LIFETIME REPRODUCTIVE SUCCESS OF SNOWY PLOVERS IN COASTAL NORTHERN CALIFORNIA

By

Dana M. Herman

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Committee Membership
Dr. Mark Colwell, Committee Chair
Dr. Daniel Barton, Committee Member
Dr. Jeff Black, Committee Member
Dr. Alison O’Dowd, Graduate Coordinator

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ABSTRACT

Lifetime Reproductive Success of Snowy Plovers in Coastal Northern California

Dana M. Herman

Conserving threatened and endangered species requires knowledge of species breeding productivity and the factors that cause variation in reproductive success. I summarized 13 years of reproductive data to quantify lifetime reproductive success (LRS) for 195 individually marked Snowy Plovers (*Charadrius nivosus*) breeding in Humboldt County. In addition, I modeled relationships between LRS and various measures of habitat quality using an information theoretic framework and a model averaging approach. LRS varied appreciably between sexes; males exceeded females in maximum LRS, mean LRS and variance in LRS. Additionally, reproductive success was highly skewed among individuals, with a small proportion of the population contributing most offspring. Thirteen percent (*n* males = 12, *n* females = 14) of males and females produced approximately 50% of fledglings. By contrast, 37% (*n* = 33) of males and 45% (*n* = 47) of female plovers produced zero fledglings and 71% (*n* = 64) of males and 72% (*n* = 76) of females produced two or fewer during their lifetime. Variance in LRS was best explained by breeding substrate, with gravel breeding birds having significantly higher LRS compared to beach breeding birds. Models containing this covariate accounted for nearly 100% of the corrected-Akaike weights based on the relative importance of model covariates. Other measures of habitat quality, including measures of nest exclosures, corvid abundance and human activity, were not significant predictors of LRS. The results
from this study provide valuable information regarding the relationship between LRS and habitat quality, and thus can be used to guide management aimed at increasing the reproductive success of this threatened species.
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INTRODUCTION

Long-term studies of individually marked birds have allowed for the quantification of lifetime reproductive success (LRS). LRS measures the total number of offspring that an individual contributes to future generations over its lifetime (Clutton-Brock 1988, Newton 1989a); consequently, it is considered to be a good approximation of biological fitness (Newton 1989a, Korpimäki 1992, Newton 1995, Jensen et al. 2004).

Prior to the 1980s, studies of avian breeding ecology often focused on analyses of single breeding attempts or annual reproductive success (Newton 1989a). Such studies, termed “cross-sectional” because they investigate data from a particular point in time (Newton 1989a, Loschl 2008), include only a fraction of the lifespan of the birds in the study population and therefore cannot elucidate how reproductive success varies with age (Newton 1989a, Loschl 2008). In addition, the identities of individual birds are often unknown in many cross-sectional studies and this makes it difficult to examine variation in breeding success (Newton 1989a).

Studies of LRS are particularly valuable when patterns of variation in reproductive success are coupled with causative factors, as this provides insight on the selective pressures affecting breeding populations (Krüger and Linström 2001, Newton 1989a). Many studies focus on the relationship between LRS and various life-history traits (Brown 1988, Grafen 1988). These studies typically partition variance in LRS into components explained by traits like lifespan, average fecundity, and offspring survival (Brown 1988). For instance, Saurola (1989) studied LRS of Ural Owls (*Strix uralensis*)
and found that lifespan and the annual number of clutches explained most of the variation in lifetime production. MacColl and Hatchwell (2004) studied LRS of Long-tailed Tits (Aegithalos caudatus) and found that offspring survival accounted for most of the variance in LRS. Oring et al. (1991) studied LRS of Spotted Sandpipers (Actitis macularia) and found that the proportion of chicks fledged accounted for the greatest proportion of variance in lifetime production.

Studies that examine the relationship between LRS and morphology are also common (Bryant 1989, Mills 1989, Krüger 2002, Blums and Clark 2004, MacColl and Hatchwell 2004). For instance, Jensen et al. (2004) studied LRS of House Sparrows (Passer domesticus) and found that morphological traits, like badge size and bill length, explained a significant proportion of variation in male LRS. In addition, Murphy (2007) studied LRS in Eastern Kingbirds (Tyrannus tyrannus), and found that large body size had a negative effect on female lifetime reproductive output. Other studies have found that LRS is closely tied to behaviors like dispersal distance (Ekman et al. 1999, Hansson et al. 2004, MacColl and Hatchwell 2004) and song repertoire (McGregor et al. 1981).

To a much lesser extent, studies have examined the effects of measures of breeding habitat quality on LRS (Hötker 1989, Newton 1989b, Owen and Black 1989, Conradt et al. 1999, Krüger 2002). For instance, Owen and Black (1989) tested whether breeding area influenced LRS of Barnacle Geese (Branta leucopsis) by comparing reproductive success of geese at two different breeding sites which vary in quality. This study revealed that geese breeding at the site with higher quality feeding habitat had higher reproductive output (Owen and Black 1989). In addition, Krüger (2002) studied
the effects of food supply and human disturbance on LRS of Common Buzzards (*Buteo buteo*) and found the latter to be a significant predictor of LRS. Dark and light morph buzzards that nested in habitats with high human disturbance had lower fitness, compared to those nesting in higher quality territories (Krüger 2002).

Information regarding the relationship between habitat and LRS is especially useful for guiding management of threatened and endangered species (Colwell et al. 2005, Colwell et al. 2010a). This study reports 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 in response to a significant population decline and a decrease in the number of breeding sites along the Pacific coast (USFWS 1993). In the species’ recovery plan, the USFWS (2007) identified three 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.

