *et al.* 2010, Leja 2015). Snowy Plovers previously bred on riverine gravel bars along approximately 15 km of the lower Eel River (Colwell *et al.* 2010); however, we excluded gravel bar sites from this analysis because these represent a different habitat type where no human-restoration occurs.

Field methods

Observers from a collaboration of agencies began surveys in March and ended monitoring when the last chick fledged (usually September). Sites with known breeding activity were systematically surveyed once or twice a week during the morning (dawn–noon), and surveyors located nests by tracking or observing adults exhibiting breeding behavior (e.g., courting, incubating). Upon discovery of a nest, observers used a GPS unit to record its location and floated the eggs to determine nest age (Liebezeit *et al.* 2007) if discovered after clutch completion (three eggs). The intensity of monitoring varied annually and across sites, such that the interval between successive nest checks to confirm status ranged from one to 15 days. Observers determined the nest to have hatched by the presence of downy chicks (nearly all broods were banded at hatch), or to have failed if the eggs were abandoned, buried, or disappeared before the expected hatch date. Surveyors inferred the cause of failure from the presence of tracks (predator, human, vehicle, horse, or dog), scat, buried eggs, or eggshell remains. The common causes of nest failure included tidal overwash, sand burial, predation, human activity, and abandonment (Colwell *et al.* 2017).

During all regular surveys for Snowy Plovers, observers collected ancillary data to index the activity of humans and predators at all sites. Observers conducted point

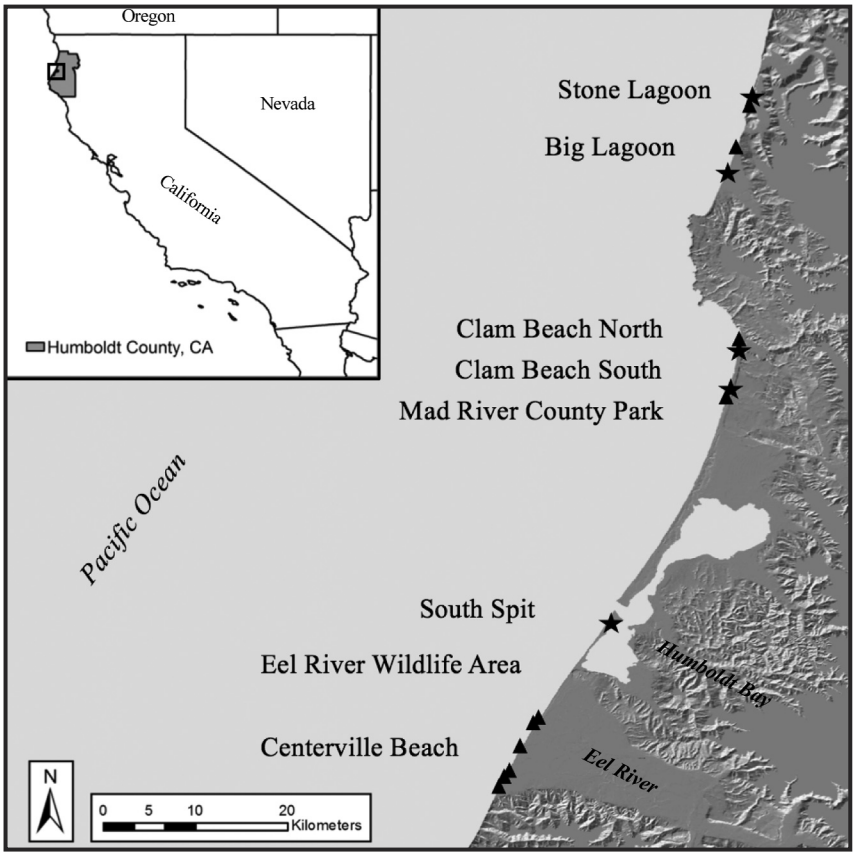

Fig. 1. Location of study sites in Humboldt County, California, USA and areas of human-implemented (★) and natural (▲) habitat restoration.

counts at 20-min intervals to record the total number of humans, dogs, horses, vehicles, raptors, and corvids within a 500-m radius of their current position on the beach, as well as visibility. Colwell *et al.* (2010, 2019) provide details on these methods.

Data and analysis

We analyzed data (n = 610 unexclosed nests) collated over 14 years (2004–2017) at eight sites in Humboldt County, California (Fig. 1). Exclosed nests (n = 67) were excluded from the analysis because these nests have artificially increased survival (Hardy & Colwell 2008, Dinsmore *et al.* 2014, Pearson *et al.* 2014).

We used annual satellite imagery in Google Earth Pro (version 7.3.14507 [64-bit], Google Inc., USA) from mid-breeding season (June) to visually assign nests to one of three restoration categories: unrestored, human-restored, or naturally restored (see Leja 2015). Human-restored areas (HRAs) occurred where agencies removed invasive plants, graded the foredune (recontouring), and/or spread oyster shells. HRAs differed in treatment method and intervals, size, and age, but limited sample size prevented further categorization of HRAs by type. We defined naturally restored areas to be sand spits, river mouths, and blowouts (hollows formed by erosion of the foredune; Hesp 2002) that showed clear signs of overwash during high tide events, winter storm surges, or seasonal flooding that resulted in natural scouring of vegetation and deposition of debris. We categorized all other stretches of beach as unrestored, as no active restoration or major scouring events occurred there (i.e., narrow beaches backed by tall *A. arenaria*-covered foredunes).

For each site, we created an annual index of corvid and human activity by calculating the average number of corvids, vehicles, and 'foot' traffic detected on point counts (i.e., annual site mean). We derived an index of foot traffic by summing the annual site means for humans, dogs, and horses. The results of a principal components analysis support the separation of human activity into foot and vehicle traffic (see Raby 2018). We did not include raptors in predator activity because they are not significant egg predators in this region (Burrell & Colwell 2012, Colwell 2019). For sites where the number of annual point counts was insufficient ($n \leq 10$) to represent activity, we imputed the 2004–2017 site mean (n = 5 site-years). We excluded point counts with visibility less than 400 m from the analysis. We assumed a high detection probability for corvids, foot traffic, and vehicles due to the open nature of the beach habitat surveyed, high frequency of point counts over multiple seasons, and their generally conspicuous behavior and comparatively large physical size.

