Factors Influencing Snowy Plover Nest Survival on Ocean-Fronting Beaches in Coastal Northern California

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Abstract.—Selection of a nest site that affords camouflage of eggs or incubating adults is thought to be strongly influenced by predation, especially for ground-nesting birds. Data from 115 Snowy Plover (*Charadrius nivosus*) nests were used to model relationships between nest survival, habitat characteristics, predator activity and human activity on four sandy, ocean-fronting beaches in coastal northern California from 2007-2009. Plover daily nest survival was higher at two southern sites (South Spit range = 0.98-0.99; Eel River Wildlife Area range = 0.91-0.96) compared with two northern sites (Mad River Beach range = 0.77-0.88; Clam Beach range = 0.79-0.89) where predator activity was appreciably higher. Nest survival was positively related to debris heterogeneity and negatively related to the amount of debris near the nest, but these relationships were weaker than the site-level effect. Although plovers select nest sites among cryptic debris in sparsely vegetated areas, restoration that creates and enhances such habitats may have limited utility at sites where predators are abundant. Thus, managers must carefully consider predator activity at the landscape level in order to maximize the effectiveness of fine-scale restoration efforts. *Received 29 August 2011, accepted 24 August 2012.*

Key words.—California, *Charadrius nivosus*, Common Raven, nest predation, nest success, nest survival, shorebird, Snowy Plover.

Predation is a leading cause of nest failure for birds (Ricklefs 1969) and is likely a strong selective force shaping the behavior of habitat selection for nest sites (Martin 1993), especially among ground-nesting birds such as waterfowl (e.g. Cowardin *et al.* 1985; Anthony *et al.* 1991; Bailey 1993), gallinaceous birds (e.g. Erikstad *et al.* 1982), and shorebirds (e.g. Grover and Knopf 1982; Haig 1992; Page *et al.* 1995). In many of these taxa, nests are concealed in vegetation and the secretive behavior of incubating adults serves to reduce the likelihood that eggs will be found by predators. In waterfowl and gallinaceous birds that conceal their nests with vegetation, hatching success often has been shown to correlate positively with increased cover (e.g. Livezey 1981; Keppie and Herzog 1978), although this result is not universal (e.g. Storaas and Wegge 1987). However, many shorebirds (e.g. plovers, avocets, stone-curlews) establish nests in open, sparsely vegetated habitats (Koivula and Rönkä 1998; Muir and Colwell 2010) where

an unobstructed view of approaching predators facilitates early detection of danger and allows incubating birds to leave the nest undetected. In these shorebird species, camouflaged eggs often blend in with substrate, debris and vegetation to enhance nest survival (Colwell *et al.* 2011). For example, Koivula and Rönkä (1998) posited that success of Temminck's Stint (*Calidris temminckii*) nests in coastal meadows was compromised in habitats where encroaching vegetation did not allow incubating birds to detect predators early, leave the nest, and allow the eggs to blend in with the surrounding habitat.

Studies of nest site selection in plovers have shown that many species select habitats that differ from surrounding landscapes, which can positively influence nest survival. For example, European Golden-Plovers (*Pluvialis apricaria*) that nest on plateaus have higher nesting success than those nesting on slopes, presumably because they detect predators early and leave the nest undetected (Whittingham *et al.* 2002). Addi-

tionally, the type of habitat in the immediate vicinity of the nest may increase nest survival by making eggs more difficult to detect following departure of the incubating adult. American Golden-Plover (*P. dominicus*) nests in lichen habitats survived better than those in non-lichen habitats (Byrkjedal 1989). Snowy Plovers (*Charadrius nivosus*) breeding in a riverine system nested in heterogeneous substrates, especially those matching the size of eggs, which enhanced egg crypsis and increased nest survival (Colwell *et al.* 2011).