Lifetime reproductive success has not been formally studied in the Snowy Plover and has rarely been studied in other shorebird species. While many studies have reported on the annual reproductive success of shorebirds (Knopf and Rupert 1996, Espie et al. 1998, Grant et al. 1999, Murphy et al. 2000, Minton et al. 2003, Takahashi and Ohkawara 2007), few studies have monitored shorebird populations long enough to capture the LRS of these long-lived organisms (Oring et al. 1991, Thompson and Thompson 1991, Holland and Yalden 1994, Van De Pol et al. 2006).
The objectives of this study were to (1) analyze 13 years of reproductive data to quantify LRS of Snowy Plovers breeding in Humboldt County, (2) quantify variation in LRS among individuals and between sexes, and (3) assess the relationship between LRS and habitat factors which are thought to influence Snowy Plover productivity (USFWS 2007).
METHODS

Study Area

I studied Snowy Plovers in Humboldt County, CA, which is near the northern limit of the species’ range. Humboldt County is part of Recovery Unit 2 (RU2), which also encompasses Del Norte and Mendocino counties and is one of six recovery units designated in the USFWS species’ recovery plan (USFWS 2007). Breeding plovers have been intensively monitored in RU2 for the past 13 years, and during this time, plovers have been found to breed almost exclusively in Humboldt County (Colwell et al. 2013). The number of breeding plovers in RU2 has fluctuated greatly over the past 13 years, varying from 72 (2004) to 19 (2009) (Colwell et al. 2013).

Plovers have bred at 19 sites in Humboldt County since intensive monitoring of a color-marked population began in 2001 (Colwell et al. 2013). Eight of these sites are ocean-fronting beaches, characterized by fine sandy substrates, scattered marine debris (algae, eel grass and invertebrate carapaces), woody debris, and dense stands of invasive European beach grass (Colwell et al. 2010a). The remaining 11 sites are gravel bars of the Eel River, which were unknown as plover breeding sites before 1996 (Tuttle et al. 1997). The gravel bars are composed of substrates varying in size from large cobble to small sand particles. Gravel bars also have scattered woody debris and are sparsely vegetated by white sweet-clover (Melilotus albus) and willows (Salix spp., Colwell et al. 2010a). There have been no known breeding records on the gravel bars since 2010.
Field Methods

For the past 13 years (2001-2013), researchers from Humboldt State University, Mad River Biologists, and county, state and federal agencies have monitored plover breeding activity in RU2 (Colwell et al. 2013). From mid-March to early September, researchers surveyed suitable plover habitat at least once a month; when plovers were observed at a site, survey frequency increased (Colwell et al. 2013). Since 2001, researchers marked virtually all breeding plovers in RU2 with a unique combination of three colored leg bands and a single metal USFWS band wrapped in colored tape (Colwell et al. 2013).

During surveys, researchers recorded nest locations using a personal data assistant (PDA; Dell Axim 50) equipped with a global positioning system (GPS; Holux GR-271, Colwell et al. 2013). Occasionally \((n = 11/678)\), researchers found broods from unknown nests; for these cases, I used the location at which the brood was first encountered in place of the nest location (Pearson 2011). Researchers determined nest ownership by observing color bands on the legs of adult plovers (Colwell et al. 2013). In addition, researchers documented the substrate type surrounding each nest (Colwell et al. 2013).

For nests found with a complete clutch (i.e., three eggs), researchers determined hatch date using egg flotation methods (Hays and Lecroy 1971) or by reviewing adult location data to determine the most likely date of incubation onset (Colwell et al. 2013). During the first six years of the study and sporadically in 2010, biologists exclosed some
nests \((n = 126/678)\) with wire cages to exclude predators and boost hatching success (Hardy and Colwell 2008, Colwell et al. 2010b). Exclosures were used at three beach sites: Clam Beach \((n = 102)\), South Spit \((n = 7)\) and Eel River Wildlife Area \((n = 17)\).

At hatch, researchers marked chicks on their right leg with a single metal band covered in brood-specific colored tape and thereafter monitored broods regularly until they fledged or failed (Colwell et al. 2013). I considered a chick to be fledged if it survived to 28 days (Page et al. 2009, Colwell et al. 2013).

Since 2004, researchers also conducted 500 m point counts at 20 minute intervals to assess the threat of predation and human activity at plover breeding sites (Colwell et al. 2010a, Burrell and Colwell 2012, Hardy and Colwell 2012). During this time, observers recorded the number of pedestrians, dogs, vehicles, horses and corvids (Common Raven, *Corvus corax*; American Crow, *C. brachyrhynchos*) detected within a 500 m radius of their location. Research was conducted under federal, state, and university permits (USFWS permit TE-823807-3; USFWS Federal banding permit #22971; California Department of Fish and Wildlife collecting permit #801059-03; State Parks collecting permit #09-635-002; Humboldt State University IACUC #11/12.W.12-A).

Data Summary

I summarized 13 years (2001-2013) of reproductive data to quantify LRS for 195 (105 females; 90 males) individually-marked plovers breeding in Humboldt County. I removed individuals from the initial dataset that were not uniquely marked \((n_{\text{males}}=17, n_{\text{females}}=8)\), those with documented breeding records outside of Humboldt County \((n_{\text{males}}=15, n_{\text{females}}=26)\), those that bred in Humboldt County before 2001 when data
collection was less reliable \((n_{\text{males}}=18, n_{\text{females}}=22)\), and those that had an equal number of nesting attempts on sand and gravel substrates \((n_{\text{males}}=3, n_{\text{females}}=4)\). I defined lifetime reproductive success as the number of fledglings produced by a plover over the course of its lifespan \((\text{Clutton-Brock 1988, Newton 1989a})\). I decided that the number of fledglings was a more accurate measure of LRS, compared to recruits, because philopatry in RU2 is extremely variable; in some years, less than 10\% of male and female chicks return to breed \((\text{Colwell et al. 2007a, Colwell et al. 2013})\). Furthermore, several LRS studies have found measures of fledgling and recruit production to be correlated \((\text{Hochachka et al. 1989, Hötker 1989, Newton 1989b, Brommer et al. 1998, Korpimäki 1992})\).

