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RESEARCH ARTICLE

Lifetime reproductive success of Snowy Plovers in coastal northern California

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ABSTRACT

Conserving threatened and endangered species requires knowledge of breeding productivity and factors that cause variation in reproductive success. We summarized 13 years of lifetime reproductive success (LRS) data for 195 individually marked Snowy Plovers (*Charadrius nivosus*) breeding in Humboldt County, CA. Reproductive success was highly skewed among individuals with 13% of individuals ($n_{\text{males}} = 12$, $n_{\text{females}} = 14$) producing ~50% of fledglings; by contrast, 71% ($n = 64$) of males and 72% ($n = 76$) of females produced 2 or fewer during their lifetime. Variance in LRS was best explained by substrate (~100% of Akaike weight), with plovers breeding on gravel having significantly higher LRS compared to those on sandy substrates. Other measures of habitat quality, including use of nest exclosures, as well as corvid and human activity, were not significant predictors of LRS. Results indicated that enhancing the cryptic nature of substrates (for eggs and chicks) may be a productive means of increasing reproductive success in this threatened species.

Keywords: Charadrius nivosus, lifetime reproductive success, LRS, habitat quality, Snowy Plover, substrate, threatened

Éxito reproductivo de vida de *Charadrius nivosus* en la costa norte de California

RESUMEN

La conservación de especies amenazadas y en peligro requiere del conocimiento de la productividad reproductiva y de los factores que causan variación en el éxito reproductivo. Resumimos 13 años de datos del éxito reproductivo de vida (ERV) de 195 individuos marcados de *Charadrius nivosus* que crían en el Condado Humboldt, CA. El éxito reproductivo estuvo altamente sesgado entre individuos, con 13% de los individuos ($n_{\text{machos}} = 12$, $n_{\text{hembras}} = 14$) produciendo ~50% de los volantones; en contraste, 71% ($n = 64$) de los machos y 72% ($n = 76$) de las hembras produjeron dos o menos volantones durante sus vidas. La varianza en ERV fue explicada mejor por el sustrato (~100% del peso de Akaike), presentando los chorlitos sobre grava un ERV significativamente más alto comparado con aquellos sobre sustratos de arena. Otras medidas de la calidad del hábitat, incluyendo el uso de clausuras de nidos, así como la actividad de cuervos y humanos, no fueron predictores significativos de ERV. Los resultados señalaron que el aprovechamiento de la naturaleza críptica de los sustratos (para huevos y polluelos) puede ser un medio productivo para aumentar el éxito reproductivo de esta especie amenazada.

Palabras clave: amenazada, calidad de hábitat, *Charadrius nivosus*, éxito reproductivo de vida, ERV, sustrato.

INTRODUCTION

Long-term studies of individually marked birds have allowed for the quantification of lifetime reproductive success (LRS), a measure of the total number of offspring that an individual contributes to future generations over its lifetime (Clutton-Brock 1988, Newton 1989a). Consequently, LRS is considered to be a good approximation of fitness (Korpimäki 1992, Newton 1995). A common result in LRS studies is that individuals vary greatly in productivity, with a majority of individuals producing no offspring and a few producing many (Newton 1989a, Newton 1995). Studies of LRS are particularly valuable when they examine the causative factors behind this variation, as this provides justification for management or conservation actions.

Numerous studies have examined relationships between variation in LRS and its components (e.g., longevity, offspring survival, number of eggs laid; Saurola 1989, Oring et al. 1991, MacColl and Hatchwell 2004) or morphological traits (e.g., body size, sexually selected badges; Jensen et al. 2004, Murphy 2007). From a conservation perspective, however, the value of LRS lies in understanding how habitat variables influence LRS, as these variables can potentially be manipulated to bolster reproductive success and/or survival. For example, LRS of Common Buzzards (*Buteo buteo*) was positively correlated with food supply and negatively correlated with human disturbance (Krüger 2002). Barnacle Geese (*Branta leucopsis*) breeding at a site with higher quality forage had higher reproductive output (Owen and Black 1989). Nest predation was found to be an important source of variance in LRS for Merlins (*Falco columbarius*; Wiklund 1996).