We used the nest survival model in MARK (White & Burnham 1999, Dinsmore *et al.* 2002) implemented in package RMark (Laake 2013) in R (R Core Team 2016) to estimate daily survival rate of nests (DSR). MARK uses a maximum likelihood approach to estimate DSR (Dinsmore *et al.* 2002) and its associated variance from exposure days (Rotella 2006). The model requires four basic inputs: 1) day of discovery, 2) last day seen active, 3) last day checked, and 4) nest fate (0 = successful; 1 = failed). There is currently no available goodness-of-fit test for the nest survival model in MARK (Dinsmore *et al.* 2002, Rotella 2006); however, we included a null model, which is relatively improbable, to help evaluate the fit (i.e., 'usefulness') of the other candidate models (Anderson 2008). We converted calendar dates to numerical days (day-of-season), which is the format required by MARK, by designating the earliest day of nest discovery over all the years as the first occasion (Day 1 = 4 March), and the latest day a nest was checked as the last occasion (Day 171 = 21 August; Dinsmore & Dinsmore 2007). We defined a nest as successful if at least one egg hatched. A few nests (n = 7) that observers checked twice in a day failed between the time of discovery and the subsequent nest check; in these instances, we used an exposure period of one day. We included up to a maximum of 39 exposure days, which is longer than the average nesting period of 33 days (5 days of laying and 28 days of incubation; Page *et al.* 2009), in order to incorporate information from successful nests that had longer laying or incubation periods than average. For eight nests with prolonged incubation (generally owing to inviable embryos), we truncated exposure days at 39 because these outliers would bias survival high. We followed Dinsmore *et al.* (2002) in including nest age in the candidate model set to help address potential issues arising from individual heterogeneity. We included an individual covariate of nest age upon discovery, which was used to calculate the age of each nest on each day of the nesting season in RMark (Rotella 2006). For nests with unknown age that were found as a full clutch (i.e., failed before the eggs could be floated; n = 110), we imputed the median nest age on discovery (7 days) of known-age (hatched) nests that were found as full clutches. The large number of imputed nest ages (18%) could make the effect of nest age less perceptible (Smith & Wilson 2010); however, we chose to include the larger dataset (imputed nest ages) to retain as much information as possible.

We used a staged modeling approach (e.g., Lebreton *et al.* 1992, Dinsmore *et al.* 2002, Hood & Dinsmore 2007, Dinsmore *et al.* 2014, Pearson *et al.* 2014) to investigate nest survival as a function of group and individual covariates. None of the covariates were highly correlated and therefore all covariates could be included in the same model (highest correlation between corvids and foot traffic [r = 0.356]; Catlin *et al.* 2011). Following Dinsmore *et al.* (2014), we first built a 'baseline model' in two stages to 'control' for known variation in nest survival that management cannot affect, as natural variation in these variables may influence the analysis. While many ecological factors (e.g., clutch size [Dinsmore *et al.* 2014], incubation behavior [Smith *et al.* 2012]) could influence nest survival, we chose to include only the four main factors most prevalent in the literature (year, site, nest age, and a within-season time trend). In stage one, we compared all single and additive combinations of year and within-season variation (constant [null model], linear [T], and quadratic time [TT] trends) to examine temporal variation within and between breeding seasons. In stage two, we added all single and additive combinations of nest age and site to the top model(s) from stage one. We chose to include nest age and a within-season time trend in the same model even though these are possibly confounded because there was considerable variation in initiation dates over the years, and Snowy Plovers can have multiple nests in a breeding season (Warriner *et al.* 1986, Smith & Wilson 2010). Likewise, we included site and year in the analysis despite also using annual site means (corvid, foot, and vehicle covariates) as they still account for unknown sources of variation (e.g., weather, prey availability, population size and density). In stage three, we examined the influence of the limiting factors (predator activity, human activity, and restoration) by adding the four main covariates singly (corvids, foot traffic, vehicle traffic, and restoration) to the top baseline model(s) from stage two.

We used an information-theoretic approach to evaluate the relative strength of candidate models. The strength of evidence for each model in each stage was assessed using Akaike Information Criteria corrected for small sample sizes (AICc), and Akaike weights (w_i) and differences (ΔAICc; Burnham & Anderson 2002). When advancing from one stage to the next, we retained the model(s) with ΔAICc ≤ 7 and a 95% CI of the effect size ($\hat{\beta}$) that did not overlap zero, and we examined deviance at each stage to look for the presence of pretending variables (Burnham & Anderson 2002, Arnold 2010). We calculated evidence ($w_{top\ model}$ / w_i) and odds ratios (OR; $e^{\beta i}$) to quantify the strength of evidence for candidate models and covariates. An odds ratio contrasts the odds of two events, such that OR = 1 would mean there is no difference in DSR between groups or with a one-unit change in the covariate. We used sum contrasts in RMark to estimate the grand mean across all sites and/or years which were used to calculate predicted DSRs and estimated the associated variance with the Delta method (White & Burnham 1999).

RESULTS

We estimated nest survival using data from 610 nests at eight sites in Humboldt County, California over 14 years (2004–2017) and spanning 4 Mar–21 Aug (effective sample size = 6,825). Apparent hatching success (AHS; number of nests that hatched at least one egg divided by the total number of nests) was 23.6% (144 hatched), with the northernmost (Stone and Big Lagoons) and southernmost (South Spit, Eel River Wildlife Area, and Centerville Beach) sites having roughly four times higher AHS than the middle sites (Clam Beach North and South, and Mad River County Park).

