WESTERN SNOWY PLOVER NEST SURVIVAL IN HUMBOLDT COUNTY, CALIFORNIA

By

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ABSTRACT

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Productivity measures, such as nest survival, are often used to indirectly assess habitat quality and guide targeted management practices for the conservation of threatened and endangered species. The coastal population of the Western Snowy Plover (*Charadrius nivosus nivosus*) is listed as threatened due to three limiting factors: human disturbance, loss and degradation of habitat as a result of invasive plants, and increasing predator populations. I examined the relative influence of these three limiting factors on nest survival, using data from 2004 to 2017 at eight sites in Humboldt County, California. I assigned nests (n = 610) to three categories of restoration (unrestored, human- and naturally restored areas) and created an index of human and predator activity using point count data. I used a staged modeling approach under an information-theoretic framework to analyze nest survival in program RMark. Survival varied by year and site, and increased with nest age and as the breeding season progressed. Restoration had the greatest influence on nest survival, and human and corvid activity had a weak effect (i.e., not strong predictors) when compared to restoration. Both natural and human-implemented restoration had a positive effect on nest survival, whereas unrestored areas had a negative effect. Natural restoration had higher and less variable nest survival (i.e., a stronger effect) than human-implemented restoration. I recommend managers focus on conserving, maintaining, and creating restoration areas to enhance nest survival.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

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 to model population growth and viability (Jones and Geupel 2007), along with other vital rates (e.g., juvenile and adult survival). Research suggests adult survival has the greatest influence on shorebird population growth, but the survival of adults is difficult to assess, let alone effectively manage (Colwell 2010, Dinsmore et al. 2010, Mullin et al. 2010, Cruz-López et al. 2017). Thus, monitoring and managing productivity is generally the focus of adaptive management efforts to increase shorebird populations, especially for threatened and endangered taxa. Additionally, scientists consider demographic measures like productivity to be one of the better ways to indirectly measure habitat quality (hereafter, defined as variation in nest survival; Johnson 2007), thereby providing managers with an indispensable means of determining the effectiveness of management actions.

The Western Snowy Plover (*Charadrius nivosus nivosus;* hereafter “plover”) is a small North American shorebird with a distinct coastal population ranging from southern Washington to Baja California, Mexico (USFWS 2007). By the 1980s, plovers were absent from many former breeding locations along the coast (33 out of 53 historical locations; Page and Stenzel 1981), and the population declined from an estimated 2,300 in 1977-1980 to 1,900 in 1988-1989 (Page et al. 1991). The United States Fish and

Wildlife Service (USFWS) listed the Western Snowy Plover population (i.e., within 50 miles of the coast) as threatened in 1993 and designated critical habitat in 1995. The three main factors limiting the coastal population of plovers are increasing predator populations (resulting in high levels of egg and chick loss), human disturbance, and the loss and degradation of habitat (owing primarily to invasive plants [e.g., *Ammophila* spp.], and urban development; USFWS 2007). USFWS assigned six recovery units to the coastal population, with Recovery Unit 2 (RU2) encompassing northern California (CA; Del Norte, Humboldt, and Mendocino counties; USFWS 2007). The plover population in RU2 has experienced large fluctuations in population size and per capita reproductive success (Feucht et al. 2018) and has been considered a population sink in most years due to low reproductive success (Eberhart-Phillips and Colwell 2014).

Of the three limiting factors listed above, 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 [*Urocyon cinereoargenteus*] and red [*Vulpes vulpes*] foxes, Northern Harrier [*Circus hudsonius*], gull [*Larus*] spp., striped [*Mephitis mephitis*] and western spotted skunks [*Spilogale gracilis*]) have been documented taking plover eggs, but corvids (*Corvus corax* and *Corvus brachyrhynchos*) are considered the most consistently significant egg predators (Liebezeit and George 2002, USFWS 2007). Because corvids are highly intelligent, human-commensal, generalist omnivores that have effectively exploited urban and agricultural landscapes (e.g., supplemental food sources), their populations have substantially increased, leading to increased nest predation of threatened and endangered species (Luginbuhl et al. 2001, Kelly et al. 2002, Liebezeit and George 2002, Marzluff and Neatherlin 2006). Video evidence from 21 nests in RU2 show predation by Common Ravens accounted for 70% of Snowy Plover nest failures. Raven activity has also been negatively correlated with per capita fledgling success (Burrell and Colwell 2012). Lethal and non-lethal (e.g., exclosures, taste aversion, translocation) predator control has been used in an effort to combat high levels of plover nest predation across their range (Liebezeit and George 2002, Colwell 2010). Of the non-lethal predator control methods, most research has been on the use of exclosures (wire cages erected to keep predators from eating eggs). Several studies have shown that exclosures can increase nest survival for Snowy Plovers along the coast, but they may also increase nest abandonment and adult mortality (Hardy and Colwell 2008, Dinsmore et al. 2014, Pearson et al. 2014). There is some evidence that lethal predator control can also improve survival of unexclosed 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 increase 8% by 2020 (NOAA 2018). This rise in human activity, and thus potential disturbance, in coastal zones could have negative effects on shorebird populations (e.g., by decreasing productivity, and altering behavior and local distribution; Colwell 2010). Nests are particularly vulnerable to the indirect and direct effects of human disturbance since plovers cannot move the nest in response to changing levels of disturbance (Colwell 2010). Vehicles, pedestrians, and dogs directly crushing eggs has been observed (Colwell et al. 2005, USFWS 2007). Human disturbance can also indirectly alter the behavior of plovers, notably by flushing incubating adults from nests, which may increase predation risk, slow embryo development, and leave the eggs vulnerable to sand burial during high winds (USFWS 2007, Colwell 2010, Burrell and Colwell 2012, Hardy and Colwell 2012). A study in RU2 found that incubating females in low human disturbance areas had higher nest attentiveness and lower variation in incubation behavior, and 11% of the incubation recesses were caused by human disturbance (Hoffmann 2005). Additionally, human activity indirectly leads to an overabundance of predators since many predators are attracted to areas of human development and refuse (Schulz and Stock 1993, USFWS 2007, Hardy and Colwell 2012). Managers have employed a variety of practices, such as symbolic fencing, seasonal beach closures, vehicle and dog restrictions, and public education, to reduce human disturbance to breeding plovers (Colwell 2010). Research has shown that vehicle closures and symbolic fencing to provide refuge to nesting and brooding Snowy Plovers from human activity has successfully improved various measures of productivity in RU2 and other recovery units (e.g., Lafferty et al. 2006, Wilson and Colwell 2010, Eberhart-Phillips and Colwell 2014).

Loss and degradation of plover breeding habitat is largely associated with the rapid expansion of non-native European beach grass (*Ammophila arenaria*; USFWS 2007), which was first planted in Humboldt County, CA in 1901 (Buell et al. 1995). Plovers prefer to nest and make courtship scrapes in relatively flat, open, sparsely vegetated habitats, probably enabling early detection of predators (Page et al. 2009, Muir and Colwell 2010). *Ammophila arenaria* creates immobile, steep, densely vegetated foredunes and backdunes (Buell et al. 1995), lowers arthropod abundance (Slobodchikoff and Doyen 1977), and potentially provides cover for predators (USFWS 2007). Habitat restoration creates suitable plover breeding habitat by using heavy equipment to flatten (recontour) or create “cut-outs” in the foredune, and removing invasive plants through mechanical (bulldozing or disking), chemical (herbicides), or manual (hand-pulling) methods (Zarnetske et al. 2010). Sometimes oyster shells are spread to increase crypsis of eggs and chicks, and, thus survival, by creating a heterogeneous substrate (Colwell et al. 2011). Leja (2015) found that plovers in RU2 preferentially selected restored habitats (84% of nests) that were generally flatter and wider with more debris and less vegetation. Along the Oregon coast, 34% of plover nests were associated with human-implemented habitat restoration areas (HRAs) from 1999 to 2004 (USFWS 2007), and habitat management significantly increased nest survival (Dinsmore et al. 2014).

Researchers have conducted studies on plover nest survival across their range, but to date, there has not been a study examining the relative influence of all three limiting factors (increasing predator populations, human disturbance, and habitat loss and degradation as a result of invasive plants) on nest survival. Furthermore, only a small number of studies (e.g., Dinsmore et al. 2014, Hunt et al. 2018) have examined the influence of natural or human-restored sites on productivity for plovers, despite the widespread use of restoration to boost population levels of Snowy and Piping (*Charadrius melodus*) plovers. While it has been demonstrated that plovers select restored areas, the influence of restoration on reproductive success has not been well-studied. To update management strategies, there is a need for current nest survival estimates, which are especially important in populations with low reproductive success, such as RU2. Nest survival has not been studied in RU2 since 2009 (Hardy and Colwell 2012). The objectives of my study are to use 14 years of nest data to 1) establish a “baseline” model of natural variation in nest survival; 2) determine the relative influences of restoration, predator activity, and human activity on nest survival; and 3) assess whether or not human- and/or naturally restored areas increase nest survival for Western Snowy Plovers at different breeding sites in Humboldt County, CA.

METHODS

Study Area and Population

I studied a small, color-marked (individually or brood-specific) group of plovers in Humboldt County, CA, which contains most of the population in RU2 (Page and Stenzel 1981, Feucht et al. 2018). Population size has varied widely over the years, ranging from 19 to 74 breeding individuals. Plovers breed on approximately 80 kilometers (km) of sandy, ocean-fronting beaches (Figure 1; Colwell et al. 2017). Beaches are backed by bluffs or dunes, and form expansive sand spits at river mouths and lagoons (Page and Stenzel 1981). Beach vegetation varies from sparse native dune flora (e.g., sand verbena [*Abronia* spp.], American searocket [*Cakile edentula*], beach bursage [*Ambrosia chamissonis*], beach morning glory [*Calystegia soldanella*], beach strawberry [*Fragaria chiloensis*]) and dunegrass (*Elymus mollis*), to dense stands of introduced plants (mainly European beach grass [*A. arenaria*], iceplant [*Carpobrotus edulis*], and yellow bush lupine [*Lupinus arboreus*]). Debris fields of driftwood, stones, shells, trash, *Velella velella*, carapaces, and dried vegetation (e.g., brown algae [*Fucus*, *Egregia*, and *Postelsia* spp.], eelgrass [*Zostera marina*]) form seasonally during winter storm events and high tides, especially on sand spits (Colwell et al. 2010, Leja 2015). Plovers have also utilized riverine gravel bars along approximately 15 km of the lower Eel River, which are characterized by egg-sized to large stones with sparse willows (*Salix* spp.) and white sweet clover (*Melilotus alba*; Colwell et al. 2010); however, I excluded gravel bar sites from my analysis because these represent a different habitat type, there are no human-restored areas, and no nests have been detected since 2010 (Feucht et al. 2018).