I quantified variation in LRS between individuals and sexes using descriptive statistics and frequency distributions of LRS values. In addition, to avoid potential bias in the data owing to truncating the breeding lifespans of extant individuals \((\text{Newton 1989a})\), I analyzed a subset of individuals \((n = 154)\) that excluded plovers known to be alive within the last two years of the study. For this analysis, I assumed that a plover was deceased, and therefore had concluded its breeding life, if it was not observed within the last two years of the study and had no documented breeding records outside of Humboldt County during that time \((\text{McCleery and Perrins 1989, Owen and Black 1989})\). The results of this analysis were nearly identical to those presented.

I calculated lifespan as the total number of years which elapsed from when a plover was first and last observed in Humboldt County. I assumed that individuals that were banded in RU2 as adults were 1 year old \((\text{Oring et al. 1991})\). Not all plovers were present throughout their lifespan because they skipped one or more breeding seasons.
(n\textsubscript{male} = 22, n\textsubscript{female} = 28). I removed plovers from the analysis that were documented breeding outside of Humboldt County during skipped years (n\textsubscript{male} = 4, n\textsubscript{female} = 7). I retained plovers whose whereabouts were unknown during skipped breeding seasons and I assumed that there was zero reproduction during those years (n\textsubscript{male} = 18, n\textsubscript{female} = 21) (Gustaffson 1989, Oring et al. 1991). I also performed analyses where I estimated reproductive success for skipped years by substituting yearly averages (Oring et al. 1991); the results of these analyses were nearly identical to those presented.

I quantified the amount of human and corvid activity that each plover was exposed to while breeding using point count data collected from 2004-2013. Previous studies have shown that patterns of human and corvid abundance are consistent across years (Colwell et al. 2013), so I pooled point count data from all years. For each individual plover, I plotted all known nest locations in ArcMap (ESRI, Redlands, CA) and isolated the point count locations that fell within 500 m of each nest. I then calculated the average corvid abundance and average human activity abundance within 500 m of each plover nest. If an individual had multiple nests, I averaged these values across nests (Appendix A).

I chose to average data from point counts within a 500 m radius of all nests because this is the scale at which observers conduct point counts during plover surveys (Colwell et al. 2013). In addition, Wilson and Colwell (2010) found that snowy plover chicks moved an average of approximately 500 m from their nests during the first three days after hatch, and I wanted to estimate the amount of human and corvid activity that each brood encountered.
I categorized plovers as occupying either sand or gravel habitats based on the substrate at the majority of their nesting sites, as identified by detailed notes from researchers. I considered a nest to be located on gravel if it was surrounded by egg sized (or larger) stones, and anything smaller was categorized as sand. Most gravel substrates were found on the Eel River Gravel bars, however, a small number of beach nests \( (n = 15/600) \) were located on patches of gravel substrate. This occurred for a few nests on Eel River Wildlife Area \( (n = 11) \), Big Lagoon \( (n = 2) \), Stone Lagoon \( (n = 1) \) and Clam Beach \( (n = 1) \). Lastly, for each individual, I calculated the proportion of nests that were protected with exclosures.

Statistical Analysis

I investigated which predictor variables (i.e., lifespan, corvid abundance score, human activity score, nesting substrate, proportion of nests that were exclosed; Table 1) best explained variance in Snowy Plover LRS using generalized linear models, with a log-link and poisson error, which are commonly used to analyze count data (Lovett and Flowerdew 1989). The response variable in my analysis was lifetime reproductive success. Reproductive success of male and female plovers was not independent, so I analyzed each sex separately.

I used Akaike’s Information Criterion corrected for small sample size (AIC\(_c\), Burnham and Anderson 2002) in Program R (R Core Team 2014) to evaluate a set of 16 candidate models. Preliminary exploratory analyses revealed that there were no significant interactions between variables. Therefore, I only included models with
Table 1. Variables hypothesized to explain variance in Snowy Plover lifetime reproductive success in coastal northern California.

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<th>Abbreviation</th>
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<td>Lifespan</td>
<td>LIFESPAN</td>
<td>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).</td>
</tr>
<tr>
<td>Corvid abundance score</td>
<td>CORVID</td>
<td>Predation by corvids is the leading cause of reproductive failure for plovers breeding in Humboldt County (USFWS 2007, Colwell et al. 2013).</td>
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<tr>
<td>Human activity score</td>
<td>HUMAN</td>
<td>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 eight of the 13 years in which plovers have been intensively monitored in RU2, and humans have been directly responsible for the failure of 29 clutches since 2001 (USFWS 2007, Colwell et al. 2013).</td>
</tr>
<tr>
<td>Nesting substrate</td>
<td>SUBSTRATE</td>
<td>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. 2007b).</td>
</tr>
<tr>
<td>Proportion of nests that were exclosed</td>
<td>EXCLOSED</td>
<td>Exclosures increased hatching success of plover nests that were located on beaches in Humboldt County (Hardy and Colwell 2008).</td>
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additive relationships, as interaction terms would have vastly inflated the size of my model set. I included the variable LIFESPAN in all of my models because previous studies have shown that lifespan explains the majority of variation in LRS for several different bird species (Newton 1989c, Wiklund 1996, Blums and Clark 2004, Murphy 2007, Schubert et al. 2007, Herényi et al. 2012). Consequently, my null model contained the variable LIFESPAN, instead of simply fitting the intercept. Additionally, I log-transformed LIFESPAN in all models because it was right skewed.