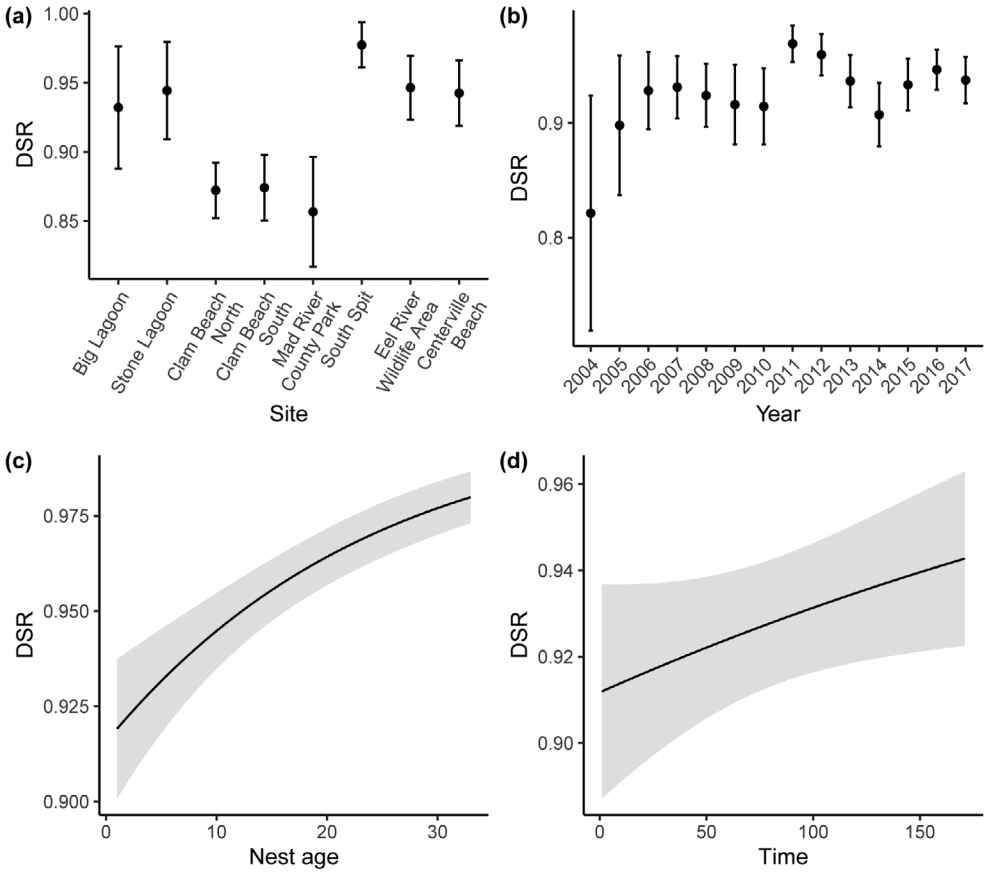

Fig. 2. Predicted daily survival rate (DSR + 95% CI) for Snowy Plover nests from the top baseline model (Year + T + Site + NestAge; Table 1) with the grand mean for site and/or year and the average day-of-season (85; 27 May) and nest age at discovery (4 days). **a)** DSR across all eight study sites. **b)** DSR across all years of the study (2004–2017). **c)** DSR across the 33-day nesting period. **d)** DSR across the 171-day nesting season.

Observers classified cause of failure as unknown (i.e., nest cup empty with no conclusive evidence of cause of failure; n = 276; 45.2% of total nests) for most nests that failed to hatch. The most prevalent known cause of nest failure was predation (n = 112; 18.4%), followed by abandonment (n = 31; 5.1%), tidal overwash (n = 19; 3.1%), sand burial (n = 18; 3.0%), and human activity (n = 10; 1.6%). Corvids were implicated in most cases of predation (78.6% of depredated nests, n = 88) and mammals (Virginia Opossum *Didelphis virginiana*, Striped Skunk, and Gray Fox) in 7.1% (n = 8) of depredated nests.

Human and corvid activity

We used a total of 21,074 point counts to derive indices of human and corvid activity. The number of annual point counts per site ranged from 17 (Stone Lagoon in 2014) to 971 (Clam Beach North in 2015). Surveyors observed corvids most frequently (non-zero counts = 28%; max = 59 on a single point count), followed by humans (non-zero counts = 23%; max = 419 [corresponding to clamming events]), dogs (non-zero counts = 13%; max = 17), vehicles (non-zero counts = 5%; max = 39), and, lastly, horses (non-zero counts = 1%; max = 7). Clam Beach (North and South) had both the highest average foot and vehicle traffic, as well as the largest variance (95% CI) in averages over the years, with Clam Beach North having the highest human activity overall. All other sites had comparatively low foot and vehicle traffic. Highest corvid activity (average number of corvids seen on a point count) occurred at Clam Beach (North and South) and Mad River County Park. The two northernmost sites (Big and Stone Lagoons) and two southernmost sites (Eel River Wildlife Area and Centerville Beach) had comparatively low corvid activity, and South Spit had the lowest average number of corvids seen on a point count overall.

Nest survival

We constructed 13 candidate nest survival models, with six models compared in stage one, three additional models in stage two, and four models added to the final stage (Table 1). A single top baseline model emerged from stage two (w_i = 1.000). In this model, nest survival varied by site and year (Fig. 2a,b), and increased with nest age and as the season progressed (positive linear time trend; Fig. 2c,d). Nest age had a strong positive effect ($\hat{\beta}$ = 0.046, 95% CI = 0.032–0.060, OR = 1.047) on DSR, whereas the evidence was weaker for a positive linear time trend ($\hat{\beta}$ = 0.003, 95% CI = –0.0004–0.006, OR = 1.003).

The top model ($w_i = 0.751$) from the final stage of analysis combined the additive effects of the baseline model (year, site, linear time trend, and nest age) with restoration (Table 1). Natural and human-implemented restoration both had a positive effect on nest survival, when contrasted with unrestored areas (natural: $\hat{\beta} = 0.391$, 95% CI = 0.115 –0.666; human: $\hat{\beta} = 0.182$, 95% CI = –0.124–0.487; Fig. 3). The absence of restoration negatively influenced DSR. Conversely, the odds of daily nest survival increased 48% (OR = 1.478, 95% CI = 1.122–1.946) in naturally restored areas when compared to unrestored habitat (with all other covariates held constant). Human-implemented restoration had a weaker and more variable effect on nest survival than natural restoration. The odds of daily nest survival were 20% higher in HRAs than in unrestored habitat (OR = 1.199, 95% CI = 0.883–1.628), but precision was low; the odds ratio 95% CI overlapped one. South Spit HRA had the highest DSR and lowest variance, and Clam Beach North HRA had the lowest DSR and a larger variance (Fig. 4). The second-ranked model ($w_i = 0.095$) was simply the baseline model (Table 1). The restoration model was approximately eight times more likely than the baseline model, and was 12–21 times more likely than the other main covariate models. The relationship between corvid activity ($\hat{\beta} = 0.142$, 95% CI = –0.116–0.400), foot traffic ($\hat{\beta} = 0.005$, 95% CI = –0.063–0.072), and vehicle traffic ($\hat{\beta} = -0.315$, 95% CI = –0.945–0.316) and nest survival was not strongly supported.