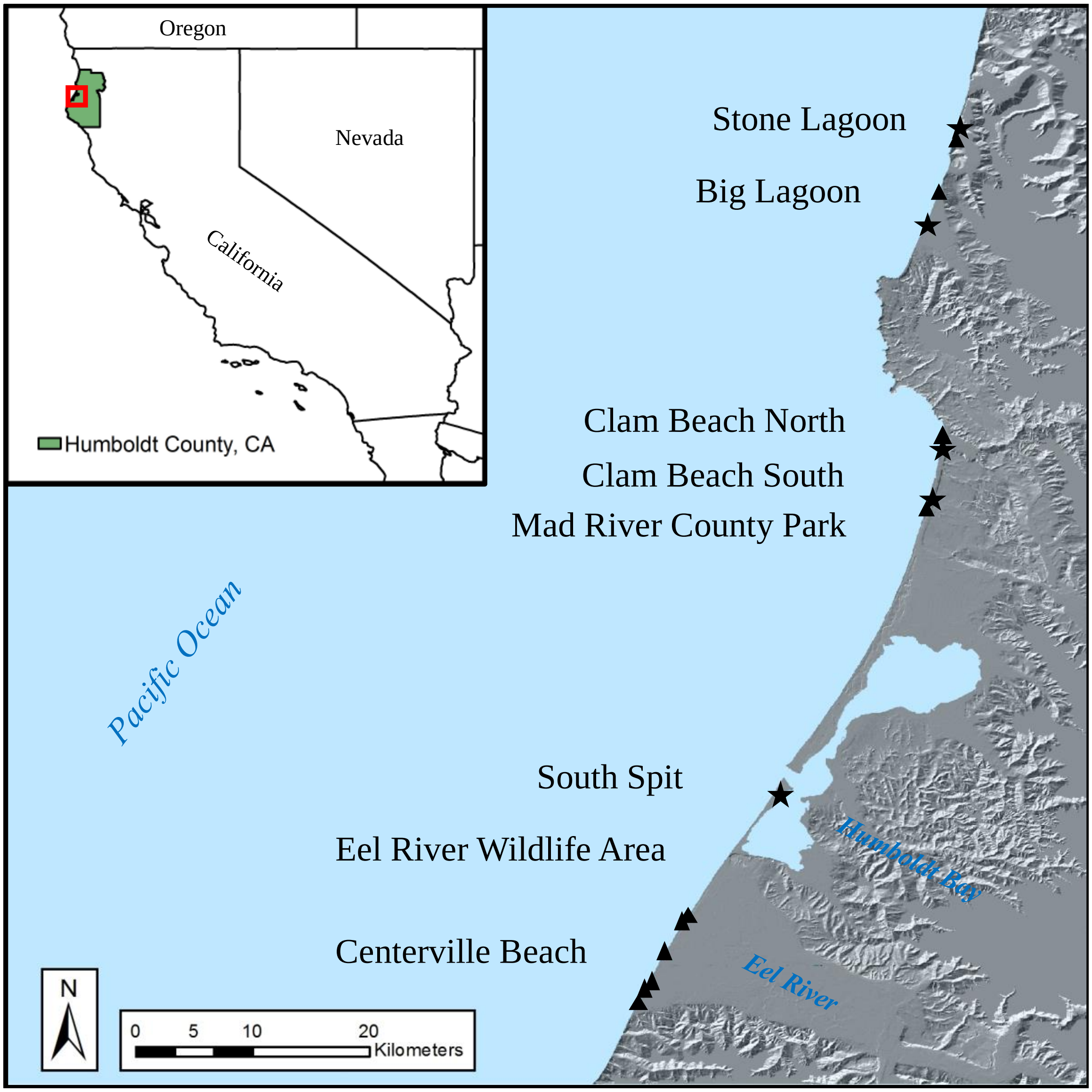

Figure 1. Location of study sites in Humboldt County, CA and areas of human-implemented (★) and natural (▲) habitat restoration (USGS 2006 and 2013, Esri 2017, Humboldt County n.d.).

Field Methods

A collaboration of agencies, including state (California State Parks, California Department of Fish and Wildlife, and Humboldt State University), federal (Bureau of Land Management, National Park Service, and USFWS), and private biological consultants, surveyed beach sites for breeding plovers. Observers began surveys in March and ended monitoring when the last chick fledged (usually late summer). Sites with known breeding activity were systematically surveyed on a biweekly to weekly basis during early morning hours, and observers located nests by tracking or observing adults showing breeding behavior (e.g., courting, incubation). Upon nest discovery, observers used a Global Positioning System (GPS) to record its location (World Geodetic System 1984 [WGS 84] / Universal Transverse Mercator [UTM] Zone 10 North), and floated the eggs to determine nest age if discovered after clutch completion (three eggs; Liebezeit et al. 2007). 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 are banded at hatch), or failed if the eggs were abandoned, buried or disappeared before the expected hatch date. The cause of failure was inferred from the presence of tracks (predator, human, vehicle, horse, or dog), scat, buried eggs, or egg shell remains. The common causes of nest failure include tidal overwash, sand burial, predation, human activity, and abandonment (Colwell et al. 2017). Monitoring is conducted under permits from multiple agencies, including Humboldt State University (IACUC #14/15.W.07-A and #14/15.W.08-A), USFWS (recovery #TE-73361A-1;

banding #23844 and #10457), California Department of Fish and Wildlife (scientific collecting #SC0496) and California Department of Parks and Recreation (scientific research #17-635-005).

During regular surveys for plovers, observers collected ancillary data to measure habitat characteristics, and index the activity of humans and predators. Observers stopped at 20 minute intervals to conduct a point count and sample a three-meter (m) radius ground plot centered on their location. For the point count, observers recorded the total number of humans, dogs, horses, vehicles, raptors, and corvids within a 500 m radius of their position and noted compliance with laws for human activity (e.g., dogs on leash, vehicles driving on waveslope), as well as visibility. After the point count, observers estimated percent cover of vegetation, shells, rocks, woody debris, garbage, wrack, and *V. velella*, and tallied the number of sets of human (e.g., vehicle, dog) or predator (e.g., corvids, fox) tracks within the ground plot. Colwell et al. (2010) provide details on these methods.

Data Set

I used data collated over 14 years (2004-2017) to examine nest survival at eight sites (Stone [SL] and Big [BL] Lagoon, North [CN] and South [CS] Clam Beach, Mad River County Park [MR], South Spit [SS], Eel River Wildlife Area [ERWA], and Centerville Beach [CV]; Figure 1) in Humboldt County, CA. I did not include data from the start of the project before point counts were recorded (2001-2003), or sites with less than ten nests in my analysis (Tolowa Dunes [n = 4], Gold Bluffs Beach [n = 6], Freshwater Lagoon [n = 2], and North Spit [n = 2]). I also omitted 67 nests with exclosures (2004-2006, 2010) since these nests have artificially increased survival (Hardy and Colwell 2008, Dinsmore et al. 2014, Pearson et al. 2014). Lastly, I removed seven nests discovered after predators had consumed eggs because these nests lacked exposure days (see below).

Statistical Analysis

I used the nest survival model (White and Burnham 1999, Dinsmore et al. 2002) with a logit link function in package RMark (Laake 2013) in RStudio (RStudio 2016) to estimate daily nest survival rate (DSR). RMark uses a maximum likelihood approach to estimate DSR (the probability that a nest will survive a single day; Dinsmore et al. 2002) and its associated variance from exposure days (Rotella 2006). The model requires four basic inputs (data) which are: 1) day of discovery, 2) last day seen active, 3) last day checked, and 4) nest fate (0 = successful; 1 = failed). The model assumptions are: 1) nests are correctly aged when discovered, 2) nest fates are known, 3) observers (i.e., discovery and nest checks) do not influence nest survival, 4) nest fates are independent, and 5) nest survival is homogeneous (Dinsmore et al. 2002). My data set meets these assumptions since observers found most nests before clutch completion (68.1%), frequent surveys allowed determination of nest fate (Mabee 1997), disturbance was minimized, and most nests are widely spaced (i.e., only 19% less than 100 m from a conspecific; Patrick and Colwell 2017). Assumption five is difficult to address, so I followed Dinsmore et al. (2002) in including nest age in my candidate model set to help address potential issues arising from individual heterogeneity. There is currently no available goodness-of-fit test for the nest survival model in RMark (Dinsmore et al. 2002, Rotella 2006); however, I included a null model, which is relatively improbable, to help evaluate the fit (i.e., "usefulness") of the other candidate models (Anderson 2008).

I converted calendar dates to numerical days, which is the format required by program MARK, by designating the earliest day of nest discovery over all the years as the first occasion (Day 1 = March 4), and the latest day a nest was checked as the last occasion (Day 171 = August 21; Dinsmore and Dinsmore 2007). Thus, the breeding season in my analysis was 171 days long. I defined a nest to be successful if at least one egg hatched. A few nests that were checked twice in a day failed between the time of discovery and the subsequent nest check (n = 7), in which case the last day checked alive was adjusted to the following day (i.e., one exposure day). I included 39 exposure days, which is longer than the average nesting period of 33 days (five 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 the average. For eight nests with prolonged incubation (generally owing to inviable embryos), I truncated exposure days at 39 since these outliers would bias survival high. Observers checked nests that were suspected to be abandoned or buried by sand at variable intervals throughout the study. I classified the second check after discovery as the last day checked alive for abandoned nests surveyed many more times (i.e., egg(s) persisted on the beach). For nests buried by wind-driven sand, I considered the last day checked to be when the clutch was first seen partially or completely covered by sand, even if eggs resurfaced on subsequent checks.

Nest survival covariates

Habitat restoration. I used Google Earth Pro (Google 2018), nest GPS coordinates, and information (e.g., maps, project initiation date) provided by state and federal agencies (Table 1) to code each nest as being in unrestored, human-restored, or naturally restored areas (see Leja 2015). Human-restored areas (i.e., HRAs) are where agencies have removed invasive plants, graded the foredune (recontouring), and/or spread oyster shells. I also included nests located west of HRAs in the human-restored category since the increased viewshed afforded by vegetation removal may have influenced nest survival. I defined naturally restored areas to be spits, river mouths, and blowouts that show clear sign of overwash during high tide events, winter storm surges or seasonal flooding that results in natural scouring of vegetation and deposition of debris. I considered all other stretches of beach to be unrestored since no active restoration or major scouring events occurred there (i.e., narrow beaches backed by tall *A. arenaria* covered foredunes). I used satellite imagery from mid-breeding season (June) to visually assign nests to restoration categories. Some sites did not have satellite imagery available for every year of the study, in which case I used the year of imagery closest to the year the nest was active. I chose to include human-implemented restoration as only a broad category, even though HRAs differed in treatment method and intervals, size, and age, because there are not enough HRAs (i.e., limited sample size) to support further categorization.