I removed one pretending model (i.e., the addition of an extra parameter did not change the deviance of the model; Anderson 2008) from the male dataset before calculating the final AICc values. In addition, I found that the full model was slightly overdispersed for both datasets ($\hat{\gamma}_{\text{female}} = 1.6$, $\hat{\gamma}_{\text{male}} = 1.4$), so I calculated quasipoisson models and quasi-AICc (i.e., QAICc). There was no clear model that came to the top with a majority of the weight, so I applied model averaging to both the female and male datasets in order to obtain model averaged estimates and 95% confidence intervals for each covariate (Burnham and Anderson 2002). Lastly, I estimated the relative importance of a given covariate by summing the weights across all the models where the variable occurred (Burnham and Anderson 2002, Burrell 2010).
RESULTS

Lifespan of plovers breeding in RU2 ranged from 1 to 12 years (µ = 2.3±1.8, σ² = 3.1) (Figure 1a). Average lifespan was higher for males (µ = 2.5±2.1, range = 1-12, σ² = 4.2) than females (µ = 2.1±1.5, range = 1-7, σ² = 2.2). Most (68%, n = 132) plovers had a lifespan of 2 years or less. Lifespan was significantly correlated with LRS for both male (r = .8, N = 90, p < 0.001) and female (r = .7, N = 105, p < 0.001) plovers (Figure 2a, Figure 2b).

I analyzed point counts that fell within 500 m of 600 nests located at nine different plover breeding sites in Humboldt County (Appendix B). The average number of point counts that fell within 500 meters of a plover nest was 823±385 (range = 17-1,476). The average corvid abundance and human activity scores were 1.2±0.5 and 1.8±2.1, respectively. Average corvid abundance scores were slightly higher for birds breeding on gravel (µ = 1.2±.63, range = 0.5-4.1, σ² = 0.4) compared to sand (µ = 1.1±.39, range = 0.1-1.8, σ² = 0.2). In contrast, the average human activity score for sand breeding birds (µ = 2.6±2.1, range = 0.03-7.0, σ² = 4.5) exceeded those on gravel (µ = 0.1±.23, range = 0.01-1.4, σ² = 0.05).

Eighty-seven percent (n = 169) of plovers nested exclusively on one type of substrate (i.e., either gravel or sand) during their lifetime, while the remaining 13% (n = 26) nested on both types of substrate and were therefore categorized based on the substrate at the majority of their nest sites. Of the birds that nested on multiple substrates, a majority had at least 75% of their nests located on a particular substrate type.
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 2001-2013.
Figure 2. Lifetime reproductive success of (a) male and (b) female plovers in relation to lifespan. Corresponding to its size, each spot represents 1-32 different individuals. (Males: r = .8, N = 90, p < 0.001; Females: r = .7, N = 105, p < 0.001).
I categorized 68% of plovers ($n = 132$) as “sand breeding” and the remaining 32% ($n = 63$) as “gravel breeding”.

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

I calculated LRS for 195 individually marked plovers (105 females; 90 males) that bred in Humboldt County from 2001-2013 (Figure 1b). During this 13 year period, plovers fledged a total of 244 young. Individuals fledged 0-20 chicks ($\mu = 1.9 \pm 2.7$, $\sigma^2 = 7.1$) over their lifetimes. Males had higher maximum (range = 0-20) LRS, mean (2.2±3.0) LRS, and greater variance ($\sigma^2 = 9.2$) in LRS than females (range = 0-11, $\mu = 1.7 \pm 2.3$, $\sigma^2 = 5.2$). Overall sex differences held for the subset of 154 plovers (85 females, 69 males) which excluded extant individuals.

Reproductive success was highly skewed among individuals, with a small proportion of the population contributing most offspring. Thirteen percent ($n_{males} = 12$, $n_{females} = 14$) of males and females produced approximately 50% of fledglings. By contrast, 37% ($n = 33$) of males and 45% ($n = 47$) of female plovers produced zero fledglings and 71% ($n = 64$) of males and 72% ($n = 76$) of females produced two or fewer during their lifetime.

For both sexes, SUBSTRATE was the most important variable predicting variance in LRS, with birds occupying gravel substrates producing significantly more fledged
young than those breeding on sandy substrates ($\beta_{\text{male}} = -0.65$, 95% CI$_{\text{male}} = [-1.0, -0.3]$, $\beta_{\text{female}} = -0.76$, 95% CI$_{\text{female}} = [-1.2, -0.3]$). Models containing the SUBSTRATE covariate accounted for nearly 100% of the model weights (Table 2, Table 3); in other words, any model that did not contain this covariate had little to no explanatory power.

The proportion of exclosed nests appeared to be the second most important predictor of LRS for both males and females; however, the relationship between LRS and this variable was weak. Models containing the EXCLOSED covariate accounted for 31 and 27% of the model weights for males and females, respectively (Table 2, Table 3). Additionally, the confidence interval for this covariate overlapped zero ($\beta_{\text{male}} = 0.26$, 95% CI$_{\text{male}} = [-0.4, 1.0]$; $\beta_{\text{female}} = 0.17$, 95% CI$_{\text{female}} = [-0.6, 0.9]$), suggesting that the proportion of exclosed nests was not a significant predictor of LRS.

