

# Direct and indirect evidence that productivity of Snowy Plovers *Charadrius nivosus* varies with occurrence of a nest predator

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## Abstract

The Snowy Plover *Charadrius nivosus* is a threatened species of shorebird that breeds along the Pacific coast of North America where predation of eggs and chicks is thought to be a principal cause of low productivity and small population size. Data were collated over nine years (2001–2009) at 19 breeding locations in northern California to evaluate relationships between the activity of the main predator (Common Raven *Corvus corax*) suspected to compromise plover reproductive success and *per capita* fledging success of plovers, including video camera evidence. An index of raven activity correlated negatively with plover productivity and appeared in the five most-competitive models, accounting for 88% of corrected-Akaike weights explaining variation in *per capita* fledging success. Activity of humans and American Crows *Corvus brachyrhynchos* was weakly correlated with plover reproductive success. Video cameras (deployed in the last two years of the study at the site where corvid activity was highest and most plovers bred) showed that ravens caused 70% of nest failures at an average of 12 ( $\pm$  2.82 s.e.) days after clutch initiation; humans (20%) or drifting sand/tidal overwash (10%) caused remaining losses. Video recordings suggested that the departure of an incubating plover prompted raven predation of eggs. These results substantiate the notion that the Common Raven is an important factor limiting plover productivity in northern California, which emphasises the need for more effective management measures for predators.

**Key words:** Common Raven, human disturbance, predation, reproductive success, video cameras.

Worldwide, wader populations are declining (Morrison *et al.* 2001; Delany *et al.* 2009). A variety of causes have been implicated in these declines, including degradation and

loss of wetland habitats in non-breeding areas (Myers *et al.* 1987), which affects adult survival (*e.g.* Burton *et al.* 2006), and low productivity on breeding grounds

(MacDonald & Bolton 2008; Teunissen *et al.* 2008). In arctic and boreal regions, low breeding productivity has been linked to elevated rates of nest predation, especially in human-altered landscapes (Evans 2004; MacDonald & Bolton 2008) that enhance populations of synanthropic species (Perry & Henry 2010). A variety of studies have implicated corvids (Family: Corvidae) as principal predators responsible for low reproductive success (see MacDonald & Bolton 2008), although evidence differs regarding the extent to which variation in corvid abundance is correlated with changes in wader productivity. For instance, Bolton *et al.* (2007) showed experimentally that Lapwing *Vanellus vanellus* nesting success was highly variable and largely unaffected (except at sites with highest predator densities) by lethal control of two predators (Red Fox *Vulpes vulpes* and Carrion Crow *Corvus corone*).

In North America, temperate latitude populations of waders that breed on ocean beaches face a variety of threats that compromise their productivity (Brown *et al.* 2001), including habitat loss (*e.g.* Aiello-Lammens *et al.* 2011), human disturbance (Lafferty *et al.* 2006) and predation of eggs and chicks by corvids (Colwell *et al.* 2010). In these habitats, negative effects of predation on wader productivity may be magnified at sites where anthropogenic refuse attracts corvids that subsequently depredate eggs and chicks. Additionally, human disturbance may lead indirectly to increased levels of nest predation, through human proximity displacing incubating birds from nests. This scenario has been exacerbated by

increases in corvid populations (Marzluff *et al.* 1994; Kelly *et al.* 2002; Perry & Henry 2010). Little evidence exists, however, for an evaluation of relationships between corvids and wader reproductive success, which are critical for the recovery of some populations of species listed under the U.S. Endangered Species Act (ESA).