Table 1. Human-implemented habitat restoration areas (HRAs) in RU2 from 2004-2017 with project initiation year and the number of nests in each area. The size of the HRA (hectares [ha]) was provided by the project management agency and do not include any beach habitat located to the west of the HRA. Spot treatment to remove invasive plants (primarily iceplant mats) occurred at Humboldt Lagoons State Park and size (ha) reflects total area surveyed for invasive plants. Maintenance is ongoing at all sites except for Clam Beach County Park. Mechanical treatment is the use of heavy equipment to grade, bulldoze, or disc. Manual treatment refers to hand removal, and shell is the spreading of oyster shell hash.

HRA	Year Initiated	Size (ha)	Treatment	Nests	Sources
Humboldt Lagoons State Park (Big and Stone Lagoons)	2002-2005	110.1	Manual	36	CSP 2006, 2011, 2014, 2017a, 2017b, M. Forys (pers. comm., 2018)
Little River State Beach	2005, 2009	17.8	Manual, mechanical	51	CSP 2006, 2011, 2014, 2017a, 2017b, Forys 2011
Clam Beach County Park	2007-2008	21.4[a]	Manual, mechanical	81	MRB 2002, Caltrans 2009
South Spit Cooperative Management Area (FRA/HRA)	2004, 2008	20.6	Manual, mechanical, shell	24	BLM 2011, J. Irwin (pers. comm., 2018)

[a] Area has been reduced since the start of the project due to the northward migration of the Mad River mouth.

<u>Predator and human activity</u>. For each site, I created an annual index of corvid and human activity by calculating the average number of corvids (*C. corax* and *C. brachyrhynchos*), vehicles, and “foot” traffic (i.e., annual site mean) detected on point counts (Appendix A). I derived an index of foot traffic by summing the annual site means

for humans, dogs, and horses (i.e., the cumulative average number of humans, horses, and dogs per site-year). The results of a principal components analysis support the separation of human activity into “foot” and vehicle traffic (Appendix B). I did not include raptors (e.g., *C. hudsonius*) in predator activity because they are not significant egg predators in this region (Burrell and Colwell 2012). For sites where the number of annual point counts was insufficient (n = 10 or fewer) to represent activity, I imputed the 2004-2017 site mean (n = 5 site-years; Appendix A). I excluded point counts with visibility less than 400 m or that were spatially inaccurate from my analysis. There were no issues with model convergence, therefore, I chose to not standardize vehicle, foot, and corvid covariates in order to facilitate visualization of results.

Nest age. I 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). I assumed that nests found with one or two eggs that subsequently failed were in the process of being completed (Warriner et al. 1986), and are, therefore, of known age since observers did not float eggs at these nests. For nests with unknown age that were found as a full clutch (i.e., failed before the eggs could be floated; n = 110), I imputed the median nest age on discovery (seven days) of known age (i.e., hatched) nests that were found as full clutches. It is possible that an effect of nest age may not be detectable because of the large number of imputed nest ages (18%; Smith and Wilson 2010); however, I chose to include the larger dataset (imputed nest ages) to retain as much information as possible.

Staged modeling approach

I used a staged (also termed “hierarchical,” “sequential,” or “stepped”) modeling approach (e.g., Lebreton et al. 1992, Dinsmore et al. 2002, Hood and Dinsmore 2007, Dinsmore et al. 2014, Pearson et al. 2014) to investigate nest survival as a function of group and individual covariates (Table 2). This approach has the advantages of parsimony by reducing the number of candidate models in the model set (Dinsmore et al. 2002), facilitating comparisons to previous Snowy Plover nest survival research (e.g., Hood and Dinsmore 2007, Dinsmore et al. 2014, Pearson et al. 2014), “controlling” for natural variation before examining main effects, as well as reducing the risk of spurious effects from running all possible models (Burnham and Anderson 2002). The disadvantages to this approach, however, are that the number and order of covariates in each “stage” is arbitrary, which might influence the results, and the inability to model average creates model selection uncertainty (Burnham and Anderson 2002). None of the covariates were highly correlated (i.e., all below 0.5), therefore all covariates could be included in the same model (highest correlation between corvids and foot traffic [$r = 0.356$]; Catlin et al. 2011). I did not include interaction terms in my analysis in order to avoid overfitting my models. It is plausible that there is an interaction between site, year, and/or a within-season time trend (Sexson and Farley 2012, Ellis et al. 2015, Cruz-López et al. 2017); however, the sample sizes for most site-years in this dataset precludes meaningful estimates from these interactions.

Table 2. Covariates used in plover nest survival analysis with description, range, mean ± standard deviation (SD), and stage in analysis. Brackets are terms used in the models. Stage one and two was used to establish a baseline model of natural variation in survival and stage three to compare the relative influence of main predictors (variables that can be influenced by management) on survival.

Stage	Predictor	Description	Range	Mean ± SD
3	Predator activity [Corvids]	Average number of corvids (American Crow and Common Raven) per point count for each site-year	0.03 - 4.13	1.17 ± 0.75
	Human activity:			
3	Foot traffic [Foot]	Summed averages of the number of humans, dogs, and horses per point count for each site-year	0 - 16.57	2.02 ± 2.62
3	Vehicle traffic [Vehicle]	Average number of vehicles seen per point count for each site-year	0 - 1.21	0.09 ± 0.24
3	Habitat restoration [Restor]	Categorical variable representing 3 types of habitat restoration	Human, unrestored, natural	NA
2	Site [Site]	Categorical variable representing 8 sites	SL, BL, CN, CS, MR, SS, ERWA, CV	NA
2	Nest age [NestAge]	The age of the nest upon discovery in days (includes laying)	1 - 32	4.32 ± 4.29
1	Year [Year]	Categorical variable representing the breeding season year to examine between season variation	2004 - 2017	NA
1	Within-season variation [Null, T, TT]	Constant, linear and quadratic time trend models to examine within-season variation	Null, T, TT	NA

Following Dinsmore et al. (2014), I first built a “baseline model” in two stages to “control” for known variation in nest survival that cannot be affected by management since natural variation in these variables may influence my analysis. While there are many ecological factors (e.g., food availability [Pruner 2010], clutch size [e.g., Dinsmore et al. 2014], and incubation behavior [e.g., Smith et al. 2012]) that could influence nest survival, I 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, I compared all single and additive combinations of year and within-season variation (constant [null model], linear, and quadratic time trends) to examine temporal variation within and between breeding seasons. In stage two, I added all single and additive combinations of nest age and site to the top model(s) from stage one. I 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 plovers can have multiple nests in a breeding season (Warriner et al. 1986, Smith and Wilson 2010). Likewise, I 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, I 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. I used 2004, Big Lagoon, and unrestored habitat as the year, site, and restoration reference groups respectively (i.e., human and natural restoration are “treatment” groups).

I 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 (AIC_c), and Akaike weights (w_i) and differences (ΔAIC_c; Burnham and Anderson 2002). I advanced the single "best" or multiple top models with $\Delta AIC_c \leq 7$ and a $\hat{\beta}$ 95% confidence interval (CI) that does not overlap zero to the next stage, and I examined deviance at each stage to look for the presence of pretending variables (Burnham and Anderson 2002, Arnold 2010). I calculated evidence ($w_{top\ model}$ / w_i) and odds ratios (e^{β_i}) to quantify the strength of evidence for candidate models and covariates. An odds ratio (OR) contrasts the odds of two events, such that a ratio of one would mean there is no difference in DSR between groups or with a one-unit change in the covariate (i.e., the null case). I used the Delta method (White and Burnham 1999) to calculate the variance of period survival rates (the probability that a nest survives the entire average nesting period [DSR^{33}]) in the "car" package (Fox and Weisberg 2011) in RStudio (RStudio 2016).

RESULTS

I estimated nest survival using data from 610 nests at eight sites in Humboldt County, CA over 14 years (2004-2017) and spanning March 4-August 21 (effective sample size = 6,825). The total number of nests at each site ranged from 241 (Clam Beach North; 39.5% of total nests) to 17 (Big Lagoon; 2.8% of total nests; Appendix C). Apparent hatching success (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 sites (South Spit, Eel River Wildlife Area, and Centerville Beach) having roughly four times higher apparent hatching success than the middle sites (Clam Beach North and South, and Mad River County Park). South Spit had the highest overall apparent hatching success (72.4%). Annual apparent hatching success varied from 6.7% (2004) to 45.2% (2011).

Apparent hatching success was highest in restored habitats, and was similar between natural and human-restored areas (30.5% [51 hatched] and 28.6% [55 hatched] respectively). Restored areas (natural and human) had roughly double the apparent hatching success of unrestored habitat (15.1%; 38 hatched). Plovers initiated slightly more nests in HRAs (n = 192; 31.5% of total nests) than in naturally restored areas (n = 167; 27.4% of total nests). Unrestored areas had only approximately 10% more nests (n = 251; 41.1% of total nests), despite there being significantly more unrestored habitat than both naturally and human-restored areas (Figure 1). The majority of hatched nests over the 14 years occurred in restored areas (73.6%, $\bar{x}$ = 72.2%). Human- and naturally restored areas each contributed on average approximately 40% of the hatched nests on an annual basis (40% and 38.2% respectively).

The HRAs at different sites had variable apparent hatching success. South Spit HRA had the highest (79.2%, $\bar{x}$ = 70%), whereas Little River State Beach and Clam Beach County Park HRAs had the lowest apparent hatching success (7.8% [$\bar{x}$ = 13.1%] and 18.5% [$\bar{x}$ = 14.9%] respectively) over the 14 years. The HRAs within Humboldt Lagoons State Park (Big and Stone Lagoons) had similar overall apparent hatching success (47.1% [$\bar{x}$ = 50%] and 47.4% [$\bar{x}$ = 52.1%] respectively). The annual mean apparent hatching success is 4.7 to 5.3 times higher at South Spit HRA than at Clam Beach HRAs, and 1.3 to 1.4 times higher than at the northernmost HRAs (Big and Stone Lagoons). Plover use of HRAs ranged from 11 years (Clam Beach County Park, n = 81 nests) to four years (South Spit, n = 24 nests).