Human activity was the third most important predictor of LRS for both sexes, followed by corvid abundance. The relationship between LRS and these two covariates was also weak. Models containing the HUMAN covariate accounted for 23 and 26% and models containing the CORVID covariate accounted for 22 and 25% of the model weights for males and females, respectively (Table 2, Table 3). The confidence intervals for both of these covariates overlapped zero (HUMAN: $\beta_{\text{male}} = -0.03$, 95% CI$_{\text{male}} = [-0.2, 0.1]$; $\beta_{\text{female}} = 0.03$, 95% CI$_{\text{female}} = [-0.1, 0.2]$; CORVID: $\beta_{\text{male}} = -0.06$, 95% CI$_{\text{male}} = [-0.4, 0.3]$; $\beta_{\text{female}} = -0.07$, 95% CI$_{\text{female}} = [-0.6, 0.4]$), suggesting that neither human activity nor corvid abundance were significant predictors of plover LRS.
Table 2. Models predicting Snowy Plover LRS for female birds, ranked according to QAIC\textsubscript{c} value. Only models that summed to 97% weight are included.

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
<th>logL</th>
<th>QAIC\textsubscript{c}</th>
<th>ΔQAIC\textsubscript{c}</th>
<th>w\textsubscript{j}</th>
<th>w\textsubscript{i}</th>
<th>cumulative w\textsubscript{i}</th>
</tr>
</thead>
<tbody>
<tr>
<td>LIFESPAN + SUBSTRATE</td>
<td>4</td>
<td>-102.44</td>
<td>213.28</td>
<td>0</td>
<td>0.40</td>
<td>0.40</td>
<td></td>
</tr>
<tr>
<td>LIFESPAN + SUBSTRATE + EXCLOSED</td>
<td>5</td>
<td>-102.33</td>
<td>215.28</td>
<td>2.00</td>
<td>0.15</td>
<td>0.55</td>
<td></td>
</tr>
<tr>
<td>LIFESPAN + SUBSTRATE + HUMAN</td>
<td>5</td>
<td>-102.35</td>
<td>215.31</td>
<td>2.03</td>
<td>0.14</td>
<td>0.69</td>
<td></td>
</tr>
<tr>
<td>LIFESPAN + SUBSTRATE + CORVID</td>
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<td>-102.42</td>
<td>215.45</td>
<td>2.16</td>
<td>0.13</td>
<td>0.82</td>
<td></td>
</tr>
<tr>
<td>LIFESPAN + SUBSTRATE + HUMAN + EXCLOSED</td>
<td>6</td>
<td>-102.23</td>
<td>217.34</td>
<td>4.05</td>
<td>0.05</td>
<td>0.87</td>
<td></td>
</tr>
<tr>
<td>LIFESPAN + SUBSTRATE + HUMAN + CORVID</td>
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<td>-102.26</td>
<td>217.39</td>
<td>4.11</td>
<td>0.05</td>
<td>0.92</td>
<td></td>
</tr>
<tr>
<td>LIFESPAN + SUBSTRATE + CORVID + EXCLOSED</td>
<td>6</td>
<td>-102.31</td>
<td>217.48</td>
<td>4.20</td>
<td>0.05</td>
<td>0.97</td>
<td></td>
</tr>
</tbody>
</table>

K: number of parameters in the model.
QAIC\textsubscript{c}: Akaike’s Information Criterion with small sample size correction and quasi-fit.
ΔQAIC\textsubscript{c}: difference in QAIC\textsubscript{c} value between each model and the top model.
w\textsubscript{j}: QAIC\textsubscript{c} weight; the proportion of total weight that can be attributed to an individual model.
Table 3. Models predicting Snowy Plover LRS for male birds, ranked according to QAIC_c value. Only models that summed to 97% weight are included.

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
<th>logL</th>
<th>QAICc</th>
<th>ΔQAICc</th>
<th>wi</th>
<th>cumulative wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>LIFESPAN + SUBSTRATE</td>
<td>4</td>
<td>-99.40</td>
<td>207.25</td>
<td>0</td>
<td>0.40</td>
<td>0.40</td>
</tr>
<tr>
<td>LIFESPAN + SUBSTRATE + EXCLOSED</td>
<td>5</td>
<td>-99.12</td>
<td>208.96</td>
<td>1.71</td>
<td>0.17</td>
<td>0.57</td>
</tr>
<tr>
<td>LIFESPAN + SUBSTRATE + CORVID</td>
<td>5</td>
<td>-99.31</td>
<td>209.34</td>
<td>2.09</td>
<td>0.14</td>
<td>0.71</td>
</tr>
<tr>
<td>LIFESPAN + SUBSTRATE + HUMAN</td>
<td>5</td>
<td>-99.38</td>
<td>209.48</td>
<td>2.23</td>
<td>0.13</td>
<td>0.84</td>
</tr>
<tr>
<td>LIFESPAN + SUBSTRATE + CORVID+ EXCLOSED</td>
<td>6</td>
<td>-99.01</td>
<td>211.04</td>
<td>3.79</td>
<td>0.06</td>
<td>0.90</td>
</tr>
<tr>
<td>LIFESPAN + SUBSTRATE + HUMAN + EXCLOSED</td>
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<td>211.19</td>
<td>3.94</td>
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<td>0.95</td>
</tr>
<tr>
<td>LIFESPAN + SUBSTRATE + HUMAN + CORVID + EXCLOSED</td>
<td>7</td>
<td>-99.01</td>
<td>213.38</td>
<td>6.13</td>
<td>0.02</td>
<td>0.97</td>
</tr>
</tbody>
</table>