In contrast, other studies of shorebird nesting have found no relationship between habitat and nest survival (e.g. Burger 1987; Powell 2001; Nguyen *et al.* 2003). For example, Piping Plover (*C. melodus*) nest sites had more stones and rocks than random sites but selection of this substrate was not associated with nest predation rates (Espie *et al.* 1996). In shorebirds that conceal their nests, measures of vegetation cover often were not associated with either hatching success or nest survival (Colwell 1992; Mabee and Estelle 2000; Smith *et al.* 2007). In their review of literature on shorebird nest predation in Europe, MacDonald and Bolton (2008) found that daily nest predation rates (DPR) were often "unsustainably high," even in otherwise high-quality habitats, and identified only one study (O'Brien 2001) that found a relationship between DPR and nest crypsis. Thus, although shorebirds often select cryptic nest sites, predation may overwhelm the more subtle effects of camouflage provided by habitat.

A threatened population of Snowy Plovers breeds along the Pacific coast of North America (U.S. Fish and Wildlife Service 2007), typically on ocean-fronting beaches amidst fine, uniform (sandy) substrates that afford minimal crypsis for eggs. However, nests are often placed in patches of driftwood, shells and other debris that hide the eggs and incubating adults (Page *et al.* 1995). Nest predation by native and introduced vertebrates, especially corvids (Common Raven, *Corvus corax*; American Crow, *C. brachyrhynchos*) has been identified as an important factor limiting recovery of this listed population (U.S. Fish and Wildlife Ser-

vice 2007). Corvids search for nests of other birds using visual cues, either the presence of eggs or the movement of adults leaving nests (Colwell *et al.* 2011). In coastal northern California, ravens are strongly implicated in predation of nests and chicks and the majority of plover nest failures are attributable to raven predation (Burrell 2010; Colwell *et al.* 2010, 2011). Managers commonly alter habitat by removing introduced vegetation to create the open habitat selected by plovers (Muir and Colwell 2010) and spreading discarded bivalve shells in order to enhance nest crypsis and reduce predation of plover nests, but plover productivity remains consistently low and the population is sustained by immigration from elsewhere along the Pacific coast (Mullin *et al.* 2010).

The objective of this study was to understand relationships between nest survival and factors limiting Snowy Plover productivity (U.S. Fish and Wildlife Service 2007). Accordingly, we used three years of data collected at four beaches in coastal northern California to model the influence of habitat characteristics, human activity and predator activity near nest sites on the daily survival rate (DSR) of plover nests. Based on previous research in our study area (Colwell *et al.* 2010, 2011) and elsewhere, we predicted that nest survival would decline with corvid activity and that survival would be enhanced by features of the habitat that afforded greater crypsis to eggs. Further, based on findings reported by the U.S. Fish and Wildlife Service (2007), we suspected that human recreational use of breeding sites might have a negative influence on nest survival.

Methods

Study Area

We monitored plover nests at four ocean-fronting beaches (Clam Beach, Mad River Beach, South Spit and Eel River Wildlife Area; Fig. 1) in northern Humboldt County, California from 2007-2009. Over the ten years that we studied plovers in this region, these four locations represented the most important breeding sites based on high occupancy and nest density, coupled with challenges associated with managing habitats frequented by humans and anthropogenic food sources that attract Common Ravens, the principal predators
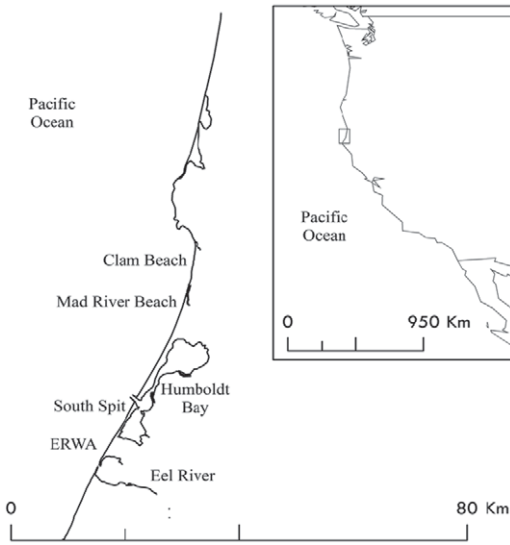
Figure 1. Snowy Plover nests were monitored from 2007-2009 at Clam Beach, Mad River Beach, South Spit and Eel River Wildlife Area (ERWA) in Humboldt County, California.

that compromise plover productivity (Burrell 2010). Beach habitats were characterized by fine, sandy substrates strewn with a mixture of driftwood of varying sizes, stones, mollusc shell fragments and crustacean remains. The dominant vegetation included both native (e.g. *Leymus mollis*, *Abronia latifolia*, *Cakile maritima*) and introduced species (*Ammophila arenaria*). Colwell *et al.* (2010) provided a detailed characterization of the study area.