The cause of failure was unknown (i.e., nest cup empty with no conclusive evidence of cause of failure) for most nests that failed to hatch (45.2% of total nests; Table 3). Known causes of failure included predation (18.4%; direct observation of predator eating eggs, eggshell fragments/yolk, and/or predator tracks directly approaching nest cup), abandonment (5.1%; no sign of attendance by adults over several visits), tide (3.1%; nest cup overwashed by high tide and egg(s) displaced or gone from cup), wind (3.0%; buried by wind-driven sand or damaged in high winds), and human activity (1.6%; human, dog, vehicle, or horse tracks directly approaching nest cup and egg(s) absent or crushed; Colwell et al. 2011). Corvids were implicated in most cases of predation (14.4%) and mammals (Virginia opossum [*Didelphis virginiana*], striped skunk, [*M. mephitis*], and gray fox [*U. cinereoargenteus*]) in 1.3% of cases.

Table 3. Plover nest fates at eight sites in Humboldt County, CA from 2004-2017. Successful nests are defined as hatching at least one egg. See text for nest fate definitions.

Fate	SL	BL	CN	CS	MR	SS	ERWA	CV	Total (%)
Hatched	9	8	28	19	5	21	25	29	144 (23.6)
Abandoned	3	-	14	5	3	3	1	2	31 (5.1)
Human	-	-	6	2	-	-	-	2	10 (1.6)
Predation	4	5	39	39	5	3	9	8	112 (18.4)
Corvid	1	2	36	33	5	2	3	6	88 (14.4)
Mammal	1	-	-	2	-	1	4	-	8 (1.3)
Unknown	2	3	3	4	-	-	2	2	16 (2.6)
Wind	-	1	7	8	1	-	-	1	18 (3.0)
Tide	-	-	5	5	3	-	4	2	19 (3.1)
Unknown [a]	3	3	142	68	38	2	9	11	276 (45.2)

[a] Includes nine cases where predation was suspected, but the evidence was not conclusive (i.e., predator tracks in general area but do not directly approach nest cup).

Disturbance Covariates

I used a total of 21,074 point counts to derive indices of human and predator activity. The number of point counts taken for a site-year ranged from 17 (SL14) to 971 (CN15; Appendix A). On point counts, 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 were the least frequently observed potential disturbance (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 North Clam Beach having relatively high human activity (Figure 2A). Big Lagoon, Stone Lagoon, and Mad River County Park had similar foot and vehicle traffic averages that are comparatively low overall. The southernmost sites (South Spit, Centerville Beach, and Eel River Wildlife Area) had similar foot and vehicle traffic averages, with higher vehicle traffic and lower foot traffic than Big Lagoon, Stone Lagoon, and Mad River County Park.

Corvid activity (average number of *C. corax* and *C. brachyrhynchos* seen on a point count) was highest at Clam Beach (north and south) and Mad River County Park (Figure 2B). 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. Big Lagoon and Mad River County Park had the largest variance in corvid averages over the 14 years of data collection.

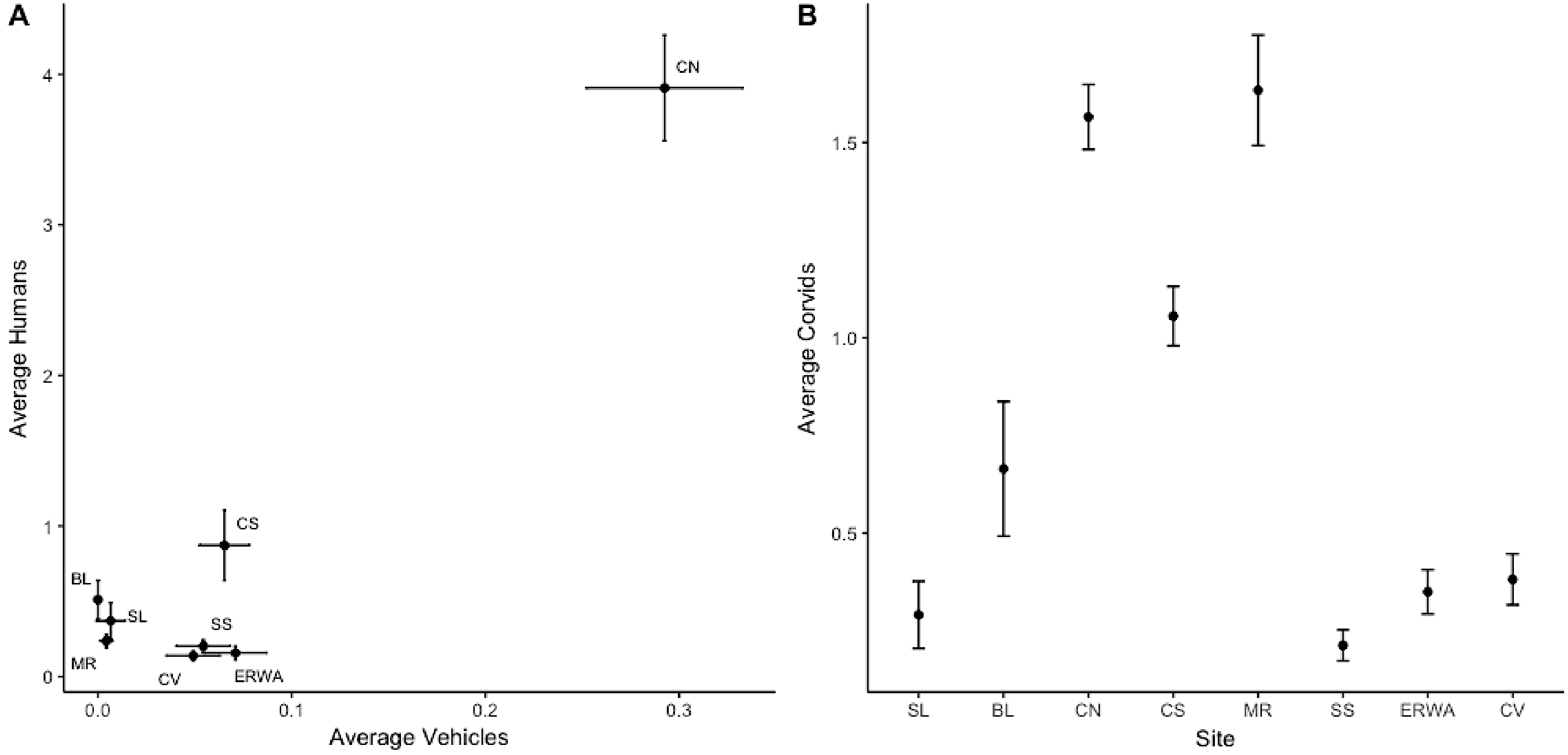

Figure 2. The average number of (A) humans, vehicles, and (B) corvids (*C. brachyrhynchos* and *C. corax*) seen per a point count at eight sites in Humboldt County, CA from 2004-2017. Error bars represent 95% CIs. Humans were chosen to represent "foot" traffic as they are the most frequently observed of the human activity variables.

Baseline Model for Nest Survival

I 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 4). The probability of surviving the entire nesting period, assuming constant daily survival (i.e., the “null” model without covariates), was 12% (real probability scale: 0.118, SE = 0.012, 95% CI = 0.095 – 0.141), which was lower than the overall apparent hatching success estimate (23.6%). The best model (given the data and the candidate model set; w_i = 0.647) from stage one of my analysis, examining temporal variation in nest survival, indicated that survival varies annually and follows a positive linear within-season time trend. The second-ranked model (w_i = 0.353) included a quadratic within-season time trend; however, the quadratic effect appeared to be a pretending variable as evidenced by a ΔAIC_c of approximately two and little change in the deviance (2279.769 versus 2278.975; Arnold 2010) and, therefore, it was not advanced to the next stage of model selection. A single top baseline model emerged from stage two (i.e., it received all of the support; w_i = 1.000). In this model, nest survival varied by site and year, and increased with nest age and as the season progressed (linear time trend). Nest age had a strong positive effect (95% CI = 0.032 – 0.060, OR = 1.047, $\hat{\beta}$/SE = 6.571) on DSR, while the evidence was weaker for a positive linear time trend (95% CI = -0.0004 – 0.006, OR = 1.003, $\hat{\beta}$/SE = 1.500; Appendix D, Figure 3A-B). DSR was highest at South Spit and in 2011, whereas Mad River County Park and 2004 had the lowest DSRs (Figure

3C-D). Predicted DSRs for sites and years followed the same general pattern as apparent hatching success estimates.

Table 4. Candidate model set for Western Snowy Plover nest survival at eight sites in Humboldt County, CA from 2004-2017. K = number of parameters in model. ΔAIC_c = difference in AIC_c ($\Delta_i = AIC_i - AIC_{min}$) from the final stage (stage three) of the analysis and from within each stage of model building (Stage ΔAIC_c). w_i = Akaike weights (i.e., probability that a model is the "best" model given the candidate model set and the data) from within each stage of model building. Cum. w_i = cumulative weight of all models. Deviance is the difference between $-2\log(\mathcal{L})$ of model$_i$ and the saturated model. Evidence ratio = $w_{top\ model} / w_i$.