DISCUSSION

Our results from a long-term dataset show that habitat restoration (natural and human-implemented) had a positive effect and the greatest influence on Snowy Plover nest survival when compared to the other variables we tested. Furthermore, we found that nest survival rates were higher in naturally restored than human-restored areas. When compared to habitat restoration, human and predator activity were not strong predictors of Snowy Plover nest survival. Collectively, these findings have important implications for the recovery of Snowy Plover populations.

Restoration enhances nest survival

Restoration had the largest influence on Snowy Plover nest survival (when compared to human and predator activity), which indicates habitat loss and degradation may be the primary threat to Snowy Plover nest survival in northern California. A large percentage (59%) of nests were in restored habitats, which supports previous research

Table 1. Candidate models for Snowy Plover nest survival at eight sites in Humboldt County, California during 2004–2017. K = number of parameters. ΔAICc = difference in AICc from the final stage (stage three) of the analysis and from within each stage of model building (Stage ΔAICc). Cum. w_i = cumulative weight of all models. Evidence ratio = $w_{top\ model} / w_i$.

Stage	Model	K	AICc	ΔAICc	Stage ΔAICc	w_i	Cum. w_i	Deviance	Evidence ratio
3	Year + T + Site + NestAge + Restor	25	2163.361	0.000	0.000	0.751	0.751	2113.170	–
2	Year + T + Site + NestAge	23	2167.492	4.130	4.130	0.095	0.846	2121.329	7.905
3	Year + T + Site + NestAge + Corvids	24	2168.328	4.967	4.967	0.063	0.909	2120.152	11.921
3	Year + T + Site + NestAge + Vehicle	24	2168.533	5.172	5.172	0.057	0.966	2120.357	13.175
3	Year + T + Site + NestAge + Foot	24	2169.489	6.127	6.127	0.035	1.000	2121.312	21.457
2	Year + T + Site + NestAge	23	2167.492	–	0.000	1.000	–	2121.329	–
2	Year + T + Site	22	2209.503	46.142	42.011	0.000	–	2165.354	–
2	Year + T + NestAge	16	2225.952	62.591	58.460	0.000	–	2193.872	–
1	Year + T	15	2309.840	146.479	0.000	0.647	–	2279.769	–
1	Year + TT	16	2311.055	147.693	1.215	0.353	–	2278.975	–
1	Year	14	2329.737	166.376	19.897	0.000	–	2301.675	–
1	TT	3	2385.386	222.024	75.546	0.000	–	2379.382	–
1	T	2	2387.282	223.920	77.442	0.000	–	2383.280	–
1	Null	1	2411.808	248.447	101.968	0.000	–	2409.808	–

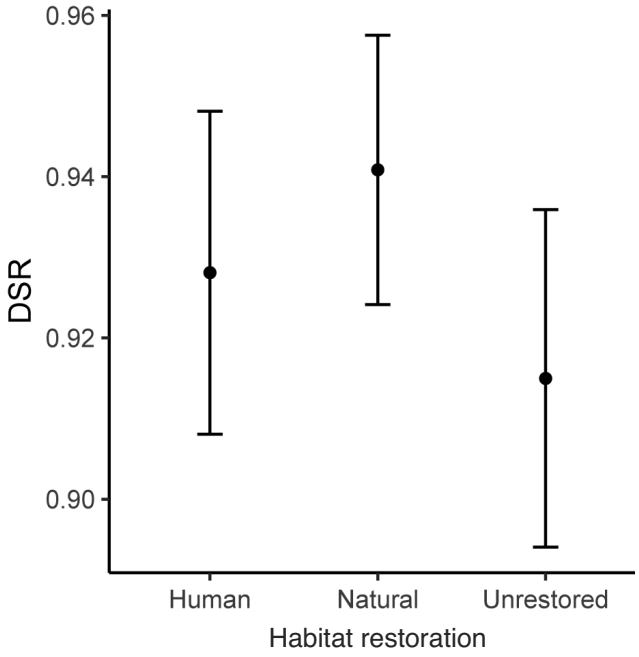

Fig. 3. Predicted daily survival rate (DSR + 95% CI) for Snowy Plover nests from the top model (Year + T + Site + NestAge + Restor; Table 1) for the three habitat restoration categories with the grand mean for site and year, and the average day-of-season (85; 27 May) and nest age at discovery (4 days).

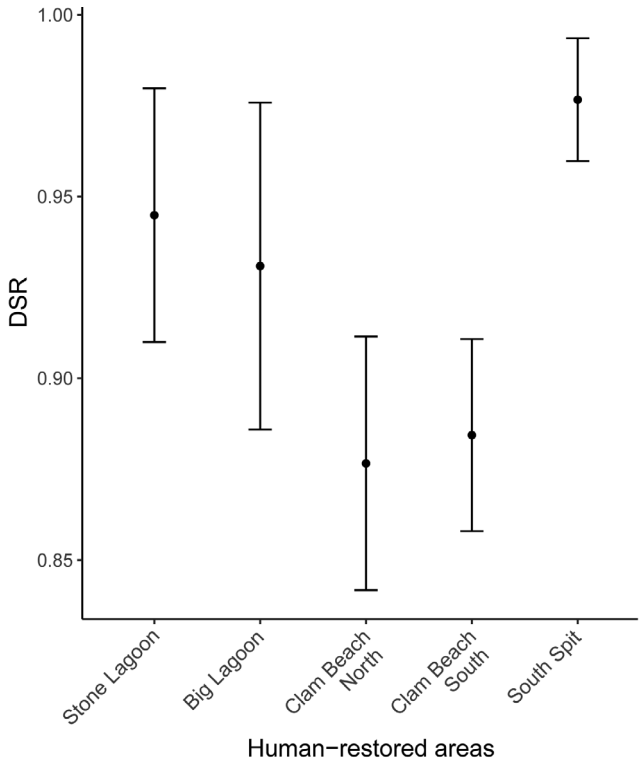

Fig. 4. Predicted daily survival rate (DSR + 95% CI) for Snowy Plover nests in each of the five human-restored areas in Humboldt County, California with the grand mean for year, and the average nest age on discovery (4 days) and day-of-season (85; 27 May).