Information regarding the relationship between habitat and LRS is especially useful for guiding management of threatened and endangered species (Colwell et al. 2010). Here, we report on the LRS of a small, isolated population of Snowy Plovers (*Charadrius nivosus*) in coastal northern California. In 1993, the United States Fish and Wildlife Service (USFWS) listed the coastal population of the Snowy Plover as threatened under the Endangered Species Act (USFWS 1993). The species' recovery plan identified 3 factors that limit plover recovery: (1) habitat loss and degradation due to the encroachment of European beach grass (*Ammophila arenaria*); (2) human disturbance; and (3) predation of eggs and chicks (USFWS 2007). Our objective was to quantify variation in LRS among individual Snowy Plovers breeding in Humboldt County. We assessed the contribution of nesting substrate choice, predator exclosures, and presence of humans and corvid predators to variation in LRS.

METHODS

Study Area

We monitored plovers from 2001 to 2013 at multiple locations in Humboldt County, CA. During this interval, plovers bred in 2 distinct habitat types (Colwell et al. 2010). Eight breeding sites were ocean-fronting beaches, adjacent to dense stands of invasive European beach grass. There, plovers nested on homogeneous sandy substrates with scattered marine debris (algae, sea grasses, invertebrate carapaces) and driftwood. The remaining 11 sites were gravel bars on the lower 15 km of the Eel River, where substrates ranged from small clay and silt particles to large cobble. Gravel bars often had scattered woody debris and were sparsely vegetated by white sweet-clover (*Melilotus albus*) and willows (*Salix* spp.). Colwell et al. (2010) provide a detailed description of the study area.

Field Methods

Starting in 2001, researchers marked nearly all breeding plovers with a unique combination of 3 colored leg bands and a single metal USFWS band wrapped in colored tape. From mid-March to early September, we surveyed suitable habitat at 7–10 day intervals between dawn and mid-day to identify plover breeding sites and find nests; we increased the frequency of surveys at a site when we detected evidence of breeding adults. Upon finding a nest, we recorded its location (i.e. UTM coordinates) using a personal data assistant (PDA; Dell Axim 50; Dell, Round Rock, Texas, USA) equipped with a global positioning system (GPS; Holux GR-271; Holux Technology, Hsinchu, Taiwan). Occasionally ($n = 11$ of 678), researchers found newly hatched chicks from unknown nests, in which case we recorded the "nest" location as the coordinate where we first encountered the brood (Pearson and Colwell 2014).

We confirmed the identity (i.e. color band combination) of adults associated with each nest based on repeated observations of individuals together and behaviors (e.g., courtship, copulation, or tending eggs or chicks). We also documented the substrate type surrounding each nest, as plovers have been shown to select nesting substrate that improve egg crypsis and survival of nests (Colwell et al. 2011) and chicks (Colwell et al. 2007). Using this information we categorized each plover as breeding on either sand or gravel based on the substrate at the majority of their nesting sites. We considered a nest to be located on gravel if it was surrounded by egg-sized (or larger) stones; we categorized any smaller substrates as sand. Most gravel substrates occurred on the Eel River gravel bars, however, a small number of beach nests ($n = 15/600$) lay amidst patches of gravel at 4 sites.

During the first 6 years of the study and sporadically in 2010, researchers erected wire cages around some nests ($n = 126$ of 678) to exclude predators and boost hatching success (Hardy and Colwell 2008), especially at 3 beach sites: Clam Beach ($n = 102$), South Spit ($n = 7$), and Eel River Wildlife Area ($n = 17$). For each individual, we calculated the proportion of nests protected with exclosures.