Stage	Model	K	AIC_c	ΔAIC_c	Stage ΔAIC_c	w_i	Cum. w_i	Deviance	Evidence ratio
3	Restor + Year + T + Site + NestAge	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	Corvids + Year + T + Site + NestAge	24	2168.328	4.967	4.967	0.063	0.909	2120.152	11.921
3	Vehicle + Year + T + Site + NestAge	24	2168.533	5.172	5.172	0.057	0.966	2120.357	13.175
3	Foot + Year + T + Site + NestAge	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	-

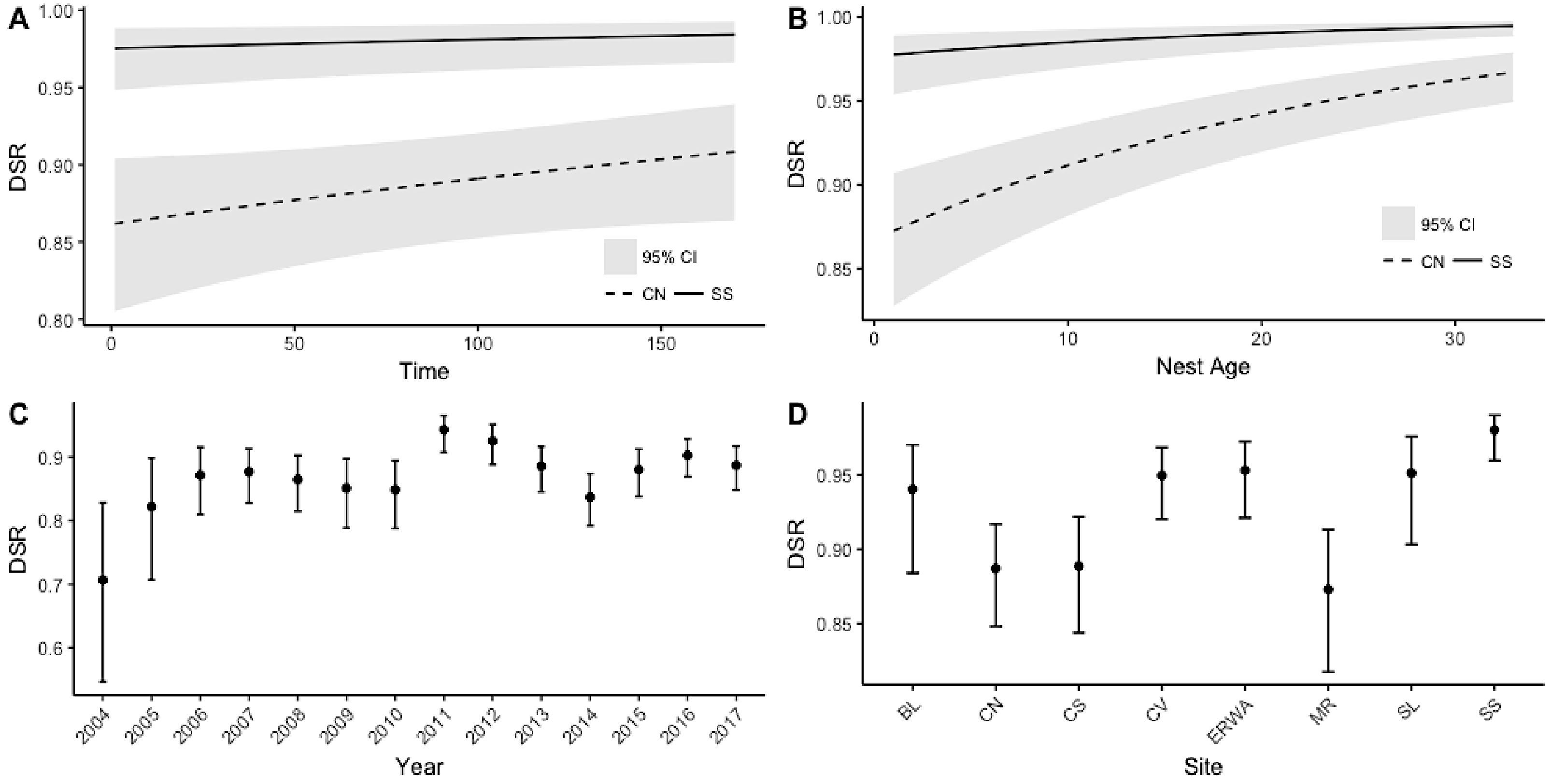

Figure 3. Predicted DSRs and 95% CIs for plover nests from the top baseline model (Year + T + Site + NestAge). A) DSR in 2017 at a site with low survival (Clam Beach North) and high survival (South Spit) with a mean nest age on discovery (four) across the 171 day nesting season. B) DSR in 2017 at a site with low survival (Clam Beach North) and high survival (South Spit) with a mean within-season date (85; May 27) across the 33 day nesting period. C) DSR at Clam Beach North (occupied for all 14 years) with the mean within-season date and nest age on discovery across all years of the study (2004-2017). D) DSR in 2017 (all sites occupied) with the mean within-season date and nest age on discovery across all eight study sites.

Relative Influence of Restoration, and Human and Predator Activity

The top model (w_i = 0.751) from the final stage of my analysis combined the additive effects of the baseline model (year, site, linear time trend, and nest age) with restoration (Table 4). Natural and human-implemented restoration both had a positive effect on nest survival, when contrasted with unrestored areas (Appendix D, Figure 4D). The absence of restoration negatively influenced DSR. Conversely, DSR increased 48% (OR = 1.478) in response to natural restoration, and nests were 1.5 times more likely to survive the day in naturally restored areas when compared to unrestored habitat (with all other covariates held constant). Human-implemented restoration increased DSR by 20% (i.e., nests were 1.2 times more likely to survive the day; OR = 1.199) when compared to unrestored habitat, but precision was low since the odds ratio 95% CI overlapped one. South Spit HRA had the highest DSR and lowest variance, and Little River State Beach HRA had the lowest DSR and a larger variance (Figure 5). Variation in DSRs at each HRA likely explains the low precision (i.e., OR 95% CI includes one) associated with human-implemented restoration. The second-ranked model (w_i = 0.095) was simply the baseline model, followed by the model combining the additive effects of the baseline model with corvid activity (w_i = 0.063), then vehicle traffic (w_i = 0.057), and lastly, foot traffic (w_i = 0.035; Table 4). The restoration model was approximately eight times more likely than the baseline model, and 12 to 21 times more likely than the other main covariate models (Table 4). The beta coefficients suggested the possibility of a positive effect of corvid activity and foot traffic, and a negative effect of vehicle traffic (Appendix

D, Figure 4A-C). The relationship between corvid activity, foot traffic, and vehicle traffic and nest survival, however, was not strongly supported (all $\hat{\beta}$ 95% CIs include zero and OR 95% CIs include one, and estimates are all approximately equal to or less than the standard errors). Reliable inference cannot be made about the sign of these effects because the wide confidence intervals indicate high variance, and all include the null case (Anderson 2008). I therefore chose not to include an additive stage three model because the second-ranked model did not include any of the main covariates, and the main covariate models hold relatively little weight (i.e., corvid activity, foot traffic, and vehicle traffic were not strong predictors of nest survival).

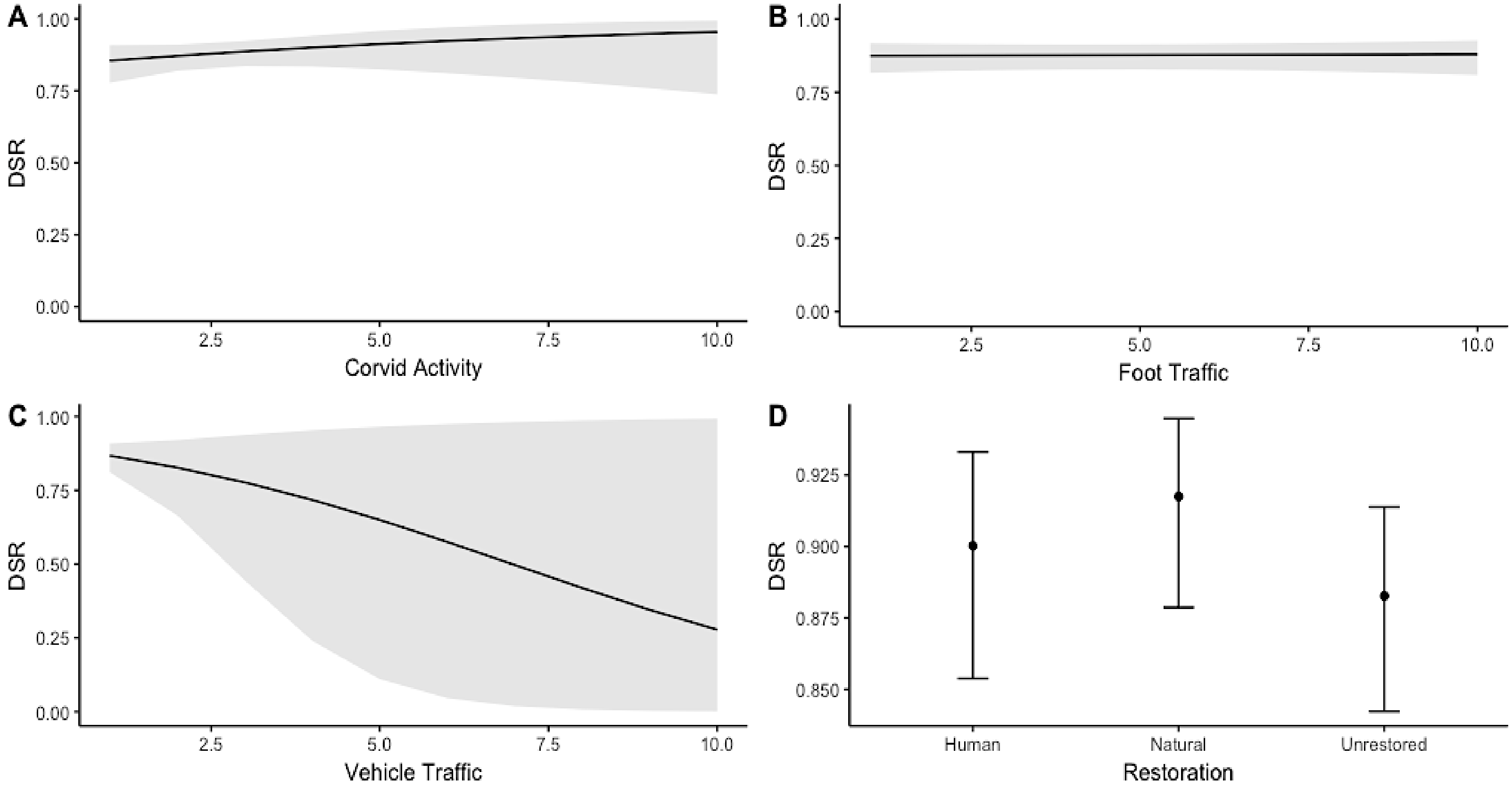

Figure 4. Predicted DSRs for plover nests and 95% CIs from the top main covariate models (restoration, and human and predator activity). DSR was calculated at Clam Beach North (has all three restoration and disturbance types) using the mean nest age on discovery (four) and within-season date (85; May 27) in 2007 (before vehicle use was prohibited) for corvid and human activity (A-C), and in 2017 for restoration (D).