K: number of parameters in the model.
QAIC_c: Akaike’s Information Criterion with small sample size correction and quasi-fit.
ΔQAIC_c: difference in QAIC_c value between each model and the top model.
w_i: QAIC_c weight; the proportion of total weight that can be attributed to an individual model.
DISCUSSION

This study revealed several important findings. First, lifetime reproductive success varied appreciably between sexes; male plovers had higher mean LRS and variance in LRS compared to females. Second, reproductive success was highly skewed among individuals, with a small proportion of the population contributing a disproportionate amount of offspring. Finally, variance in LRS was best explained by breeding substrate, with gravel breeding birds having higher LRS compared to beach breeding birds; measures of nest exclosures, as well as corvid abundance and human activity, were not significant predictors of LRS.

Patterns of variance between sexes

On average, male plovers had higher LRS compared to females. Intuitively, one might expect the reverse to be true given typical sex roles in parental care: males are responsible for rearing chicks for an additional 28 days after hatch (USFWS 2007, Page et al. 2009). As a result, females may breed successfully up to three times a year, whereas males may only breed successfully twice annually (USFWS 2007, Page et al. 2009). However, this was likely outweighed by (1) the high rate of nest failure in RU2 (Colwell et al. 2013) leading females to lay multiple replacement clutches with the same male over the course of the breeding season (Pearson 2011), and (2) the fact that males have higher survival (Mullin et al. 2010, Stenzel et al. 2011).

Another factor that may contribute to sex differences in LRS is that females have a greater tendency to disperse during and between breeding seasons (Stenzel et al. 1994).
My analysis revealed that males in RU2 had a maximum lifespan of 12 years, as opposed to only 7 years for females. While I presumed that failure to return meant that a bird had died, it is possible that some females dispersed to other breeding sites along the Pacific Coast (Oring et al. 1991, Stenzel et al. 1994). I attempted to control for this issue by removing birds from the analysis that were later documented breeding outside of Humboldt County, however, I had limited outside breeding information at my disposal. Nevertheless, I feel confident in my assumption as Pearson (2011) found that most plovers (85-92%) in RU2 dispersed less than 10 km between and within breeding seasons.

Male plovers had higher variance in LRS than females. It is common for LRS studies to reveal intra- and inter-sexual differences in the distribution of LRS (Payne 1979, Wade 1979, Mills 1989, Newton 1989c, Owen and Black 1989, Oring et al. 1991); these differences are often a consequence of the species’ mating system. Snowy Plovers on the Pacific coast exhibit a sequentially polygamous mating system, with both sexes obtaining multiple mates within a breeding season (USFWS 2007, Page et al. 2009). Typically, intrasexual variance in LRS is greater in polygamous species, compared to those that are monogamous (Newton 1989c, Nunney 1993, Storz et al. 2002). This pattern is most pronounced in lekking species where mating opportunities are monopolized by a few dominant males (Johnson et al. 2004, Stiver et al. 2008, Ryder 2009).

Sex differences in reproductive variance can also arise due to differences in survival, as mediated through a biased sex ratio (Newton 1989c). This pattern results because a larger proportion of individuals of the longer-lived sex will remain unpaired, compared to the limiting sex (Newton 1989c). However, while a male-biased sex ratio
has been reported for two populations of plovers in California (Warriner et al. 1986, Stenzel et al. 2011), Mullin et al. (2010) found that the sex ratio of plovers in northern California was not skewed toward either sex. In addition, plovers in RU2 rarely go unpaired during a breeding season.

A large part of this inter-sexual difference in variance was likely due to a single male plover with uncharacteristically high lifetime reproductive success (LRS = 20); removal of this outlier from the dataset resulted in a substantial decrease ($\sigma^2_{\text{male,new}} = 5.7$) in male variance. This high LRS value resulted from a long life (9 years) spent breeding exclusively on gravel substrate, where nest success and chick survival is significantly higher than on beaches (Colwell et al. 2005, Colwell et al. 2007b, Colwell et al. 2010a). This contrasts with a similarly-aged male of 12 years, who bred exclusively on sandy substrates and fledged only 8 young.

**Skew in reproductive success**

Lifetime reproductive success was right skewed for both sexes. Most individuals produced few or no offspring and a small percentage accounted for greater than 50% of young. This is a common trend in LRS studies; Newton (1989b) found that for 12 different bird species, 14-31% of breeders were responsible for producing 50% of offspring. In a study of Common Sandpipers, fledgling output was highly skewed, with 12.5% of females and 9% of males producing 55% of fledglings (Holland and Yalden 1994). In addition, Oring et al. (1991) studied LRS in Spotted Sandpipers and found that for both sexes, the majority of birds fledged zero young during their lifetime.
Understanding variance in reproductive success is especially important for small, isolated populations because it allows for the estimation of effective population size ($N_e$) (Kimura and Crow 1963, Barrowclough and Rockwell 1993). $N_e$ can be defined as “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). $N_e$ is a useful parameter in conservation biology because it predicts how quickly a given population will lose genetic variation (Kimura and Crow 1963).

With such high variance in reproductive success, plovers in RU2 may be vulnerable to genetic issues like drift and inbreeding; four instances of inbreeding have been observed in RU2 over the past 13 years, one of which may have resulted in an unviable embryo (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 1,855 individuals (Colwell et al. 2013). Based on lifetime reproductive success, I 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.