At hatch, we marked chicks on their right leg with a single metal band covered in brood-specific colored tape; thereafter, we monitored broods every 1–4 days to determine whether they successfully fledged (i.e. survived to 28 d; Page et al. 2009) or died (Colwell et al. 2010). We determined that chicks had died if we did not detect them on multiple subsequent attempts to relocate them, in combination with changes in the behavior of the tending parent (e.g., adult paired and courting another plover prior to the time when chicks would have fledged).

Beginning in 2004, we collected data on the activity of humans and predators using instantaneous point counts every 20 minutes as determined by a preset alarm (Colwell et al. 2010). During each point count, observers immediately stopped surveying or observing plovers and counted the number of pedestrians, dogs, vehicles, horses, and corvids (Common Raven, *Corvus corax*; American Crow, *C. brachyrhynchos*) within 500 m of their location, which they recorded as UTM coordinates in the PDA. Observers

TABLE 1. Covariates hypothesized to explain variance in Snowy Plover lifetime reproductive success in coastal northern California.

Covariate	Abbreviation	Justification
Lifespan	lifespan	Multiple studies have shown that lifespan is an important predictor of LRS (Newton 1989c, Wiklund 1996, Blums and Clark 2004, Murphy 2007, Schubert et al. 2007, Herényi et al. 2012).
Corvid abundance score	corvid	Predation by corvids is the leading cause of reproductive failure for plovers breeding in Humboldt County (USFWS 2007, Colwell et al. 2014).
Human activity score	human	Studies have demonstrated negative impacts of human disturbance on Snowy Plovers during the breeding season, including low nest attentiveness (Hoffmann 2005), decreased hatching success (Warriner et al. 1986), and reduced chick survival (Ruhlen et al. 2003). In addition, human disturbance has directly resulted in clutch failures in 8 of the 13 years in which plovers have been intensively monitored in Humboldt County, and humans have been directly responsible for the failure of 29 clutches since 2001 (USFWS 2007, Colwell et al. 2014).
Nesting substrate	substrate	Studies of annual reproductive success have shown that plovers breeding on gravel substrates have higher nest success compared to those breeding on sand (Colwell et al. 2005, Colwell et al. 2011). In addition, plover chicks have higher survival on gravel substrates, compared to sandy substrate (Colwell et al. 2007).
Proportion of nests that were exclosed	exclosed	Exclosures increased hatching success of plover nests that were located on beaches in Humboldt County (Hardy and Colwell 2008).

conducted point counts throughout the time that they surveyed for plovers at all locations, although they occasionally ignored a 20-min observation if they were recording other essential data (e.g., plover identification and behavior); these point counts were not associated with nest locations. Details are provided elsewhere (Colwell et al. 2010, Burrell and Colwell 2012, Hardy and Colwell 2012).

Data Summary

We summarized 13 years of reproductive data to quantify LRS for 105 females and 90 males that were uniquely color-banded. For purposes of understanding LRS, we considered the population to be closed, although individuals occasionally move and breed at other locations along the Pacific coast. We defined LRS as the number of fledglings produced by a plover during the years it bred in Humboldt County (Clutton-Brock 1988, Newton 1989a). We used fledglings because philopatry in our study area is variable (8–33% annually; Colwell et al. 2014) and some birds disperse to breed elsewhere along the Pacific coast.

We calculated lifespan as the total number of years a plover bred in Humboldt County. We assumed that individuals banded in our study area as adults were 1 year old (Oring et al. 1991). Some plovers skipped one or more breeding seasons ($n_{\mathrm{male}} = 22$, $n_{\mathrm{female}} = 28$). We removed plovers from the analysis that bred outside of Humboldt County based on communications with researchers elsewhere ($n_{\mathrm{male}} = 4$, $n_{\mathrm{female}} = 7$). We retained plovers whose whereabouts were unknown during skipped breeding seasons and assumed that there was zero reproduction during those years ($n_{\mathrm{male}} = 18$, $n_{\mathrm{female}} = 21$) (Gustaffson 1989). We conducted several alternate analyses (e.g., omitting all individuals that skipped years, inserting average reproductive success for skipped years, excluding plovers known to be alive within the last 2 years of the study) and obtained virtually identical results to those presented.