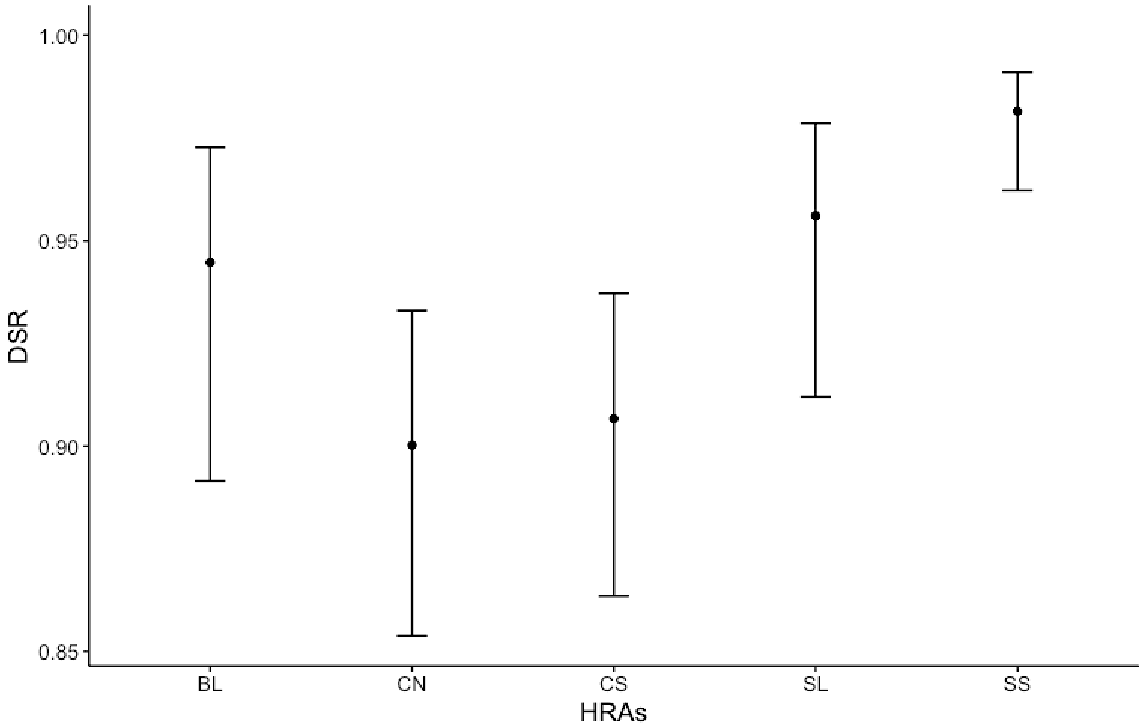

Figure 5. Predicted DSR and 95% CIs for plover nests in each of the five HRAs in Humboldt County, CA in 2017 with the mean nest age on discovery (four) and within-season date (85; May 27).

DISCUSSION

The federal government outlined three factors limiting productivity and population growth for Western Snowy Plovers (USFWS 2007), and this study is the first to rank the relative influence of all three limiting factors on nest survival. The key findings from this study are the following: 1) nest survival varied annually and by site, and increased with nest age and as the season progressed; 2) restoration had a positive effect on nest survival; and 3) restoration had the greatest influence on nest survival when compared to human and predator activity.

Baseline Nest Survival

Nest survival was low overall (apparent hatching success = 23.6%; null model period survival = 12%) and influenced by site, year, nest age, and a within-season linear time trend. Many studies have found that plover nest survival can be highly variable between sites and years (e.g., Sexson and Farley 2012, Dinsmore et al. 2014, Ellis et al. 2015); however, two studies on coastal plovers using seven to nine years of data did not find an annual effect (Colwell et al. 2011, Pearson et al. 2014). I found that the effect of year was generally stronger than the site effect (Appendix D). Survival differences among sites and years may be attributable to natural variation in size and structure of breeding habitat, weather, food availability, management practices (e.g., law enforcement), and fluctuations in predator distribution, abundance, and species (Hood and Dinsmore 2007, Colwell 2010, Pearson et al. 2014). The comparatively weak effect of site could be a result of how I defined a “site,” which I based on agency ownership (e.g., county, state, federal). Some sites, however, are geographically adjacent (e.g., Clam Beach North and South, and Mad River County Park) and likely have similar environmental conditions. Nonetheless, I found that the middle sites (Clam Beach North and South, and Mad River County Park) had lower DSRs than the northernmost and southernmost sites (Big and Stone Lagoons, South Spit, Eel River Wildlife Area, and Centerville Beach). Hardy and Colwell (2012) reported the same pattern using a smaller dataset that included some of the same nests I analyzed. Their DSRs were similar to my results, although the higher predicted confidence interval range in my results suggests nest survival has improved since 2009 (e.g., Mad River County Park range = 0.77 – 0.88 [Hardy and Colwell 2012] versus 0.82 – 0.91 [my results]).

I found a strong positive relationship between nest age and nest survival, despite the high number of imputed means. Other studies on inland plovers also found that nest survival increased as the nest aged, though the evidence was generally weak (Hood and Dinsmore 2007, Sexson and Farley 2012, Ellis et al. 2015). Smith and Wilson (2010) reported a strong interaction between nest defense and nest age for five shorebird species, especially for bi-parental incubators, which was driven by an increase in nest defense intensity as the nest ages (i.e., an older nest is more “valuable”). It has also been suggested that the effect of nest age could be explained by and confounded with individual heterogeneity since more vulnerable nests fail earlier in laying or incubation (Klett and Johnson 1982, Dinsmore et al. 2002).

The within-season time trend seen in my results supports, albeit weakly, previous research showing plover nest survival varies within a breeding season. The type of relationship between breeding season date and plover nest survival is inconsistent, with some studies indicating a positive linear (e.g., Colwell et al. 2011, Saalfeld et al. 2011), negative linear (Hood and Dinsmore 2007, Saalfeld et al. 2011), or quadratic time trend (e.g., Dinsmore et al. 2014, Pearson et al. 2014). The hypothesized causes of within-season changes in nest survival are similar to those posited for annual and site variation (e.g., seasonal changes in weather, predation rates, predator diet, vegetation; MacDonald and Bolton 2008, Pearson et al. 2014), and likely underlie variation in the type of within-season time trends seen at different locations as well (but see Smith and Wilson 2010). Previous work in RU2 found that nest survival was highest mid-season (quadratic time trend; Hardy and Colwell 2012), which contrasts with my finding of a positive linear time trend.

Influence of Three Limiting Factors

Restoration

Restoration had the largest influence on plover nest survival (when compared to human and predator activity), which indicates habitat loss and degradation is the primary threat to nest survival in RU2. I found that a significant percentage (59%) of nests were in restored habitats, which corroborates previous research in RU2 indicating plovers select restored areas (Leja 2015). Snowy and Piping plovers are often quickly attracted to restored areas, likely due to the highly dynamic and ephemeral nature of their breeding habitat (e.g., Powell and Collier 2000, Hunt et al. 2018). In this case, habitat selection equates to habitat quality since the majority of hatched nests over the years have been initiated in restored areas, where nest survival is higher. My 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, Hunt et al. (2018) found that Piping Plover nest survival was higher on flood-created than on engineered sandbars along the Missouri River. I also found that human-implemented restoration increased nest survival, but the effect was more variable than natural restoration. The few other studies that have investigated the influence of habitat restoration on Snowy Plover productivity have also mostly found a positive relationship, but none have compared it to the effect of natural restoration. Dinsmore et al. (2014) found that human-implemented habitat management in Oregon resulted in a greater than two-fold increase in nest survival. Additionally, two other studies found that HRAs positively influenced other measures of productivity (Powell and Collier 2000, Zarnetske et al. 2010). In contrast, Pearson et al. (2014) concluded that whether or not a nest was inside a HRA was not a strong predictor (did not rank above their baseline model) of nest survival in Washington, although it was included within the range of plausible models (i.e., $\Delta AIC_c \leq 7$; Anderson 2008).

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 and 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 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 and Colwell 2012, Sexson and Farley 2012, Pearson et al. 2014), which contrasts with my results that habitat loss and degradation (i.e., habitat characteristics) has the largest influence on plover nest survival. This contrast could be caused by the different scales of analysis (site-level in my analysis and nest-site in other analyses). Additionally, Powell and 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). More research is needed to substantiate this hypothesis, and elucidate the mechanism(s) by which restoration increases nest survival.

It has been argued that HRAs may become a sink over time as predators discover the new nesting areas, nest density increases, and vegetation encroaches (Powell and Collier 2000, Catlin et al. 2011 and 2015, Hunt et al. 2018). Low productivity at a sink site could translate to depressed productivity over the whole recovery unit because of plovers’ site fidelity (Powell and Collier 2000). There is some preliminary evidence from a study conducted at Little River State Beach HRA that raven activity on the ground is possibly higher in HRAs, as they provide preferable foraging habitat (i.e., more debris and less vegetation; King 2016). The increased raven activity in Little River State Beach HRA could also simply be a reflection of higher raven activity in the area that is attributable to larger landscape factors, such as close proximity to agricultural lands and low intensity urban areas (Lau 2015).

Importantly, this study suggests that not all HRAs have a similar effect on nest survival. HRAs at Stone Lagoon, Big Lagoon, and South Spit are primarily driving the positive effect of human-implemented restoration in my results, as nest survival is low at both Clam Beach HRAs. South Spit also had very high nest success in 2018 (Feucht et al. 2018), and including 2018 data would likely strengthen the relationship between human-implemented restoration and nest survival. It is unlikely that factors relating to the age of the HRA, such as increasing vegetation, are driving these differences, as Little River State Beach and South Spit HRAs are similar in age and Clam Beach County Park HRA was initiated after restoration at the lagoons and South Spit. South Spit is the only HRA in RU2 with shell hash, and the exceedingly 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 RU2, and Pearson et al. (2014) did not find an effect of shell cover on nest survival in Washington. The influence of shell cover on nest crypsis requires further study and, moreover, does not explain increased nest survival at Big and Stone Lagoons. The comparatively low nest survival and high corvid and human activity at Clam Beach than at other sites suggests that there might be an interaction between restoration, and corvid and human activity. Little River State Beach and Clam Beach County Park HRAs may be an example of an ecological trap, where there is a discrepancy between the indirect environmental cues plovers use to assess habitat quality (e.g., open and sparsely vegetated) and actual habitat quality, which is low because of comparatively high human activity and the overabundance of ravens (Kokko and Sutherland 2001, Battin 2004).

Human and predator activity

I did not find a strong relationship between corvid and human activity and nest survival when compared to habitat restoration. The ranking of the three limiting factors indicated that the addition of corvid or human activity covariates do not explain much more variation in nest survival than the baseline model representing natural variation in survival. This suggests that the influence of corvids, foot traffic, and vehicle traffic on nest survival has been variable over the years, but the relationship between restoration and habitat loss (unrestored areas) and nest survival has been more predictable. The last study on nest survival in RU2 found a similar ranking, although the relationships were weak, with microhabitat nest characteristics (heterogeneity and clutter) ranked first, then corvid activity, and finally human activity (indexed by dog tracks; Hardy and Colwell 2012). Similarly, Herman and Colwell (2015) demonstrated that the strongest predictor of lifetime reproductive success (LRS) was substrate, and human and corvid activity were not significant predictors of LRS.