Survey Methods

Each year, observers (eleven in 2007 and 2008, 15 in 2009) surveyed suitable habitat (i.e. debris fields upslope from the wrack line, foredunes and sparsely-vegetated backdunes) for breeding plovers from early March until late summer when the last young had fledged. Ten observers conducted surveys in all three years and individuals without prior experience surveying in our study area were paired with an experienced observer. Observers systematically surveyed the full length of each of the four sites at a minimum of seven to ten day intervals and supplemented these full surveys with occasional partial surveys to check known nest locations and areas where courting plovers had been observed. Surveys were conducted from 0600-1100 h. During surveys, nests were found by observing courting plovers, following their tracks in sandy substrates, and observing incubating adults. When a nest was found, its location was recorded using a personal digital assistant (PDA) equipped with a global positioning system (GPS) unit and ArcPad 6.0 Software (Environmental Systems Research Institute, Inc. 2002). In nearly all cases, the age of eggs was known because observers found nests prior to the completion of the three-egg clutch. When

nests were discovered after clutch completion, the eggs were floated to determine their age (Liebezeit *et al.* 2007). Nests were monitored at one to seven day intervals until the eggs hatched or the nest failed. Nests were checked daily as they approached the end of the 28-day incubation period. From these observations, we maintained an annual record of each nest, including its fate (hatched at least one chick or failed).

During nest visits, surveyors confirmed that a nest was active by observing an incubating adult through a spotting scope. During most visits, the incubating adult did not leave the nest. After initial discovery, observers did not approach active nests except when 1) an adult was not incubating, 2) both parents had been observed elsewhere since the previous nest visit, 3) the nest was 1-2 days from the expected hatch date (i.e. to check eggs for pipping/starring), or, in rare cases, 4) to float eggs when a nest was discovered after clutch completion. When incubating adults were not present, observers only approached close enough to confirm that eggs were present in the nest cup (typically through binoculars). In all cases, observers were careful to minimize disturbance to the substrate near the nest and the time spent at the nest. Consequently, we are confident that the vast majority of nest checks were not likely to have an appreciable effect on DSR.

During surveys for plovers, observers sampled habitat using three methods and geo-referenced the data using the GPS-equipped PDA. These three approaches characterized habitat near the nest (i.e. within 15 cm and 3 m radii), within 100 m of the nest and throughout the study area. To describe fine-scale variation in habitat near the nest, observers counted the number of objects (sticks, shells, live vegetation, dead vegetation and garbage) within 15 cm of the nest cup. Then, observers visually estimated percentage of debris cover (0; 1-10%; 11-50%; 51-90% and >90%) within 3 m of the nest and estimated the number of objects (0; 1-10; 11-100; 101-1000; >1000) in various debris categories (large stumps, smaller wood, shells, live vegetation, dead vegetation, garbage, brown algae, bundles of eelgrass (*Zostera marina*), stones and dried husks of cnidarians (*Velella velella*). Finally, observers characterized danger posed to eggs by humans and corvids by recording an index of tracks (none; 1-10 sets; >10 sets) left within 3 m of the nest by vehicles, pedestrians, dogs, horses and corvids, respectively, in the prior 24 h.

To describe habitat, observers recorded the same set of variables that were recorded within 3 m of the nest in randomly-placed plots sampled throughout the study area. Observers sampled these plots during regular surveys (i.e. Mar-Aug) for plovers at all sites by stopping every 20 min as signaled by a pre-determined wristwatch alarm. When observers stopped, they also recorded an instantaneous point count of the number of vehicles, pedestrians, dogs, horses and corvids within 500 m of their location. We used the subset of these 3-m plots that fell within 100 m of a nest to calculate incidence values (i.e. proportion of plots where a given track or debris type was detected) for each of the habitat features. Similarly, we derived incidence values from

point counts for vehicles, pedestrians, dogs, horses and corvids within 100 m of a nest.