indicating Snowy Plovers select restored areas (Leja 2015, Colwell *et al.* 2019). In this case, habitat selection may equate to habitat quality because the majority of successful nests were in restored areas (73.6% of total hatched nests), where nest survival is higher. Our results are the first to suggest a strong positive effect of natural restoration on Snowy Plover nest survival. Similarly, Piping Plovers experienced increased productivity when natural overwash processes were restored (Schupp *et al.* 2013), and nest success was elevated in storm-created habitat (Cohen *et al.* 2009). Moreover, Piping Plover nest survival was higher on flood-created sandbars than on engineered sandbars along the Missouri River (Hunt *et al.* 2018). In our study, human-implemented restoration increased nest survival as well, but the effect was more variable than that of natural restoration. The few other studies that have investigated the influence of human-implemented habitat restoration on Snowy Plover productivity have also mostly found a positive relationship, but none have compared the effects of human versus natural restoration processes. For example, Dinsmore *et al.* (2014) found that human-implemented habitat management in Oregon resulted in a greater than two-fold increase in Snowy Plover nest survival. In contrast, Pearson *et al.* (2014) concluded that whether or not a Snowy Plover nest was inside an HRA was not a strong predictor of nest survival in Washington State.

Increased nest survival in restored areas may be due to beneficial changes in habitat characteristics that increase the viewshed (i.e., wider beaches with shorter, sparser vegetation; Koivula & Rönkä 1998) and egg crypsis (more woody debris and shells). Interestingly, the relationship between nest microhabitat characteristics, such as the amount of vegetation and debris, and nest survival is inconsistent among breeding sites across the coastal and interior Snowy Plover populations (Ellis *et al.* 2015). Most studies have found the relationship between nest-site habitat characteristics and survival to be weak or unsupported (e.g., Hardy & Colwell 2012, Sexson & Farley 2012, Pearson *et al.* 2014). This contrast with our results could be caused by the different scales of analysis (site-level in our analysis and nest-site in other analyses). Additionally, Powell & Collier (2000) found that nest survival peaked in the initial year following restoration, and speculated that increased nest survival in newly restored areas might be caused by lower predation rates (predators have not yet found the new nesting area). It has been argued that HRAs may become a population sink over time as predators discover the new nesting areas, nest density increases, and vegetation encroaches (Powell & Collier 2000, Catlin *et al.* 2011, 2015, Hunt *et al.* 2018) while locally breeding Snowy Plovers show high site-fidelity (Powell & Collier 2000). More research is needed to evaluate this hypothesis and elucidate the mechanism(s) by which restoration increases nest survival.

Importantly, our study also suggests that not all HRAs have a similar effect on nest survival. HRAs at Stone

Lagoon, Big Lagoon, and South Spit were the primary drivers of the positive effect of human-implemented restoration in our results, as nest survival was low at both Clam Beach HRAs. It is unlikely that factors relating to the age of the HRA, such as increasing vegetation, caused these differences, as the Clam Beach HRAs are either similar in age or younger than restoration at South Spit and the lagoons. South Spit is the only HRA in our study with shell hash, and the especially high nest survival there could be due to increased egg crypsis. There is little support in the literature, however, to show that nest crypsis is positively related to nest survival for shorebirds (Colwell 2010). For example, Colwell *et al.* (2011) found only weak evidence that crypsis (measured by the number of egg-sized stones) affected nest survival on gravel bars in Humboldt County, California, and Pearson *et al.* (2014) found no effect of shell cover on nest survival in Washington State. The influence of shell cover on nest crypsis requires further study and, moreover, does not explain the increased nest survival we documented at Big and Stone Lagoons. The variation in nest survival rates in human-restored habitat that we found could also stem from differences in treatment method (e.g., manual, mechanical) and intervals between HRAs; however, a previous study in Oregon and Washington State did not find a strong correlation between treatment method and overall Snowy Plover productivity (nest and fledging success; Zarnetske *et al.* 2010). In summary, the underlying cause of variation in nest survival rates between HRAs in our study remains unclear.

Corvid and human activity

We did not find a strong relationship between corvid and human activity and nest survival when compared to habitat restoration in this study. The addition of corvid or human activity covariates did not explain much more variation in nest survival than the baseline model representing natural variation in survival. The last study in 2009 on nest survival in northern California found only weak relationships, with microhabitat nest characteristics (heterogeneity and clutter) ranked first, then corvid activity, and finally human activity (indexed by dog tracks; Hardy & Colwell 2012). Similarly, Herman & Colwell (2015) demonstrated that the strongest predictor of lifetime reproductive success (LRS) in Snowy Plovers was substrate, and human and corvid activity were not significant predictors of LRS. In contrast, a recent study in northern California found that average fledging success was negatively correlated with human and corvid activity (Colwell *et al.* 2019). This suggests that the relative influence of the three limiting factors may vary among different life stages and measures of productivity.

The weak effect of corvid activity on nest survival seemingly contradicts evidence that corvids are the principal nest predators in this region and cause most nest failure (Burrell & Colwell 2012, Colwell 2019); however, other studies in this region also did not find a strong relationship between corvid activity and productivity. For example, reproductive success was higher on gravel bars in northern California despite higher levels of corvid activity (Colwell *et al.* 2005) and Hardy & Colwell (2012) found that the relationship between fine-scale corvid activity (within 100 m of a nest) and nest survival was weak. Alternatively, it is possible that individual corvid behavior is more influential than overall corvid activity (i.e., there is not a simple linear increase in nest mortality with increasing corvid detections). Egg predation is likely opportunistic and influenced by incubation behavior of individual adults (Burrell & Colwell 2012), but single 'problem' corvids can learn to specifically seek out Snowy Plover nests (Liebezeit & George 2002). These individuals conceivably exert a more significant influence on nest survival than overall corvid activity.