Predators and humans are hypothesized to have a strong effect on plover reproductive success (USFWS 2007). Therefore, we summarized point count data collected from 2004 to 2013 to index the activity of corvids (principally Common Raven) and humans near an individual's breeding locations. We collated data for each individual by taking the point count data collected within 500 m of all its nests initiated each year, averaging values for multiple nest locations. Next, we averaged data across the years in which an individual bred to obtain an index of corvid and human activity. We used 500 m to summarize these data because this is the scale at which observers conducted point counts (Colwell et al. 2014); plover chicks move an average of 500 m from their nests during the first 3 days after hatch (Wilson and Colwell 2010). Therefore, we used this as an estimate of the amount of human and corvid activity that broods encountered when they are most vulnerable (Colwell et al. 2007).

Statistical Analysis

We used generalized linear models to examine relationships between LRS and covariates of habitat quality (i.e. corvid abundance score, human activity score, nesting substrate, proportion of nests with predator exclosures; Table 1); models included a log-link and Poisson error. We included a lifespan covariate in all models because studies have shown that lifespan explains the majority of variation in LRS for several different bird species (Newton 1989c,

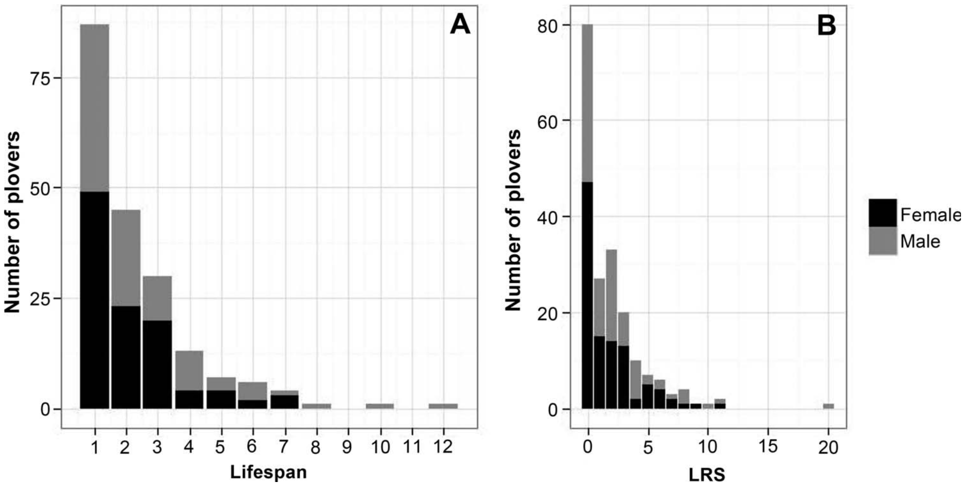

FIGURE 1. Distribution of (**A**) lifespan and (**B**) lifetime reproductive success (number of fledged young) for 195 plovers that bred in Humboldt County, CA from 2001 to 2013.

Schubert et al. 2007, Herényi et al. 2012). Consequently, the null model contained lifespan, instead of simply fitting the intercept. Additionally, we log-transformed lifespan in all models because it was right skewed. Reproductive success of male and female plovers was not independent, so we analyzed each sex separately.

We used Akaike's Information Criterion corrected for small sample size ($\mathrm{AIC_c}$; Burnham and Anderson 2002) in Program R (R Core Team 2014) to evaluate a set of 16 candidate models. Preliminary analyses revealed that there were no significant interactions between variables; therefore, we only present additive models. The full model was slightly overdispersed for both datasets ($\hat{c}_{\mathrm{female}} = 1.6$, $\hat{c}_{\mathrm{male}} = 1.4$), so we calculated quasipoisson models and quasi-$\mathrm{AIC_c}$ (i.e. $\mathrm{QAIC_c}$). As no single model had the majority of the weight, we averaged results of multiple models to produce estimates and 95% confidence intervals (Burnham and Anderson 2002). We determined the relative importance of a given covariate by summing weights across all the models where the variable occurred (Burnham and Anderson 2002). We present means ± 1 SD.