Observers conducted 5,754 point counts (2007: N = 1,985, 2008: N = 2,185, 2009: N = 1,584) and recorded data in a total of 6,130 3-m plots (2007: N = 2,056, 2008: N = 2,284, 2009: N = 1,790) between 2007 and 2009; only a small percentage of these observations occurred near nests. Overall, there were only minor (i.e. non-significant) annual differences in the average number of points sampled within 100 m of nests (2007: range = 3-22, $\overline{x}$ =12.9, SE = 5.5; 2008: range = 3-28, $\overline{x}$ =12.4, SE = 6.1; 2009: range = 2-25, $\overline{x}$ =12.4, SE = 6.1).

Modeling Approach

We developed an index of debris heterogeneity at the 100 m scale using the Shannon-Wiener index (H') of diversity [$-\Sigma p_i \ln(p_i)$], with p_i values calculated from the proportional abundance of small debris types (small woody debris, shells, stones and *Velella*) sampled in 3-m plots within 100 m of a nest. We selected these debris types because they afford camouflage to eggs and incubating adults without interfering with the adult's ability to detect approaching predators. We derived an additional habitat variable ("clutter") based on the mean number of occurrences of small woody debris, shells, stones and *Velella* in 3-m plots sampled within 100 m of a nest. We included these two variables in our set of candidate models because we knew that nesting substrates affected egg crypsis and influenced nest survival elsewhere in our study area (Colwell *et al.* 2011) and because managers frequently alter habitats by supplementing debris that increases heterogeneity and clutter with the aim of enhancing nest survival (e.g. Powell and Collier 2000).

We used program MARK to calculate the daily survival rate of nests and evaluate the effects of danger posed by humans and corvids, habitat at the nest, site, and time (Table 1). Initially, we tested for correlations among variables and used nests monitored in 2007 (N = 37) to develop a set of preliminary models. We then ranked models according to Akaike's Information Criterion corrected for small sample size, (AIC$_c$; Burnham and Anderson 2002) and reduced the number of explanatory variables based on a combination of model ranking and biological relevance (i.e. when two variables related to nest crypsis, predation threat or human

Table 1. Variables representing habitat characteristics, human activity and predator activity within 15 cm, 3 m, and 100 m of Snowy Plover nests at four sites in coastal northern California. The influence of these variables on plover nest survival was investigated in preliminary analyses (p) using data from 2007 and the most informative variables were included in final analyses (f) using pooled data from 2008-2009.

Variable	Description	15 cm	3m	100 m[a]
Debris				
stump	Large ($\geq$ 10 cm diameter) woody debris	—	p	p
woody	small (< 10 cm diameter) woody debris	p	p	p
shell	mollusk shells and crustacean carapaces	p	p	p
vegetation	live (green) vegetation	p	p	p, f
deadveg	dead (brown) vegetation	p	p	p
garbage	anthropogenic refuse	p	p	p
algae	brown algal mats (e.g., *Macrocystis, Fucus, Postelsia, Egregia*)	—	p	p
eelgrass	*Zostera marina* bundles	—	p	p
stone	stones	—	p	p
Velella	dry and fresh *Velella*	—	p	p
cover	visual estimate of percent debris cover	—	p	—
clutter	index of cryptic debris $\leq$ 100 m from the nest[b]	—	—	p, f
H'	index of debris diversity $\leq$ 100 m from the nest[c]	—	—	p, f
Tracks (< 24 hold)				
human	human tracks	—	p	p
dog	dog tracks	—	p	p, f
horse	horse tracks	—	p	p
vehicle	vehicle tracks	—	p	p
corvid	corvid tracks	—	p	p
Human and predator activity				
humans	humans detected during point counts $\leq$ 100 m from the nest	—	—	p
dogs	dogs detected during point counts $\leq$ 100 m from the nest	—	—	p
horses	horses detected during point counts $\leq$ 100 m from the nest	—	—	p
vehicles	vehicles detected during point counts $\leq$ 100 m from the nest	—	—	p
corvids	corvids detected during point counts $\leq$ 100 m from the nest	—	—	p, f

[a]For all variables except clutter and H', incidence = proportion of plots $\leq$ 100 m from the nest where at least one observation occurred.