Which predictors best explain variance in Snowy Plover LRS?

Plovers breeding on gravel substrates had significantly higher LRS than sand-breeding birds. This finding is similar to two other studies that compared annual reproductive success of plovers on beach and gravel habitats (Colwell et al. 2005, Colwell et al. 2010a). Colwell et al. (2005, 2010) found that birds breeding on gravel bars laid fewer eggs, yet fledged significantly more young than those on beaches. In addition,
by their sixth year, gravel bar birds had fledged four times as many young compared to similarly aged beach breeding plovers (Colwell et al. 2010a).

These differences in habitat quality, as indexed by reproductive success, are somewhat surprising given that (1) management efforts aimed at increasing reproductive success (i.e., nest exclosures, habitat restoration, fencing and signage) are utilized at beaches, while there has been little to no management efforts on gravel bars (Cowell et al. 2005, Colwell et al. 2010a), (2) birds breeding along the Eel River initiated clutches two to three weeks later than beach breeding birds (Colwell et al. 2010a), and (3) corvid activity is relatively similar between habitats, if not slightly higher on gravel bars (Colwell et al. 2010a).

Despite differences in management, I found that plovers breeding on gravel produced more than twice the number of young during their lifetime, compared to those breeding on sand. Differences in reproductive success likely stem from the crypsis of eggs and chicks, and their detectability in different substrates (Colwell et al. 2005, Colwell et al. 2010a, Colwell et al. 2011). Plovers nest in open, thinly vegetated habitats and rely on early predator detection and egg crypsis to camouflage nests (Lauro and Nol 1995, Winkler 2001, Muir and Colwell 2010). Colwell et al. (2011) studied habitat selection by gravel breeding plovers and found that they nested in habitats with enhanced egg crypsis (i.e., more egg sized stones), compared to random sites.

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. 2005, Colwell et al. 2010a, Colwell et al. 2011). Studies
of other shorebird species corroborate these results. Mayer et al. (2009) studied egg crypsis in Piping Plovers (*Charadrius melodus*) and found that eggs were more likely to be depredated when they contrasted with background substrates. Similarly, Solis and de Lope (1995) found that Stone Curlew (*Burhinus oedicnemis*) eggs suffered higher rates of predation when they differed in color from the ground.

It is important to note that Hardy and Colwell (2012) found little evidence of a relationship between substrate and nest survival for plovers breeding on beaches in Humboldt county. There was a positive relationship between nest survival and debris heterogeneity, but this relationship was weak. The authors speculated that landscape scale differences in predator abundance may have overwhelmed the effects of habitat characteristics at the nest site (Hardy and Colwell 2012).

Corvid abundance was not a significant predictor of plover LRS for either sex; this result contrasts with a similar study by Burrell (2010), who found that corvid activity was a strong predictor of daily predation rate and per capita fledging success in RU2. I expected to find a strong relationship between these variables because corvid predation is the foremost issue preventing recovery of plovers in RU2 (Colwell et al. 2013). Video footage confirmed that corvids depredated 70% of 20 nests that were under camera surveillance in 2008 and 2009 (Colwell et al. 2009); over the past 13 years, up to 46% (319/691) of nests failed due to corvids (Colwell et al. 2013).

There is a vast amount of evidence demonstrating the negative impacts of corvid predation on plover reproductive success in RU2 (Colwell et al. 2009, Burrell 2010, Colwell et al. 2013). Why, then, did this relationship not show up in my analysis? It is
possible that the methods I used to summarize corvid activity obscured the relationship between these two variables. Firstly, I pooled point count data from 2004-2013, so any year-to-year variation in corvid abundance was not reflected in my analysis. Previous studies have shown that relative patterns of corvid abundance are consistent across years (Colwell et al. 2013). However, it is likely that there was yearly variation in corvid abundance within sites. In addition, my goal was to produce a single value for each plover that approximated corvid activity encountered while breeding; this often required me to average corvid activity across multiple nests from different years, which may have affected the results. Lastly, I chose to consider point counts that fell within 500 m of each nest and effects may have been more noticeable if I examined corvid abundance on a larger scale.

I did not find a strong relationship between human activity and LRS; this result is consistent with findings from other studies of plover reproductive success in RU2 (Burrell 2010, Hardy and Colwell 2012). There are a few plausible explanations for the weak relationship between these two variables. Firstly, this study was conducted in an area with low human use and where a small percentage of reproductive failures are directly attributable to humans (Hardy and Colwell 2012, Colwell et al. 2013). A stronger relationship between LRS and human activity may have resulted if this study took place in central or southern California, where human activity at plover breeding sites is higher (Powell et al. 2002, Ruhlen et al. 2003, Lafferty et al. 2006). The weak relationship between human activity and LRS might also be explained by the fact that, due to high rates of nest and chick depredation in RU2, eggs and chicks may have little contact with
humans (Burrell 2010, Hardy and Colwell 2012, Colwell et al. 2013). Lastly, this relationship may have been weak due to the scale and methods that I used to summarize human activity for each plover.

I also found a weak relationship between the use of nest exclosures and LRS for plovers breeding in RU2. This is not surprising given that Hardy and Colwell (2008) found no difference in fledging success between chicks that hatched from exclosed versus unexclosed nests. While exclosures increase hatching success by protecting eggs from predators (Estelle et al. 1996, Johnson and Oring 2002, Hardy and Colwell 2008), nidifugous young are immediately vulnerable to predation once they leave the exclosure. Most of the exclosed nests in this study (102/126) were located on Clam Beach, where chicks are already extremely susceptible to predation due to a high abundance of ravens and crows (Colwell et al. 2013).