RESULTS

Lifespan of plovers attaining 1 or more years of age and breeding in Humboldt County ranged from 1 to at least 12 years ($\mu = 2.3 \pm 1.8$) (Figure 1A). Most (68%, $n = 132$) plovers bred for 2 or fewer years. We calculated LRS for 195 individually marked plovers (105 females; 90 males) that bred from 2001 to 2013 (Figure 1B). During this period, a total of 244 young fledged in the population. Individuals fledged 0–20 chicks ($\mu = 1.9 \pm 2.7$) over their lifetimes. Males averaged 2.2 ± 3.0 fledglings and females 1.7 ± 2.3 fledglings over their lifetimes. Reproductive success was highly skewed among individuals, with 13% ($n_{\mathrm{males}} = 12$, $n_{\mathrm{females}} = 14$) of males and females producing ~50% of fledglings. By contrast, 37% ($n = 33$) of males and 45% ($n = 47$) of females produced zero fledglings and 71% ($n = 64$) of males and 72% ($n = 76$) of females produced 2 or fewer fledglings during their lifetime.

Average corvid abundance scores were similar for birds breeding on gravel ($\mu = 1.2 \pm 0.6$, range = 0.5–4.1, $\sigma^2 = 0.4$) and sand substrates ($\mu = 1.1 \pm 0.4$, range = 0.1–1.8, $\sigma^2 = 0.2$). In contrast, average human activity scores were higher for sand ($\mu = 2.6 \pm 2.1$, range = 0.03–7.0, $\sigma^2 = 4.5$) than gravel habitats ($\mu = 0.1 \pm .23$, range = 0.01–1.4, $\sigma^2 = 0.05$).

Eighty-seven percent ($n = 169$) of plovers nested exclusively on one type of substrate, while the remaining 13% ($n = 26$) nested on both types. We categorized 68% of plovers ($n = 132$) as "sand breeding" and the remaining 32% ($n = 63$) as "gravel breeding". On average, plovers breeding on gravel substrates fledged more than 2 times the number of young over their lifetime ($\mu = 3.1 \pm 3.5$, range = 0–20, $\sigma^2 = 12.5$) compared to those breeding on sand ($\mu = 1.4 \pm 1.9$, range = 0–9, $\sigma^2 = 3.5$).

Thirty-three percent ($n = 65$) of plovers had at least one of their nests protected with an exclosure. Among these birds, the average percentage of exclosed nests was 63% (range = 7–100%). Eleven percent ($n = 21$) of plovers had all of their nests protected with exclosures; however, 16 of these individuals had only one nest during their lifespan.

For both sexes, substrate was the most important covariate predicting variation in LRS. Individuals breeding on gravel substrates fledged significantly more young than those breeding on sand (Table 2). Models containing the substrate covariate accounted for nearly 100% of the model weights (Table 3 and 4).

Only weak relationships existed between LRS and other covariates. Models containing the exclosed covariate

TABLE 2. Unconditional beta coefficient estimates (β) with associated standard error (SE) and 95% confidence intervals (CI).

	Covariate	β [a]	SE [a]	95% CI [a]
Males				
	LIFESPAN	1.18	0.12	0.94, 1.42
	CORVID	–0.06	0.14	–0.4, 0.3
	HUMAN	–0.03	0.06	–0.2, 0.1
	SUBSTRATE	–0.69	0.20	–1.1, −0.3
	EXCLOSED	0.26	0.36	–0.4, 1.0
Females				
	LIFESPAN	1.26	0.15	0.97, 1.56
	CORVID	–0.07	0.26	–0.6, 0.4
	HUMAN	0.03	0.07	–0.1, 0.2
	SUBSTRATE	–0.76	0.22	–1.19, −0.33
	EXCLOSED	0.17	0.38	–0.57, 0.91

[a] Derived from model averaging

accounted for 31 and 27% of the model weights for males and females, respectively (Table 3 and 4). Models containing variables that indexed activity of humans and corvids accounted for 23 and 26% and 22 and 25% of model weights for males and females, respectively (Table 3 and 4). The confidence intervals for all 3 of these covariates overlapped zero (Table 2).