[b]Mean number of detections of woody debris, shells, stones, and *Velella* within ground plots $\leq$ 100 m of the nest.

[c]Shannon-Weiner Index of diversity; considers woody debris, shells, stones, and *Velella* within ground plots $\leq$ 100 m of the nest.

disturbance were positively correlated, we retained the variable that we thought would have the most direct effect on DSR based on *a priori* knowledge of plover breeding biology).

We used the results of preliminary analysis with 2007 data (Hardy 2010) to develop a set of 21 candidate models and fitted them to pooled data from nests monitored in 2008 (N = 39) and 2009 (N = 25). Our 2008-2009 models included combinations of the most informative indices of predation threat (incidence of corvids), nest crypsis (clutter, H', and incidence of vegetation) and human activity (incidence of dog tracks) within 100 m of nests (Table 1). Each model included a site effect because the various beaches differ in activity of humans and corvids, as well as being managed by separate county, state and federal agencies. Each model also included a quadratic time effect owing to the general observation that nest survival varies seasonally, especially in our study area where plovers initiate nests over ~120 days from early March until mid-August. None of our candidate models included ≥2 correlated covariates.

RESULTS

During 2007-2009, observers found 115 plover nests distributed unevenly among four sites (Table 2). Most nests (N = 95) were on Clam Beach, where apparent nest success was especially low, ranging from 5-8% annually. In final (2008-2009) analyses, daily nest survival was higher at two southern sites (South Spit range = 0.98-0.99; Eel River Wildlife Area range = 0.91-0.96; Fig. 2) compared with two northern sites (Mad River Beach range = 0.77-0.88; Clam Beach range = 0.79-0.89; Fig. 2). In contrast, human and corvid activity during 2007-2009 was appreciably higher at the northern sites than at the southern sites (Burrell 2010).

Results of preliminary analysis using 2007 data (Hardy 2010) showed that habitat variables measured within 15 cm and 3 m of the nest described very little of the variation in DSR: each variable explained 0-4% of the null model deviance. Furthermore, variables calculated using point counts and ground plots within 100 m of nests described only slightly more variation in DSR than did those nearer the nest (0-6% deviance explained). A site-level effect accounted for ~10% of the null deviance and indicated that DSR was higher at the two southern sites than at the two northern sites. A quadratic time trend better captured variation in DSR than did a linear trend (deviance explained = 12% and 6%, respectively) and suggested that nest survival was highest mid-season. Based on these results, we retained five covariates (H', clutter, and incidence of dog tracks, corvids and vegetation) to use in final (2008-2009) analyses. Additionally, each of the 21 models in the final set included a site effect, a quadratic time trend, or both.

Most (95%) of the final models performed better than the null model, but no model explained more than 7% of the null deviance. The top model (Table 3) indicated that DSR varied appreciably among sites, with higher nest survival on South Spit and Eel River Wildlife Area compared with Mad River Beach and especially Clam Beach, although 95% confidence intervals for Mad River Beach and Eel River Wildlife Area included zero. There was only limited evidence that habitat characteristics in the vicinity of the nest influenced nest survival. Nest survival was positively correlated with H' but negatively associated with clutter. Two other models were within two AIC_c units of the top model. In the second-ranked model, H' was replaced with corvid incidence (these two variables were correlated; r = 0.48, $P < 0.05$). A third-ranked model was identical to the top model but also included the incidence of dog tracks.

Table 2. Apparent hatching success of Snowy Plover nests monitored at four sites in coastal northern California. Apparent nesting success is the number of nests hatching at least one chick divided by the total (x100).

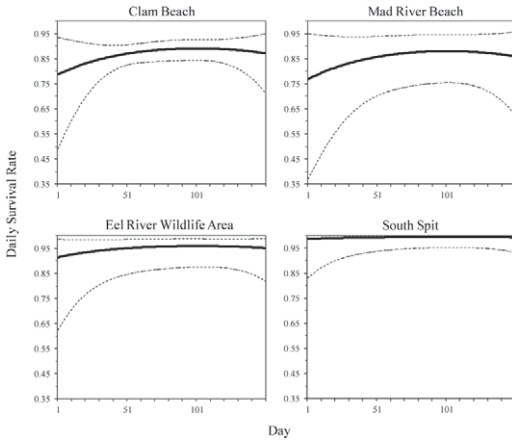| Site	2007		2008		2009	
	N	% hatched	N	% hatched	N	% hatched
Clam Beach	31	6.5	39	5.1	25	8.0
Mad River Beach	3	33.3	3	0	3	0
Eel River Wildlife Area	2	100	2	50.0	3	33.3
South Spit	1	100	3	33.3	0	—
All nests	37	16.2	47	8.5	31	12.9