Management implications

Conserving threatened and endangered species requires knowledge of species breeding productivity and the factors which cause variation in reproductive success. In addition, information regarding habitat quality is useful for guiding management aimed at increasing reproductive success (Colwell et al. 2005, Colwell et al. 2010a). Several important management implications emerge from this study.

Plovers breeding on gravel habitats had higher LRS than those breeding on sand, despite similar corvid abundance. This suggests that habitat restoration which increases nest crypsis on beaches may be an effective method for increasing lifetime reproductive output. Typically, this is accomplished by spreading bivalve shells (i.e., shell hash) on
otherwise homogeneous substrates (Powell and Collier 2000). Shell hash is currently being utilized at one plover breeding site (South Spit) in RU2; however, I cannot yet comment on the effectiveness of this method as there hasn’t been any breeding at this site for several years (Colwell et al. 2013).

Nest exclosures did not have a significant impact on plover LRS. While exclosures have been shown to increase hatching success, they do not improve fledging success (Hardy and Colwell 2008). Consequently, plovers may be receiving a false message about habitat quality, causing them to continue nesting at sites where fledging success is low (Hardy and Colwell 2008). This, coupled with disconcerting results from a previous study suggesting that exclosures promote: (1) nest abandonment and (2) depredation of adults as they leave the nest (Hardy and Colwell 2008), lead me to recommend against the reestablishment of exclosure use in RU2.

Despite the fact that my study revealed a weak relationship between LRS and human activity, I recommend the continuation of management efforts aimed at reducing human disturbance (i.e., restrictions on vehicles and dogs, fencing, signage). Plovers of the genus *Charadrius* are especially vulnerable to disturbance because (1) they nest directly on the ground (Colwell 2010), where eggs are easily trampled or destroyed by vehicles (Warriner et al. 1986, Dowling and Weston 1999) and (2) they flee from their nests in response to approaching predators and rely on habitat features and egg crypsis to camouflage nests (Gochfeld 1984, Šálek and Cepáková 2006). Consequently, at highly disturbed sites, plovers may be forced to take more nest recesses (Hoffmann 2005), and this may leave eggs more vulnerable to predation.
Currently, there are no management efforts aimed at decreasing predation in RU2 (Colwell et al. 2013). While I found that corvid abundance was not a significant predictor of lifetime reproductive success, several studies have demonstrated the negative impacts of predation on reproductive success in RU2 (Colwell et al. 2005, Colwell et al. 2007b, Colwell et al. 2010a, Burrell 2010, Colwell et al. 2013). In most years, and largely due to corvid predation, annual estimates of per capita reproductive success fall below the recovery objective set forth by the USFWS (USFWS 2007, Colwell et al. 2013). Given this information, I recommend that management continue to explore lethal and non-lethal predator control options as they have proven to be successful at other breeding sites along the Pacific Coast (Knapp and Peterson 2011, Lauten et al. 2011, USFWS 2007).
LITERATURE CITED


Appendix A. Determining corvid and human abundance scores.

To index the amount of corvid and human activity that each plover was exposed to while breeding, I plotted all point counts collected from 2004-2013 and all known nest locations from 2001-2013 in ArcMap (ESRI, Redlands, CA). I then used the Spatial Join tool to link the attributes from the point count shapefile (join feature) to the nest shapefile (target feature), based on their spatial relationship. I specified the Intersect match option and provided a search radius of 500 meters; this ensured that any point count would be matched with a nest if it fell within 500 meters of that nest. The Spatial Join tool also provides a series of “merge rules” which can be applied when multiple join features are matched to a given target feature. I applied a mean merge rule, which allowed me to calculate the mean corvid and human abundance within 500 meters of each nest; if a plover had multiple nests during its lifetime, I averaged these values across nests. Corvid abundance included counts of ravens and crows and human activity included any detection of dogs, vehicles, horses or pedestrians.

As an example, GV:WB is a male plover that bred in RU2 in 2004 and had a total of two nests during his lifespan. Using the Spatial Join tool I found that 1,013 point counts fell within 500 meters of the first nest, and 1,154 point counts fell within 500 meters of the second. Subsequently, using the mean merge rule I found that observers detected an average of 1.15 corvids within 500 meters of the first nest, and an average of
1.62 within 500 meters of the second nest. I then averaged these two values to produce an overall corvid abundance score of 1.385 for GV:WB.
Appendix B. The number of point counts and nests at 10 different plover breeding sites in Humboldt County.

<table>
<thead>
<tr>
<th>Site</th>
<th>Number of Point counts</th>
<th>Number of nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Lagoon</td>
<td>583</td>
<td>7</td>
</tr>
<tr>
<td>Clam Beach</td>
<td>8,008</td>
<td>346</td>
</tr>
<tr>
<td>Centerville</td>
<td>874</td>
<td>12</td>
</tr>
<tr>
<td>Dry Lagoon</td>
<td>194</td>
<td>0</td>
</tr>
<tr>
<td>Eel River Wildlife Area</td>
<td>1,097</td>
<td>39</td>
</tr>
<tr>
<td>Gold Bluffs Beach</td>
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<tr>
<td>Eel River Gravel Bars</td>
<td>4,109</td>
<td>147</td>
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<tr>
<td>Mad River</td>
<td>1,221</td>
<td>28</td>
</tr>
<tr>
<td>Stone Lagoon</td>
<td>385</td>
<td>5</td>
</tr>
<tr>
<td>South Spit</td>
<td>1,498</td>
<td>15</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>18,262</strong></td>
<td><strong>600</strong></td>
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</table>