My study suggests restoration overrides the negative effect of corvid activity on nest survival, despite evidence that corvids are the principal nest predators in this region (Burrell and Colwell 2012). Other studies in RU2 also did not find a strong relationship between corvid activity and productivity. Reproductive success was higher on gravel bars despite higher levels of corvid activity (Colwell et al. 2005) and Hardy and Colwell (2012) found that the relationship between fine-scale corvid activity (within 100 m of a nest) and nest survival was weak. Similarly, corvid activity within 500 m of a nest was a poor predictor of LRS (Herman and Colwell 2015). Authors of both these studies suggested that broad-scale differences in corvid activity could be more influential than nest-level corvid indices. My results using an index of site-level corvid activity, however, did not support this hypothesis. 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). Daily or seasonal changes in predator hunting methods, foraging locations, and diet are not reflected in my index using point count data. Egg predation is likely opportunistic and influenced by incubation behavior of individual adults (Burrell and Colwell 2012), but single “problem” corvids can learn to specifically seek out plover nests (Liebezeit and George 2002). These individuals conceivably exert a more significant influence on nest survival than overall corvid activity. Additionally, the cause of failure for the majority of failed nests was unknown, and more conclusive research (such as cameras) is needed to determine the impact of corvid predation and individual (predator and plover) behavior on nest survival.

Human activity (vehicle and foot traffic) also was not a strong predictor of plover nest survival in my study. My results support previous studies that did not find a correlation between human activity and nest survival, LRS, or nest daily predation rate in RU2 (Burrell and Colwell 2012, Hardy and Colwell 2012, Herman and Colwell 2015). The most probable explanation for this is the low level of human activity on beaches in northern CA, when compared to more urban coastal areas (Herman and Colwell 2015). Alternatively, the lack of correlation between human activity and nest survival may be attributable to limitations of the point count data. Point counts may not capture true activity levels well. For example, I noted vehicle tracks at certain sites, but no vehicles were recorded on any point counts throughout the season. The index of human activity I used also did not reflect within-season variation in human activity, such as a peak in mid-summer, or individual human behavior. 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 than foot traffic and had a similar model ranking to corvid activity. DSR decreased most rapidly (i.e., steepest slope) with increasing vehicle traffic than increasing foot traffic or corvid activity (Figure 4A-C), but precision was low, indicating that the effect of vehicle traffic was highly variable. 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 and Paton (1989) demonstrated that just a few vehicles led to an 81% probability of a nest being crushed before hatching for Hooded Plovers (*Thinornis rubricollis*). Accordingly, vehicle closures would be the most beneficial for nest survival out of the common strategies used to manage human disturbance.

MANAGEMENT IMPLICATIONS

Productivity studies are a valuable tool used to guide adaptive management strategies by indirectly assessing habitat quality and identifying factors limiting reproductive success. Productivity in RU2 has exceeded recovery unit objectives (1.0 fledglings per male; USFWS 2007) in recent years (2016-2018), but renewed consideration of Western Snowy Plover management practices is still warranted since this recent improvement is driven by a single site (South Spit; Feucht et al. 2018). Based on my results, I recommend managers in RU2 focus on restoration to improve plover nest survival. Conserving naturally restored areas, and maintaining and creating HRAs would benefit nest success, as plovers both select (Leja 2015) and have higher nest survival in restored areas. 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 and 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). My results suggest that restoration could be a more effective long-term solution to low productivity than other management strategies, such as predator control (Dinsmore et al. 2014).

There are several factors that should be considered when creating HRAs. First, managers should evaluate the levels of predator and human activity at a site to avoid attracting plovers to low quality habitat, as there may be an interaction between restoration and exceptionally high site-level activity. Second, they should consider the role of conspecific attraction in habitat selection (Leja 2015, Patrick and Colwell 2017) and on nest survival (Pearson et al. 2014). It might be advantageous to place HRAs near or at established breeding sites, although managers must be careful about attracting plovers to sites that are a potential sink (Ahlering and Faaborg 2006). Third, managers should consider proximity to brood-rearing and foraging habitat when placing HRAs, as long-distance movements between natal site and brood-rearing locations can decrease chick survival (Blomqvist and Johansson 1995, Kosztolányi et al. 2007, Wiltermuth et al. 2015). Fourth, managers should consider adding oyster shells to attract plovers and enhance survival of nests and chicks, although more research is needed to determine the influence of shell cover on productivity. Lastly, the size of the HRA should incorporate information on flushing distance to create an adequate buffer from human disturbance (minimum size of approximately 100 m; Muir and Colwell 2010).

I recommend managers also restore or mimic natural restoration processes to improve nest survival. Creating many temporary small-scale breeding areas by clearing vegetation at different sites in different years may mimic natural restoration and the ephemeral nature of habitat availability that plovers are adapted to (Powell and Collier 2000, Catlin et al. 2011). Bulldozing or creating cuts in the foredune would help restore natural disturbance regimes (i.e., overwash), which could be a self-sustaining way to create new naturally restored areas with minimal effort (Zarnetske et al. 2010, Schupp et al. 2013). Additionally, more naturally restored areas might not “pinch” plovers into close quarters with ravens, considering preliminary evidence that ravens are also possibly attracted to HRAs (King 2016).

Habitat restoration to improve nest survival should be combined with management actions aimed at other life stages (e.g., adult survival) since high nest survival alone might not lead to population growth (Dinsmore et al. 2014). Managing human activity could have the greatest benefits for plovers overall. For example, human disturbance can decrease fledging success (Wilson and Colwell 2010), plovers may avoid breeding sites with high human activity (e.g., Schulz and Stock 1993, Lafferty et al. 2006, Webber et al. 2013), and trash removal and limiting human activity could help alleviate the overabundance of predators (Peterson and Colwell 2014). More importantly, Eberhart-Phillips and Colwell (2014) found that managing human activity (symbolic fencing and vehicle closures) had the greatest influence on population growth in northern CA.

I emphasize the need to measure Western Snowy Plover nest survival across time and space since nest survival can vary dramatically, which may be a function of a dynamic and fluid environment. I suggest researchers examine the influence of natural restoration on plover productivity in other recovery units, and continue monitoring productivity in HRAs. Ultimately, management actions are 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 and Farley 2012).

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APPENDIX A

Appendix A: Annual site means for humans, dogs, horses, vehicles, and corvids (*C. corax* and *C. brachyrhynchos*) on eight plover breeding sites in Humboldt County, CA from 2004-2017. Includes only site-years with nests used in the analysis. n = number of point counts.

Site-Year	Dogs	Vehicles	Horses	Humans	Corvids	n
BL05[a]	0.101	0.000	0.000	0.511	0.664	742
BL11[a]	0.101	0.000	0.000	0.511	0.664	742
BL12[a]	0.101	0.000	0.000	0.511	0.664	742
BL14	0.050	0.000	0.000	0.475	0.850	40
BL15	0.012	0.000	0.000	0.000	0.030	166
BL16	0.194	0.000	0.000	0.624	0.278	263
BL17	0.009	0.000	0.000	0.000	0.387	111
CN04	1.734	0.266	0.042	1.448	0.744	308
CN05	0.525	1.211	0.061	3.725	1.627	899
CN06	0.463	0.087	0.019	1.023	1.517	795
CN07	0.750	1.087	0.144	4.411	2.599	416
CN08	0.661	0.094	0.073	1.470	1.121	372
CN09	0.834	0.401	0.014	2.924	1.717	421
CN10	0.980	0.000	0.005	2.005	1.608	398
CN11	1.000	0.004	0.016	15.557	2.396	548
CN12	1.481	0.000	0.068	5.363	1.373	322
CN13	0.334	0.000	0.014	4.141	0.533	632
CN14	0.593	0.000	0.000	1.611	2.018	113
CN15	0.249	0.001	0.004	2.896	1.674	971
CN16	0.804	0.000	0.000	2.264	1.946	148
CN17	0.787	0.000	0.040	1.120	1.127	150
CS04	0.242	0.059	0.017	0.211	0.567	289
CS05	0.041	0.049	0.001	0.179	1.196	709
CS06	0.129	0.346	0.000	0.674	0.894	341
CS07	0.175	0.057	0.018	0.300	1.193	280
CS08	0.138	0.042	0.013	0.360	1.841	239
CS09	0.397	0.028	0.007	0.454	1.273	282
CS10	0.557	0.000	0.032	0.781	1.247	219
CS11	0.473	0.005	0.000	1.887	1.247	186

Site-Year	Dogs	Vehicles	Horses	Humans	Corvids	n
CS12	0.358	0.000	0.027	7.568	0.750	148
CS13	0.409	0.000	0.000	0.722	0.383	230
CS14	0.311	0.000	0.000	1.934	0.787	61
CS15	0.451	0.000	0.000	0.561	0.415	82
CS16	0.625	0.000	0.000	0.875	0.875	32
CS17	0.535	0.000	0.000	0.512	1.186	43
CV04	0.000	0.000	0.000	0.000	0.205	39
CV06	0.000	0.000	0.000	0.000	1.040	25
CV10	0.033	0.152	0.000	0.185	0.598	92
CV11	0.038	0.124	0.000	0.343	0.514	105
CV12	0.048	0.032	0.000	0.214	0.556	126
CV13	0.032	0.036	0.000	0.094	0.106	501
CV14	0.043	0.029	0.014	0.107	0.350	140
CV15	0.005	0.035	0.000	0.073	0.123	423
CV16	0.012	0.042	0.018	0.156	0.964	167
CV17	0.010	0.050	0.000	0.099	1.079	101
ERWA07	0.019	0.046	0.000	0.120	0.213	108
ERWA08	0.027	0.137	0.000	0.199	0.541	146
ERWA09	0.007	0.086	0.000	0.184	0.750	152
ERWA10	0.047	0.129	0.000	0.316	0.561	171
ERWA11	0.000	0.175	0.000	0.149	0.370	154
ERWA12	0.091	0.000	0.000	0.591	0.364	22
ERWA13	0.004	0.018	0.000	0.082	0.113	450
ERWA14	0.015	0.060	0.000	0.187	0.463	134
ERWA15	0.004	0.024	0.000	0.036	0.060	250
ERWA16	0.000	0.038	0.000	0.057	0.352	105
ERWA17	0.024	0.202	0.000	0.298	1.107	84
MR06	0.053	0.000	0.000	0.368	0.684	19
MR07	0.197	0.007	0.000	0.565	3.095	147
MR08	0.095	0.006	0.000	0.260	2.923	169
MR09	0.077	0.005	0.000	0.257	2.131	183
MR10	0.085	0.000	0.000	0.092	2.373	142
MR11	0.162	0.006	0.000	0.437	1.808	167
MR12	0.134	0.000	0.000	0.348	1.321	112
MR13	0.057	0.000	0.000	0.132	0.607	582
MR14	0.211	0.008	0.000	0.461	2.063	128