Human activity (vehicle and foot traffic) also was not a strong predictor of Snowy Plover nest survival. Our results support previous studies that did not find a correlation between human activity and nest survival, LRS, or nest daily predation rate in northern California (Burrell & Colwell 2012, Hardy & Colwell 2012, Herman & Colwell 2015). The most probable explanation for this is the low level of human activity on beaches in northern California, when compared to more urban coastal areas (Herman & Colwell 2015). Alternatively, the lack of correlation between human activity and nest survival may be attributable to limitations of the index used. Within-season variation in human activity, such as a peak in mid-summer, and individual human behavior was not reflected in our index. Similar to corvids, certain 'problem' human behaviors could exert a stronger influence on nest survival than overall human activity levels (e.g., static versus mobile disturbances; Weston *et al.* 2011). Even though human activity did not have a strong effect on nest survival, it should be noted that the effect of vehicle traffic was stronger (i.e., steepest slope, though with high uncertainty) than foot traffic and had a similar model ranking to corvid activity. This result is unsurprising given that the 'footprint' of a single vehicle can quickly cover considerably more beach than a pedestrian, and thus the potential to crush eggs is higher. Buick & Paton (1989) demonstrated that the presence of just a few vehicles led to an 81% probability of a nest being crushed before hatching for Hooded Plovers *Thinornis cucullatus*. Accordingly, of the common strategies used to manage human disturbance, vehicle closures would be the most beneficial for improving nest survival.

Conservation implications

Productivity studies are a valuable tool used to guide adaptive management strategies by indirectly assessing habitat quality and identifying factors limiting reproductive success. We conclude that conserving naturally restored areas and maintaining and creating HRAs would benefit nest success, as Snowy Plovers both select (Leja 2015, Colwell *et al.* 2019) and have higher nest survival in restored areas. Habitat restoration to improve nest survival should be combined with management actions aimed at other life stages (e.g., adult and chick survival) because high nest survival alone might not lead to population growth (Dinsmore *et al.* 2014). Managers should be careful

not to attract Snowy Plovers to sites that are a potential sink (Ahlering & Faaborg 2006), and should therefore consider factors such as human and predator activity levels (Colwell *et al.* 2019) and proximity to brood-rearing and foraging habitat (Blomqvist & Johansson 1995, Kosztolányi *et al*. 2007, Wiltermuth *et al.* 2015) when creating restoration areas. Creating many temporary, small-scale breeding areas, such as by clearing vegetation at different sites in different years, may mimic natural restoration and the ephemeral nature of habitat availability to which Snowy Plovers are adapted (Powell & Collier 2000, Catlin *et al.* 2011). Bulldozing or creating 'cut-outs' in the foredune could restore natural disturbance regimes (overwash), which may be a self-sustaining way to create new naturally restored areas with less effort (Zarnetske *et al.* 2010, Schupp *et al.* 2013). HRAs are generally closed to the public, which has the added benefit of providing refuge from human disturbance for broods and non-breeding flocks (Powell & Collier 2000, Lafferty *et al.* 2006). Restoration of native dune ecosystems also benefits other wildlife (e.g., native plants and bees) and represents a more integrated ecosystem management approach (Zarnetske *et al.* 2010). Ultimately, management actions should be highly site-specific for this species, and careful and continual evaluation of factors influencing nest survival is recommended before and after implementing targeted management strategies (Sexson & Farley 2012).

ACKNOWLEDGEMENTS

We are indebted to the many field observers who have collected data for this long-term monitoring project, including K. Brindock, S. Brinkman, N. Burrell, A. DeJoannis, L. Eberhart-Phillips, J. Hall, M. Hardy, J. Harris, D. Herman, A. Hoffmann, S. Hurley, T. King, T. Kurz, M. Lau, S. Leja, S. McAllister, J. Meyer, C. Millett, M. Morrissette, J. Muir, S. Mullin, Z. Nelson, D. Orluck, N. Papian, A. Patrick, W. Pearson, S. Peterson, C. Ryan, K. Sesser, A. Transou, and C. Wilson. A special thank you to E. Feucht for helpful insight, and to M. Forys, D. Walker-Brown, T. Camper, and J. Irwin for providing information regarding restoration. We thank K. Hunt and an anonymous reviewer for providing useful comments on this manuscript, and D. Barton for statistical advice. Logistical support and funding was provided by U.S. Bureau of Land Management, U.S. Fish and Wildlife Service, California Department of Parks and Recreation, California Department of Fish and Wildlife, The Wildlands Conservancy, Calaveras Big Trees Association, Chevron Oil Corporation, Eureka Rotary Club, Humboldt County Fish and Game Advisory Commission, Humboldt County Planning Department, Marin Rod and Gun Club, Redwood Region Audubon Society, Stockton Sportsmen's Club, Western Section of The Wildlife Society and the California Department of Fish and Game's Oil Spill Response Trust Fund through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis. Monitoring was conducted under permits from multiple agencies, including Humboldt State University, U.S. Fish and Wildlife Service, California Department of Fish and Wildlife, and California Department of Parks and Recreation.

REFERENCES

Ahlering, M.A. & J. Faaborg. 2006. Avian habitat management meets conspecific attraction: If you build it, will they come? *Auk* 123: 301–312.

Anderson, D.R. 2008. *Model Based Inference in the Life Sciences: a Primer on Evidence*. Springer, New York, NY, USA.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74: 1175–1178.

Blomqvist, D. & O.C. Johansson. 1995. Trade-offs in nest site selection in coastal populations of Lapwings *Vanellus vanellus*. *Ibis* 137: 550–558.

Buell, A.C., A.J. Pickart & J.D. Stuart. 1995. Introduction history and invasion patterns of *Ammophila arenaria* on the north coast of California. *Conservation Biology* 9: 1587–1593.

Buick, A.M. & D.C. Paton. 1989. Impact of off-road vehicles on the nesting success of Hooded Plovers *Charadrius rubricollis* in the Coorong region of South Australia. *Emu* 89: 159–172.

Burnham, K.P. & D.R. Anderson. 2002. *Model Selection and Inference: A Practical Information-Theoretic Approach. Second Edn.* Springer-Verlag, New York, NY, USA.

Burrell, N.S. & M.A. Colwell. 2012. Direct and indirect evidence that productivity of Snowy Plovers *Charadrius nivosus* varies with occurrence of a nest predator. *Wildfowl* 62: 204–223.

Catlin, D.H., J.D. Fraser, J.H. Felio & J.B. Cohen. 2011. Piping plover habitat selection and nest success on natural, managed, and engineered sandbars. *Journal of Wildlife Management* 75: 305–310.