DISCUSSION

This study revealed 2 main findings, both of which have strong conservation value. First, reproductive success was highly skewed among individuals, with a small proportion of the population contributing disproportionately to future generations. Second, variance in LRS was best explained by breeding substrate; LRS was appreciably higher for plovers breeding on gravel substrates.

Variance in Reproductive Success

The strong skew in LRS, with most individuals producing few or no offspring and a small percentage accounting for greater than 50% of young, is a commonly reported pattern in birds. Newton (1989b) summarized data for 12 bird species, and reported that 14–31% of breeders were responsible for producing 50% of offspring. Our estimates of Snowy Plover LRS are similar to those reported for other shorebirds. Female Common Sandpipers (*Actitis hypoleucos*) fledged an average of 1.5 ± 2.2 chicks during their lifetime; 12.5% of females and 9% of males produced 55% of fledglings (Holland and Yalden 1994). Female and male Spotted Sandpipers (*Actitis macularius*) produced 5.2 ± 5.2 and 3.3 ± 4.1 fledglings during their lifetime, respectively (Oring et al. 1991). While a single individual of each sex fledged 23 chicks, birds that fledged zero chicks accounted for the largest single category (Oring et al. 1991). Our estimates of LRS share a limitation with other studies seeking to quantify it—we based our analyses on individuals who remained in our study population and have no knowledge of the reproductive success of those who emigrated to breed elsewhere. Our sample consisted of a mix of individuals of known age ($n = 92$) and immigrants of unknown age ($n = 103$). It is likely, however, that immigrants were unsuccessful breeders with low reproductive success at their prior breeding locations, as evidenced by a general pattern of dispersal following reproductive failure in shorebirds (Oring and Lank 1984, Flynn et al. 1999, Skrade and Dinsmore 2010, Rioux et al. 2011) and in this population of Snowy Plover (Pearson and Colwell 2014). Nevertheless, our results were robust to permutations of this total sample (see Methods).

Quantifying variance in reproductive success is especially important for small, isolated populations because it allows estimation of effective population size (N_e) (Kimura and Crow 1963, Barrowclough and Rockwell 1993), which is "the size of an idealized population that would have the same amount of inbreeding or random gene frequency drift as the population under consideration" (Kimura and Crow 1963). Parameter N_e is useful in conservation biology because it predicts how quickly a given population will lose genetic variation (Kimura and Crow 1963). Best estimates of N_e are based on LRS (Koenig 1988).

With high variance in reproductive success, plovers in Humboldt County may be vulnerable to genetic drift and

TABLE 3. Models predicting Snowy Plover LRS for male birds, ranked according to Akaike's Information Criterion with small sample size correction and quasi-fit. Only models that summed to 97% weight are included.

Models	Parameters	logL	$\Delta QAIC_c$ [a]	w_i
LIFESPAN+SUBSTRATE	4	–99.40	0	0.40
LIFESPAN+SUBSTRATE+EXCLOSED	5	–99.12	1.71	0.17
LIFESPAN+SUBSTRATE+CORVID	5	–99.31	2.09	0.14
LIFESPAN+SUBSTRATE+HUMAN	5	–99.38	2.23	0.13
LIFESPAN+SUBSTRATE+CORVID+EXCLOSED	6	–99.01	3.79	0.06
LIFESPAN+SUBSTRATE+HUMAN+EXCLOSED	6	–99.09	3.94	0.05
LIFESPAN+SUBSTRATE+HUMAN+CORVID+EXCLOSED	7	–99.01	6.13	0.02

[a] QAIC value of the best model was 207.25.