Figure 2. Daily survival rates and 95% confidence intervals for Snowy Plover nests at four sites in Humboldt County, California, 2008-2009. Day 1 corresponds to 4 March and day 150 corresponds to 31 July.

However, dog tracks were an exceptionally poor predictor of variation in DSR: the coefficient estimate was not significantly different from zero and the addition of dog tracks to the top model only explained an additional 0.05% of the null model deviance.

DISCUSSION

Our results are noteworthy for several reasons. First, the beach-nesting plovers we studied experienced very low reproductive success, a pattern that has prevailed over much of the 10+ years that we have monitored the population. Secondly, we found weak relationships between plover nest survival and habitat characteristics near the nest, whereas our strongest modeling result showed that nest survival was appreciably lower at two northern sites (Clam Beach and Mad River Beach) where corvid activity was especially high (Burrell 2010). Finally, the absence of strong statistical relationships between nest survival, habitat, and human and predator activity near the nest suggests that the influence of habitat characteristics (e.g.

Table 3. Coefficient estimates and 95% confidence intervals for the three top-ranked models examining variation in daily survival rate (DSR) of Snowy Plover nests in relation to indices of human and corvid activity, habitat characteristics within 100 m of nests, site, and time (TT = quadratic time trend).

Model	ΔAIC_c	Covariate	Estimate	Lower 95% CI	Upper 95% CI
S(site + H' + clutter + TT)	—	*Intercept*	1.6325	-0.6377	3.9026
		Eel River Wildlife Area	1.0564	-0.2105	2.3233
		Mad River	-0.1090	-1.0423	0.8242
		South Spit	3.0086	0.7984	5.2188
		H'	2.4408	0.2834	4.5983
		clutter	-1.5317	-2.6434	-0.4199
		T	0.0160	-0.0207	0.0527
		TT	-0.0001	-0.0003	0.0001
S(site + corvids + clutter + TT)	1.117	*Intercept*	2.2513	-0.0305	4.5331
		Eel River Wildlife Area	1.0026	-0.2468	2.2519
		Mad River	-0.4713	-1.4435	0.5008
		South Spit	2.6841	0.8101	4.5581
		corvids	1.8087	0.0160	3.6014
		clutter	-1.1535	-2.0469	-0.2601
		T	0.0230	-0.0150	0.0610
		TT	-0.0001	-0.0003	0.0001
S(site + H' + clutter + dog tracks + TT)	1.893	*Intercept*	1.7484	-0.6044	4.1012
		Eel River Wildlife Area	0.9784	-0.3472	2.3039
		Mad River	-0.1535	-1.1135	0.8065
		South Spit	3.0312	0.7877	5.2747
		H'	2.5701	0.2941	4.8461
		clutter	-1.5989	-2.7785	-0.4193
		dog tracks	-0.4669	-2.7385	1.8047
		T	0.0145	-0.0232	0.0521
		TT	-0.0001	-0.0003	0.0002

enhanced camouflage of nests and incubating adults; Colwell *et al.* 2011) may be minimal at sites where predators are abundant. Collectively, these results pose challenges to the conservation and management of plovers in our study area and throughout the range of the listed population segment (USFWS 2007).

Although reproductive success of shorebirds is known to vary considerably from year to year (Colwell 2010), apparent hatching success (Table 2) was low in each of the three years we quantified relationships between plover nest site characteristics and nest survival, and this pattern of low hatching success has been the case for beach-nesting plovers throughout the 10+ years that we have studied plovers in northern California (Colwell *et al.* 2005, 2010). Elsewhere we showed that corvids are the main predator affecting plover productivity in our study area (Burrell 2010) and that cryptic substrates enhanced nest survival (Colwell *et al.* 2011). Therefore, we expected to find strong relationships between nest survival and variables describing corvid activity and habitat characteristics near the nest. However, these relationships were weak in both preliminary analyses and final model results.