Catlin, D.H., J.D. Fraser & J.H. Felio. 2015. Demographic responses of Piping Plovers to habitat creation on the Missouri River. *Wildlife Monographs* 192: 1–42.

Cohen, J.B., L.M. Houghton & J.D. Fraser. 2009. Nesting density and reproductive success of Piping Plovers in response to storm- and human-created habitat changes. *Wildlife Monographs* 173: 1–24.

Colwell, M.A. 2010. *Shorebird Ecology, Conservation, and Management*. UC Press, Berkeley, CA, USA.

Colwell, M.A. 2019. Predation and predator management. Pp. 127–147 in: *The Population Ecology and Conservation of Charadrius Plovers* (M.A. Colwell & S.M. Haig, Eds.). Studies in Avian Biology No. 52. Taylor Francis, Boca Raton, FL, USA.

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

Colwell, M.A., N.S. Burrell, M.A. Hardy, K. Kayano, J.J. Muir, W.J. Pearson, S.A. Peterson & K.A. Sesser. 2010. Arrival times, laying dates, and reproductive success of Snowy Plovers in two habitats in coastal northern California. *Journal of Field Ornithology* 81: 349–360.

Colwell, M.A., J.J. Meyer, M.A. Hardy, S.E. McAllister, A.N. Transou, R.R. LeValley & 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., E.J. Feucht, M.J. Lau, D.J. Orluck, S.E. McAllister & A.N. Transou. 2017. Recent Snowy Plover population increase arises from high immigration rate in coastal northern California. *Wader Study* 124: 40–48.

Colwell, M.A., M.J. Lau, E.J. Feucht & J.J. Pohlman. 2019. Corvids and humans create ecological traps in otherwise suitable Snowy Plover habitat. *Wader Study* 126: 178–189.

Cruz-López, M., L.J. Eberhart-Phillips, G. Fernández, R. Beamonte-Barrientos, T. Székely, M.A. Serrano-Meneses & C. Küpper. 2017. The plight of a plover: viability of an important snowy plover population with flexible brood care in Mexico. *Biological Conservation* 209: 440–448.

Dinsmore, S.J. & J.J. Dinsmore. 2007. Modeling avian nest survival in program MARK. Pp. 73–83 in: *Beyond Mayfield: measurements of nest-survival data* (S.L. Jones & G.R. Geupel, Eds.). Studies in Avian Biology 34, Cooper Ornithological Society, Camarillo, CA, USA.

Dinsmore, S.J., G.C. White & F.L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83: 3476–3488.

Dinsmore, S.J., M.B. Wunder, V.J. Dreitz & F.L. Knopf. 2010. An assessment of factors affecting population growth of the Mountain Plover. *Avian Conservation & Ecology* 5: art 5.

Dinsmore, S.J., D.J. Lauten, K.A. Castelein, E.P. Gaines & M.A. Stern. 2014. Predator exclosures, predator removal, and habitat improvement increase nest success of Snowy Plovers in Oregon, USA. *Condor* 116: 619–628.

Eberhart-Phillips, L.J. & M.A. Colwell. 2014. Conservation challenges of a sink: the viability of an isolated population of the Snowy Plover. *Bird Conservation International* 24: 327–341.

Ellis, K.S., J.F. Cavitt & R.T. Larsen. 2015. Factors influencing Snowy Plover (*Charadrius nivosus*) nest survival at Great Salt Lake, Utah. *Waterbirds* 38: 58–67.

Hardy, M.A. & M.A. Colwell. 2008. The impact of predator exclosures on Snowy Plover nesting success: a seven-year study. *Wader Study Group Bulletin* 115: 161–166.

Hardy, M.A. & M.A. Colwell. 2012. Factors influencing Snowy Plover nest survival on ocean-fronting beaches in coastal northern California. *Waterbirds* 35: 503–511.

Herman, D.M. & M.A. Colwell. 2015. Lifetime reproductive success of Snowy Plovers in coastal northern California. *Condor* 117: 473–481.

Hesp, P.A. 2002. Foredunes and blowouts: Initiation, geomorphology and dynamics. *Geomorphology* 48: 245–268.

Hood, S.L. & 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. Pp. 124–135 in: *Beyond Mayfield: measurements of nest-survival data* (S.L. Jones & G.R. Geupel, Eds.). Studies in Avian Biology 34, Cooper Ornithological Society, Camarillo, CA, USA.

Hunt, K.L., J.D. Fraser, M.J. Friedrich, S.M. Karpanty & D.H. Catlin. 2018. Demographic response of Piping Plovers suggests that engineered habitat restoration is no match for natural riverine processes. *Condor* 120: 149–165.

Johnson, M.D. 2007. Measuring habitat quality: a review. *Condor* 109: 489–504.

Jones, S.L. & G.R. Geupel. (Eds.) 2007. *Beyond Mayfield: measurements of nest-survival data.* Studies in Avian Biology 34, Cooper Ornithological Society, Camarillo, CA, USA.

Kelly, J.P., K.L. Etienne & J.E. Roth. 2002. Abundance and distribution of the Common Raven and American Crow in the San Francisco Bay area, California. *Western Birds* 33: 202–217.

Koivula, K. & A. Rönkä. 1998. Habitat deterioration and efficiency of antipredator strategy in a meadow-breeding wader, Temminck's stint (*Calidris temminckii*). *Oecologia* 116: 348–355.

Kosztolányi, A., T. Székely & I.C. Cuthill. 2007. The function of habitat change during brood-rearing in the precocial Kentish plover *Charadrius alexandrinus*. *Acta Ethologica* 10: 73–79.

Laake, J.L. 2013. *RMark: an R interface for analysis of capture-recapture data with MARK.* U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Seattle, WA, USA.

Lafferty, K.D., D. Goodman & C.P. Sandoval. 2006. Restoration of breeding by Snowy Plovers following protection from disturbance. *Biodiversity & Conservation* 15: 2217–2230.

Lebreton, J.-D., K.P. Burnham, J. Clobert & D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67–118.

Leja, S.D. 2015. *Habitat selection and response to restoration by breeding Western Snowy Plovers in coastal northern California*. M.Sc. thesis, Humboldt State University, CA, USA.