TABLE 4. Models predicting Snowy Plover LRS for female birds, ranked according to Akaike's Information Criterion with small sample size correction and quasi-fit. Only models that summed to 97% weight are included.

Models	Parameters	logL	$\Delta QAIC_c$ [a]	w_i
LIFESPAN + SUBSTRATE	4	–102.44	0	0.40
LIFESPAN + SUBSTRATE + EXCLOSED	5	–102.33	2.00	0.15
LIFESPAN + SUBSTRATE + HUMAN	5	–102.35	2.03	0.14
LIFESPAN + SUBSTRATE + CORVID	5	–102.42	2.16	0.13
LIFESPAN + SUBSTRATE + HUMAN + EXCLOSED	6	–102.23	4.05	0.05
LIFESPAN+ SUBSTRATE + HUMAN + CORVID	6	–102.26	4.11	0.05
LIFESPAN + SUBSTRATE + CORVID + EXCLOSED	6	–102.31	4.20	0.05

[a] QAIC value of the best model was 213.28.

inbreeding; 5 instances of inbreeding have been observed in Humboldt County over the past 13 years, one of which resulted in inviable embryos (Colwell and Pearson 2011). If other plover breeding sites along the Pacific coast are characterized by a similar pattern of unequal progeny production, N_e of the listed population segment is likely to be much less than the most recent censused total of 1,831 individuals (Colwell et al. 2014). Based on lifetime reproductive success, we estimate that N_e is less than half of the censused total because the correction factor (F_{rs}) for unequal progeny production (Koenig 1988) is 0.41 for males and 0.45 for females.

Predictors of Variance in LRS

Our finding that plovers breeding on gravel substrates had significantly higher LRS than those occupying sandy substrates builds on earlier papers (Colwell et al. 2010, 2011) studying habitat correlates of productivity. Gravel-breeding plovers laid fewer eggs, yet fledged significantly more young than those on sandy ocean-fronting beaches, such that by their sixth year, they had fledged ~4× as many young as similarly aged plovers breeding on beaches (Colwell et al. 2010). Differences in reproductive success likely stem from the crypsis of eggs and chicks, and their detectability in different substrates (Colwell et al. 2005, 2010, 2011). Plovers nest in open, sparsely vegetated habitats and rely on early predator detection and egg crypsis to camouflage nests (Amat and Masero 2004, Muir and Colwell 2010). In our study area, plovers breeding on gravel had enhanced egg crypsis (i.e. more egg-sized stones), compared to random sites (Colwell et al. 2011).

Higher reproductive success on gravel substrate, despite similar corvid abundance on beaches, suggests that ravens and crows are less able to detect eggs and chicks among gravel substrates (Colwell et al. 2007, 2010, 2011). Studies of other shorebird species corroborate these results. Piping Plover (*Charadrius melodus*) eggs were more likely to be depredated when they contrasted with background substrates (Mayer et al. 2009). Similarly, Stone Curlew (*Burhinus oedicnemus*) eggs suffered higher rates of predation when they differed in color from the ground (Solis and de Lope 1995).

Interestingly, corvid abundance was not a significant predictor of LRS for Snowy Plovers. Evidence strongly implicates corvids as the main cause of low reproductive success for plovers across the range of the listed population (USFWS 2007), especially in coastal northern California (Colwell et al. 2014). Moreover, previous studies demonstrated that per capita fledging success correlated negatively with an index of raven activity (i.e. *incidence* or the proportion of point counts with at least one raven; Burrell and Colwell 2012) and that ravens were the cause of consistently low nest survival (Hardy and Cowell 2012). Additionally, video footage showed that ravens caused 70% of nest failures at the site with the highest raven activity (Burrell and Colwell 2012).