Site-Year	Dogs	Vehicles	Horses	Humans	Corvids	n
MR15	0.037	0.016	0.000	0.057	0.732	246
MR16	0.100	0.000	0.000	0.211	4.133	90
MR17	0.200	0.000	0.000	0.200	0.700	50
SL10[a]	0.033	0.007	0.000	0.370	0.291	457
SL11[a]	0.033	0.007	0.000	0.370	0.291	457
SL14	0.000	0.000	0.000	0.353	0.412	17
SL15	0.000	0.000	0.000	0.000	0.075	80
SL16	0.063	0.000	0.000	0.554	0.188	224
SL17	0.016	0.000	0.000	0.000	0.143	63
SS07	0.021	0.048	0.000	0.116	0.384	146
SS08	0.012	0.027	0.000	0.115	0.065	260
SS16	0.024	0.056	0.000	0.356	0.324	250
SS17	0.015	0.030	0.000	0.119	0.259	135

[a] Imputed site mean

APPENDIX B

Appendix B: Principal Components Analysis

I justified the separation of human activity into “foot” and “vehicle” traffic by conducting a preliminary principal components analysis (PCA) using the 2004-2017 site means. Principal component two (PC2) of the PCA showed a clear separation of human activity into foot (humans, dogs, and horses) and vehicle traffic (Table 5, Figure 6). In addition, a cluster analysis also showed the same groupings as the PCA.

Table 5. Principal components (PC) loadings for each of the variables using means from 2004-2017 point counts for all RU2 sites. Cumulative proportion is the amount of variation in the data explained by each PC.

Variables	PC1	PC2
Dogs	0.4949	-0.6605
Vehicles	0.4910	0.7483
Horses	0.5089	-0.0571
Humans	0.5050	-0.0228
Cumulative Proportion	0.9568	0.9897

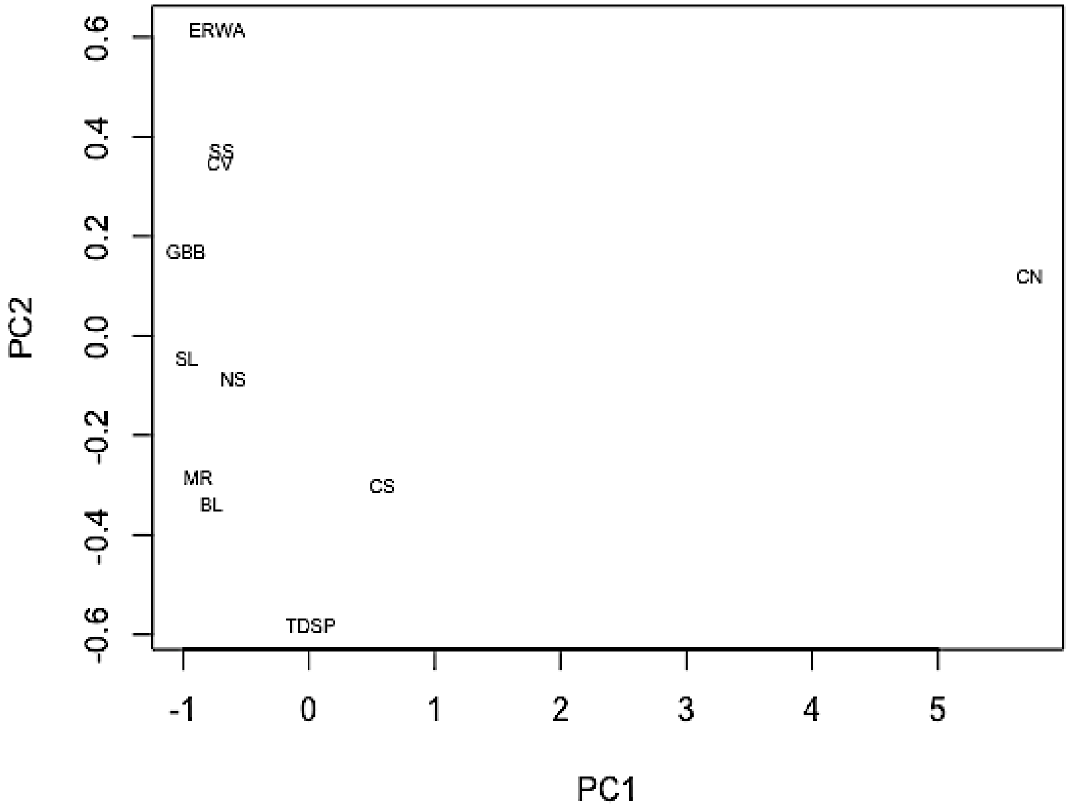

Figure 6. PCA for human disturbance data (vehicles, humans, dogs, and horses) using site means from 2004-2017 point counts for all RU2 sites. PC1 represents the overall disturbance level, and PC2 represents the contrast between humans, dogs and horses, and vehicles.

APPENDIX C

Appendix C: Number of nests (n) and apparent hatching success (%[a]) in each site-year used in the analysis at eight breeding sites in Humboldt County, CA from 2004-2017. Dash indicates no known breeding activity for that site-year or nests were not used in the analysis. Sites are arranged in order from north to south.

	SL		BL		CN		CS		MR		SS		ERWA		CV		Total	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
2004	-	-	-		5	0	9	0	-	-	-	-	-	-	1	100	15	6.7
2005	-	-	2	100	9	0	3	0	-	-	-	-	-	-	-	-	14	14.3
2006	-	-	-	-	15	6.7	5	20.0	3	0	-	-	-	-	1	100	24	12.5
2007	-	-	-	-	20	5.0	11	9.1	3	33.3	1	100	2	100	-	-	37	16.2
2008	-	-	-	-	12	8.3	26	3.8	3	0	3	33.3	2	50.0	-	-	46	8.7
2009	-	-	-	-	12	8.3	13	7.7	3	0	-	-	3	33.3	-	-	31	9.7
2010	2	100	-	-	12	8.3	12	0	3	0	-	-	4	25.0	1	0	34	11.8
2011	1	100	3	66.7	9	33.3	9	44.4	3	33.3	-	-	3	33.3	3	66.7	31	45.2
2012	-	-	2	50.0	13	23.1	16	31.3	2	0	-	-	2	100	4	75.0	39	35.9
2013	-	-	-	-	24	20.8	13	30.8	9	0	-	-	5	40.0	3	0	54	20.4
2014	2	0	1	0	40	0	9	0	11	9.1	-	-	6	50.0	6	83.3	75	12.0
2015	4	75.0	2	0	21	14.3	9	0	5	0	-	-	13	76.9	8	37.5	62	30.6
2016	8	37.5	1	100	25	28.0	6	0	4	25.0	9	66.7	7	14.3	12	58.3	72	36.1
2017	2	0	6	33.3	24	8.3	5	40.0	6	16.7	16	81.3	1	100	16	43.8	76	36.8
Total	19	47.4	17	47.1	241	11.6	146	13.0	55	9.1	29	72.4	48	52.1	55	52.7	610	23.6

[a] Apparent hatching success = (total number of nests that hatched at least 1 egg / total number of nests) x 100

APPENDIX D

Appendix D: Maximum likelihood estimates ($\hat{\beta}$), standard error (SE), and 95% confidence intervals (CI) on logit scale, and odds ratios and their 95% confidence intervals for all parameters. Effect size relative to standard error is provided ($\hat{\beta}$/SE). Intercept is from the top stage three model (Restor) and all baseline covariates (year, site, time, and nest age) estimates are from the top baseline model from stage two.

Parameter	$\hat{\beta}$	SE	$\hat{\beta}$/SE	CI	Odds Ratio	Odds Ratio CI
Intercept	1.016	0.503	2.02	0.031 – 2.001	–	–
Natural Restor	0.391	0.141	2.77	0.115 – 0.666	1.478	1.122 – 1.946
Human Restor	0.182	0.156	1.167	-0.124 – 0.487	1.199	0.883 – 1.628
Corvids	0.142	0.131	1.084	-0.116 – 0.400	1.153	0.891 – 1.491
Vehicle	-0.315	0.322	-0.978	-0.945 – 0.316	0.730	0.389 – 1.372
Foot	0.005	0.035	0.143	-0.063 – 0.072	1.005	0.939 – 1.075
2005	0.650	0.468	1.389	-0.267 – 1.568	1.916	0.766 – 4.797
2006	1.034	0.424	2.439	0.203 – 1.865	2.812	1.225 – 6.456
2007	1.082	0.395	2.739	0.308 – 1.856	2.951	1.361 – 6.398
2008	0.974	0.374	2.604	0.241 – 1.707	2.649	1.273 – 5.512
2009	0.864	0.396	2.182	0.087 – 1.640	2.373	1.091 – 5.155
2010	0.844	0.394	2.142	0.071 – 1.617	2.326	1.074 – 5.038
2011	1.922	0.423	4.544	1.094 – 2.751	6.835	2.986 – 15.658
2012	1.643	0.398	4.128	0.862 – 2.423	5.171	2.368 – 11.280
2013	1.166	0.378	3.085	0.425 – 1.908	3.209	1.530 – 6.740
2014	0.756	0.372	2.032	0.026 – 1.486	2.130	1.026 – 4.419
2015	1.115	0.382	2.919	0.365 – 1.864	3.050	1.441 – 6.449
2016	1.349	0.382	3.531	0.599 – 2.098	3.854	1.820 – 8.150
2017	1.181	0.383	3.084	0.430 – 1.933	3.258	1.537 – 6.910
Time	0.003	0.002	1.500	-0.0004 – 0.006	1.003	0.100 – 1.006
CN	-0.699	0.358	-1.953	-1.400 – 0.001	0.497	0.247 – 1.001
CS	-0.683	0.367	-1.861	-1.402 – 0.037	0.505	0.246 – 1.038
CV	0.177	0.402	0.440	-0.610 – 0.964	1.194	0.543 – 2.622
ERWA	0.253	0.413	0.613	-0.557 – 1.063	1.288	0.573 – 2.895
MR	-0.833	0.386	-2.158	-1.590 – -0.075	0.435	0.204 – 0.928
SL	0.212	0.480	0.442	-0.729 – 1.153	1.236	0.482 – 3.168
SS	1.145	0.500	2.290	0.166 – 2.125	3.142	1.181 – 8.373
Nest Age	0.046	0.007	6.571	0.032 – 0.060	1.047	1.033 – 1.062