In 1993, the United States Fish and Wildlife Service (hereafter USFWS) listed the Pacific coast population segment of the Snowy Plover *Charadrius nivosus* (hereafter plover) as threatened under the ESA (USFWS 1993), following evidence of a reduction in number of breeding locations and a declining population (Page & Stenzel 1981; Page *et al.* 1991). The plover's recovery plan (USFWS 2007) identified three factors that are thought to have led to its small population size by reducing reproductive success: 1) loss and degradation of breeding habitats stemming from the spread of invasive vegetation (*e.g.* European Marram Grass *Ammophila arenaria*), which converts sparsely vegetated coastal habitats that are favoured by plovers (Muir & Colwell 2010) to dense vegetative cover; 2) direct and indirect impacts imposed by human activity (Lafferty *et al.* 2006); and 3) direct mortality of eggs and chicks arising from predation by native and non-native (*e.g.* Red Fox) vertebrates (Neuman *et al.* 2004; Colwell *et al.* 2011). While there is evidence that some mammalian predators occasionally depredate Snowy Plover nests, corvids (Common Raven *Corvus corax* and American Crow *Corvus brachyrhynchos*) are thought to be the most important predators of eggs and chicks throughout the plover's range

(USFWS 2007; Demers & Robinson-Nilsen 2012). Yet quantitative evidence for assessing the relationships between corvid abundance and plover productivity is limited.

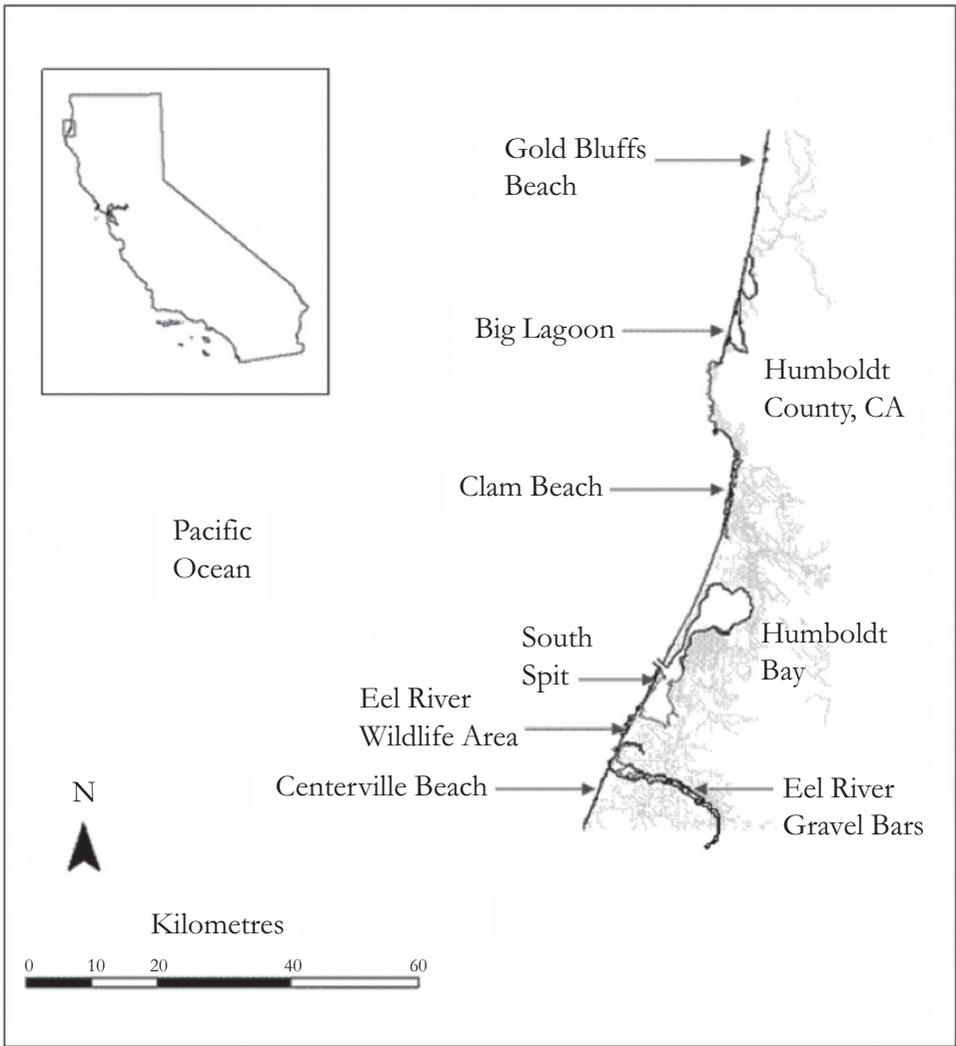
Since the plover's listing under the ESA, efforts have increased to quantify factors affecting the species' demography, especially those compromising reproductive success. To date: 1) the population continues to be stable, yet depressed (*i.e.* < 2,000 breeding adults; USFWS 2007); 2) reproductive success is often low as a result of high predation of eggs and chicks (Neuman *et al.* 2004; Colwell *et al.* 2010; Demers & Robinson-Nilsen 2012), despite efforts to manage predators using non-lethal (Hardy & Colwell 2008) and lethal means (Neuman *et al.* 2004); and 3) at least one subpopulation with chronically low productivity is maintained by immigration from more productive areas (Mullin *et al.* 2010). However, precise relationships between low productivity and predator identity and abundance are generally lacking. Corvid populations have increased dramatically in the western United States (Robbins *et al.* 1986; Marzluff *et al.* 1994, 2001; Kelly *et al.* 2002; Perry & Henry 2010). Given the above, we undertook a multi-year study to evaluate relationships between Snowy Plover reproductive success and two potentially important causes of breeding failure: predators and humans. We use direct (*e.g.* video camera) and indirect (*e.g.* correlational analyses) evidence to determine whether predation of eggs by Common Ravens is an important factor limiting productivity of plovers in our study area.