Unlike many other ground-nesting birds, plovers nest in sparsely-vegetated habitats that afford an unobstructed view of surrounding landscapes; they rely on early predator detection and departure from the nest, coupled with nest crypsis, to avoid egg predation (Colwell 2010). Studies on several plover species that demonstrate selection for breeding in open habitats (e.g. Whittingham *et al.* 2002; Muir and Colwell 2010), selection of nesting substrates that camouflage eggs (e.g. Flemming *et al.* 1992; Colwell *et al.* 2011), and relationships between these habitat features and nest success (Colwell *et al.* 2011) support this generalization. Why, then, did we find weak relationships between habitat characteristics and nest survival? We think there may be several contributing factors, including: 1) small sample size, with most nests concentrated at one site (Clam Beach) where overall corvid activity was especially high and nest success was

low; 2) differences in predator abundance at the landscape level overwhelming the effects of within-site variation in predator activity, human activity and habitat characteristics; and 3) the importance of adult responses to predators near the nest (Koivula and Rönkä 1998; Colwell *et al.* 2011).

Although our index of corvid activity within 100 m of nests was only weakly associated with nest survival, we note that the incidence of corvids at the site level varies considerably within our study area and is strongly correlated with the daily predation rate of plover nests (Burrell 2010). We believe that these broad-scale differences in corvid activity, and thus nest predation, are driven largely by differences in land use and human activity near plover breeding sites. Specifically, residential development and public campgrounds adjacent to Clam Beach and Mad River Beach subsidize high numbers of corvids that depress nest survival through frequent opportunistic predation of plover nests. Human recreational activity is also more common at Clam Beach and Mad River Beach than at other sites in our study area (Burrell 2010), which may directly or indirectly influence nest survival. For example, video evidence from nest cameras at Clam Beach showed that ravens often depredated eggs immediately after incubating plovers flushed from nests in response to disturbance, suggesting that they used the movement of plovers to locate nests amidst cryptic debris. Thus, numerous factors interact to influence plover reproductive success in our study area, emphasizing the importance of understanding relationships among behavior of incubating adults, physical features of habitat, human activity and predator activity at multiple spatial scales.

We found no evidence that variation in human activity near the nest correlated with nest survival. In fact, only an index of dog activity entered the final set of models (Table 3), albeit with low explanatory power. The absence of a strong relationship between human activity and nest survival is, perhaps, not surprising given that in our study area: 1) human use is low compared to other locations along the Pacific coast (e.g. Lafferty *et*

al. 2006); 2) humans have only occasionally caused nest failure (e.g. vehicle strike, trampling, taking of eggs; Colwell *et al.* 2011); and 3) most nests were depredated by corvids shortly after the onset of incubation and thus were not exposed to human-related disturbance for extended periods. Nevertheless, the U.S. Fish and Wildlife Service (2007) lists human disturbance as one of several factors negatively affecting plover reproductive success and population recovery, and we note that humans can indirectly influence nest survival by 1) leaving garbage on the beach, which attracts corvids; and 2) flushing incubating plovers from nests, which provides a visual cue to nest predators. We further note that efforts to manage human activity in the vicinity of breeding plovers in our study area (Wilson and Colwell 2010) and elsewhere along the Pacific coast (Lafferty *et al.* 2006) have produced positive results.

Habitat restoration for plovers often is coupled with measures to enhance survival of nests and broods by adding clutter to substrates in the form of discarded bivalve shells (i.e. shell hash; Powell and Collier 2000). However, our results, combined with evidence that corvids (Common Ravens and American Crows) are efficient egg predators in much of our study area (Burrell 2010), suggest that the benefits of increased nest crypsis may be overwhelmed at sites (e.g. Clam Beach and Mad River Beach) where corvids are particularly abundant. In these scenarios (i.e. suitable breeding habitat and high predator activity), habitat enhancement alone is probably insufficient to boost plover productivity. Therefore, we suggest that managers carefully consider the landscape context of the danger posed by predators if the objective is to restore and enhance habitats to increase plover reproductive success and achieve recovery of the listed population.

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