Consequently, we were surprised by the weak relationship between corvid activity and LRS (Table 2), although the relationship was in the predicted direction (i.e. negative coefficient). This apparent contradiction may arise from the different methods we used to summarize data across studies, as well as the imperfect nature in which our field-based measures of corvid activity index the risk to plovers of reproductive failure. First, in this study we indexed corvid activity by combining counts for ravens and crows; Burrell and Colwell (2012) analyzed them separately. Second, we collated point count data at different spatial (individual home ranges of several hundred meters vs. "sites" spanning several linear kilometers of beach or gravel bar) and temporal (averages summed across an individual's lifetime vs. annual averages) scales. Finally, although strong evidence links corvids (especially ravens) with low plover productivity, it is difficult to collect data to clearly demonstrate a causal relationship. At best, our point counts produced an average value for corvids, a measure that lacks critical information to index danger posed by corvids to eggs and chicks. Specifically, our index ignores proximity of corvids to nests and broods, as well as their behaviors (e.g., foraging on the ground vs. merely flying over). In summary, while our results appear to contradict earlier findings regarding corvid impacts on plover productivity (Burrell and Colwell 2012), we conclude that field and analytical methods make comparisons between studies difficult at best.

The recovery plan for the Snowy Plover identifies human disturbance as an important factor limiting population recovery (USFWS 2007). We did not find a strong relationship between human activity and LRS. This result is consistent with results reported elsewhere for our study population (Burrell and Colwell 2012, Hardy and Colwell 2012) but it differs from elsewhere in the species' range (Ruhlen et al. 2003, Lafferty et al. 2006). The weak relationship may arise because human activity is infrequent at most locations where plovers bred in our study area and humans account for only a small percentage of reproductive failures (Hardy and Colwell 2012, Colwell et al. 2014). At the southern extent of the plover's range in California, human activity is higher (Ruhlen et al. 2003, Lafferty et al. 2006). The synergistic relationship between humans and corvids may also influence predation risk when human activity is higher (e.g., Walker and Marzluff 2015).

The result that nest exclosures were not associated with higher LRS is surprising, although earlier analyses of annual reproductive success hinted at this result (Hardy and Colwell 2008). While exclosures increase hatching success by protecting eggs from predators (Amat et al. 1999, Johnson and Oring 2002, Hardy and Colwell 2008), nidifugous young are vulnerable to predation once they leave the exclosure. Dinsmore et al. (2014) monitored Snowy Plover nests over 20 years in coastal Oregon and found that while apparent nesting success was greater for exclosed nests, fledging success between exclosed and unexclosed nests did not differ. Most of the exclosed nests in our study (102/126) were located on Clam Beach, where chicks are highly susceptible to predation due to a high abundance of ravens and crows (Colwell et al. 2014).

Management Implications

Our results have several important management implications. First, higher LRS on gravel substrates suggests that enhancing sandy substrates with debris such as shell hash or driftwood may improve reproductive success (Powell and Collier 2000). Second, while exclosures appear to improve hatching success (Johnson and Oring 2002, Hardy and Colwell 2008, Dinsmore et al. 2014), their use does not improve LRS and has been associated with several costs, including increased mortality risk to incubating adults (Neuman et al. 2004, Hardy and Colwell 2008), increased nest abandonment (Hardy and Colwell 2008), and providing false information on habitat quality (Hardy and Colwell 2008, Dinsmore et al. 2014).

The influence of corvid predation on plover reproductive success remains a complex issue. It is clear that where especially abundant, corvids depress reproductive success (Burrell and Colwell 2012, Colwell et al. 2014). Largely due to corvid predation, annual estimates of per capita reproductive success in our study area fall below the recovery objective set forth by the USFWS (USFWS 2007, Colwell et al. 2014). However, the variation in corvid activity from year to year makes analyses of lifetime reproductive data challenging.

The plover population we studied has been characterized as a "sink" owing to low reproductive success and occasionally low survival of adults and juveniles (Eberhart-Phillips and Colwell 2014). The LRS data, although not independent of this modeling effort, provide additional insights into the contribution of low productivity to the recovery of the species.

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