## Methods

### Study area

Researchers studied breeding plovers at 19 sites in Humboldt County, California from mid-March to early September over a nine year period, from 2001–2009 inclusive. Eight sites were ocean-fronting beaches and 11 sites were gravel bars on the lower 15 km of the Eel River (Fig. 1; Colwell *et al.* 2010). A breeding site was defined as a beach or gravel bar, separated from other sites by unsuitable habitat (*e.g.* river channel, estuary, rocky headland) or distances of several km of unoccupied habitat (Colwell *et al.* 2007a), which exceeds the average home range size and movements of individuals (Pearson 2011). For example, adults tending broods rarely crossed river channels between sites and adults infrequently moved among sites within a reproductive attempt. In most instances, different county, state and federal agencies managed sites.

The two habitat types, sandy beach and riverine gravel bar, differed greatly in substrate and vegetation. Coarse, heterogeneous substrates varying in size from sand and pea-sized gravel to large cobble and sparse vegetation (sedges *Salix* sp., White Sweetclover *Melilotus alba*) characterised gravel bars (Colwell *et al.* 2010, 2011). Ocean-fronting beaches had relatively homogeneous sandy substrates interspersed with dense stands of Marram Grass. On beaches, plovers tended to nest in expansive, unvegetated patches of sand (Muir & Colwell 2010) with debris fields of wood, shells and crustacean carapaces, small tufts of vegetation (*e.g.* Marram Grass and Sea Rocket *Cakile* sp.)



**Figure 1.** Location of the main study area where Western Snowy Plovers bred in Humboldt County, California from 2001–2009.

and miscellaneous refuse (Colwell *et al.* 2010).

### Field methods

Intensive monitoring of plovers in Humboldt County commenced in 2001

(Colwell *et al.* 2010, 2011; Mullin *et al.* 2010). Each year, researchers captured and banded nearly all unmarked breeding plovers and newly hatched chicks in the study area. Adult plovers were marked with a unique combination of three coloured leg bands

and a USFWS metal band wrapped with coloured tape; newly hatched chicks were marked with a single metal band wrapped with brood-specific coloured tape to distinguish between chicks of similar age in a common area (Colwell *et al.* 2007b).