Liebezeit, J.R. & T.L. George. 2002. *A summary of predation by corvids on threatened and endangered species in California and management recommendations to reduce corvid predation*. California Department of Fish and Game, Species Conservation and Recovery Program Report 2002-02, Sacramento, CA, USA.

Liebezeit, J.R., P.A. Smith, R.B. Lanctot, H. Schekkerman, I. Tulp, S.J. Kendall, D.M. Tracy, R.J. Rodrigues, H. Meltofte, J.A. Robinson, C. Gratto-Trevor, B.J. McCaffery, J. Morse & S.W. Zack. 2007. Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. *Condor* 109: 32–47.

Luginbuhl, J.M., J.M. Marzluff, J.E. Bradley, M.G. Raphael & D.E. Varland. 2001. Corvid survey techniques and the relationship between corvid relative abundance and nest predation. *Journal of Field Ornithology* 72: 556–572.

Martin, T.E. 1993. Nest predation and nest sites. *BioScience* 43: 523–532.

Marzluff, J.M. & E. Neatherlin. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biological Conservation* 130: 301–314.

Muir, J.J. & M.A. Colwell. 2010. Snowy Plovers select open habitat for courtship scrapes and nests. *Condor* 112: 507–510.

Mullin, S.M., M.A. Colwell, S.E. McAllister & S.J. Dinsmore. 2010. Apparent survival and population growth of Snowy Plovers in coastal northern California. *Journal of Wildlife Management* 74: 1792–1798.

National Oceanic & Atmospheric Administration (NOAA). 2018. *What percentage of the American population lives near the coast?* U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service website. Accessed 10 Aug 2018 at: *https://oceanservice.noaa.gov/facts/population.html*

Page, G.W. & L.E. Stenzel. (Eds.) 1981. The breeding status of the Snowy Plover in California. *Western Birds* 12: 1–40.

Page, G.W., L.E. Stenzel, W.D. Shuford & C.R. Bruce. 1991. Distribution and abundance of the Snowy Plover on its western North American breeding grounds. *Journal of Field Ornithology* 62: 245–255.

Page, G.W., L.E. Stenzel, J.S. Warriner, J.C. Warriner & P.W.C. Paton. 2009. Snowy Plover (*Charadrius nivosus*). In: *The Birds of North America*, No. 154 (A. Poole & F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, PA and American Ornithologists' Union, Washington, D.C., USA.

Pearson, S.F., S.M. Knapp & C. Sundstrom. 2014. Evaluating the ecological and behavioural factors influencing Snowy Plover *Charadrius nivosus* egg hatching and the potential benefits of predator exclosures. *Bird Conservation International* 26: 100–118.

Powell, A.N. & C.L. Collier. 2000. Habitat use and reproductive success of Western Snowy Plovers at new nesting areas created for California Least Terns. *Journal of Wildlife Management* 64: 24–33.

R Core Team. 2016. *R: a language and environment for statistical computing.* Version 3.3.2. R Foundation for Statistical Computing, Vienna, Austria. Accessed at: *https://www.R-project.org/*

Raby, K.M. 2018. *Western Snowy Plover nest survival in Humboldt County, California*. M.Sc. thesis, Humboldt State University, CA, USA.

Rotella, J.J. 2006. Nest survival. Chapter 17 in: *Program MARK: A Gentle Introduction* (E. Cooch & G. White, Eds.). Colorado State University, Fort Collins, CO, USA. Accessed 3 Jul 2018 at: *http://www.phidot.org/software/mark/docs/book/*.

Schulz, R. & M. Stock. 1993. Kentish Plovers and tourists: competitors on sandy coasts? *Wader Study Group Bulletin* 68: 83–91.

Schupp, C.A., N.T. Winn, T.L. Pearl, J.P. Kumer, T.J.B. Carruthers & C.S. Zimmerman. 2013. Restoration of overwash processes creates Piping Plover (*Charadrius melodus*) habitat on a barrier island (Assateague Island, Maryland). *Estuarine, Coastal & Shelf Science* 116: 11–20.

Sexson, M.G. & G.H. Farley. 2012. Snowy Plover nest survival in Kansas and effective management to counter negative effects of precipitation. *Journal of Wildlife Management* 76: 1587–1596.

Smith, P.A. & S. Wilson. 2010. Intraseasonal patterns in shorebird nest survival are related to nest age and defence behaviour. *Oecologia* 163: 613–624.

Smith, P.A., I. Tulp, H. Schekkerman, H.G. Gilchrist & M.R. Forbes. 2012. Shorebird incubation behaviour and its influence on the risk of nest predation. *Animal Behaviour* 84: 835–842.

United States Fish & Wildlife Service (USFWS). 2007. *Recovery plan for the Pacific Coast population of the Western Snowy Plover (Charadrius alexandrinus nivosus).* U.S. Department of the Interior, Fish & Wildlife Service, Sacramento, CA, USA.

Warriner, J.S., J.C. Warriner, G.W. Page & L.E. Stenzel. 1986. Mating system and reproductive success of a small population of polygamous Snowy Plovers. *Wilson Bulletin* 98: 15–37.

Weston, M.A. 2019. Disturbance of plovers. Pp. 277–310 in: *The Population Ecology and Conservation of Charadrius Plovers* (M.A. Colwell & S.M. Haig, Eds.). Studies in Avian Biology No. 52. Taylor Francis, Boca Raton, FL, USA.

Weston, M.A., G.C. Ehmke & G.S. Maguire. 2011. Nest return times in response to static versus mobile human disturbance. *Journal of Wildlife Management* 75: 252–255.

White, G.C. & K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(Suppl.): S120–S139.

Wilson, C.A. & M.A. Colwell. 2010. Movements and fledging success of Snowy Plover (*Charadrius alexandrinus*) chicks. *Waterbirds* 33: 331–340.

Wiltermuth, M.T., M.J. Anteau, M.H. Sherfy & A.T. Pearse. 2015. Habitat selection and movements of Piping Plover broods suggest a tradeoff between breeding stages. *Journal of Ornithology* 156: 999–1013.

Zarnetske, P.L., E.W. Seabloom & S.D. Hacker. 2010. Non-target effects of invasive species management: beachgrass, birds, and bulldozers in coastal dunes. *Ecosphere* 1: art 13.