Each year, observers surveyed the 19 sites at 7–10 day intervals from 15 March until late August or early September to locate nests, monitor broods and re-sight banded birds. Observers often surveyed sites occupied by breeding plovers more frequently (at 1–4 day intervals). Site visits continued until the last young fledged at 28 days old. Observers conducted nearly all surveys between dawn and 12:00 h. During surveys, observers stopped frequently to search for plovers using binoculars and spotting scopes. Observers recorded the location of courtship scrapes, nests, broods and adults using a global positioning system (GPS; WGS 84 datum) in ArcPad 6 and a Dell Axim X50 Personal Digital Assistant (PDA) fitted with an auxiliary GPS unit (GPS Ultra Holux). From 2004–2009, observers also used this automated system to record instantaneous 500 m point counts, determined by an alarm at fixed 20 min intervals (*i.e.* at 07:00 h, 07:20 h, *etc.*), during regular surveys at 18 of 19 sites (Colwell *et al.* 2010). During a point count, observers counted the number of pedestrians, dogs, vehicles, horses and corvids (Common Ravens and American Crows separately) within 500 m of their location.

In 2008 and 2009, a video camera system was used to monitor a subset ( $n = 25$ ) of plover nests at the breeding site (Clam Beach) where corvid activity was known to

be comparatively high and the highest concentration of plovers bred (Appendix 1). Upon discovery of a nest, two individuals (*i.e.* camera crew) set up the video system late in the evening so as to minimise attracting corvids and humans to the site. The system consisted of a video camera, 100 m of cable, digital video recorder and 12 V deep-cycle battery. The camera had 15 large 850 nm infrared light-emitting diodes to facilitate recording at night up to 80 m away. The digital video recorder operated at 30 frames per second, 24 h a day. The camera crew placed the system in a protective container, buried in the sand, to protect it during inclement weather and to prevent damage when camouflaging necessitated partial burial of the camera. The camera was installed 15–90 m from the nest, camouflaged with vegetation, driftwood and sand so as to disguise its presence from predators and humans. The camera system was close enough to the nest to provide adequate illumination at night, but sufficiently distant to ensure that any effects on nest survival were kept to a minimum. That cameras did not influence plover nesting success was shown by similar daily survival rates of nests with (mean = 0.915, 95% CI = 0.875–0.944,  $n = 25$ ) and without (mean = 0.862, 95% CI = 0.813–0.899,  $n = 39$ ) cameras. Control nests were selected at random from within the study area using Geographical Information System (GIS) software.

The video cameras were used to evaluate: 1) the success with which field observers could determine accurately the cause of nest failure, by identifying a predator via the

nest camera, and 2) the behaviour of predators that depredated eggs. Specifically, researchers were interested in whether or not corvids found nests based on the contrast of eggs with surrounding sandy substrates (and plover tracks that were often visible in the sand), or by the behavioural response of adults (*i.e.* corvids observed an incubating adult leave the nest). Events surrounding nest failure therefore were reviewed to determine: 1) the interval (in seconds) between departure of the incubating plover from the nest and arrival at the nest cup of a corvid, and 2) proximity to the nest (< 1 m; 1–5 m; > 5 m) of the corvid when it landed.

### Data summary and analyses

For each year (2004–2009), data from point counts were collated to develop an index of corvid and human activity at each site (Appendix 1). Incidence was defined as the proportion of  $n$  point counts during which observers detected at least one form of human activity or at least one corvid. Plover productivity was indexed each year at a site as the average number of young fledged (*i.e.* reaching 28 days) per male.

Measures of corvid incidence and abundance from point counts were highly correlated for beach ( $r_6 = 0.93$ ,  $P < 0.01$ ) and river ( $r_{10} = 0.95$ ,  $P < 0.01$ ) sites individually and for all sites combined ( $r_{17} = 0.97$ ,  $P < 0.01$ ). Similarly, incidence and abundance of human activity on point counts was positively correlated for beach ( $r_6 = 0.46$ ,  $P < 0.01$ ) and river ( $r_{10} = 0.99$ ,  $P < 0.01$ ) sites individually and for all sites combined ( $r_{17} = 0.99$ ,  $P < 0.01$ ). Consequently, two covariates (*ravens* and

*crows*) were used based on the incidence of these two potential predators derived from point counts to characterise the predation threat to plover chicks and eggs. Similarly, three additional covariates (*pedestrians*, *dogs* and *vehicles*) were based on their incidences on point counts to characterise the potential negative impacts of humans to breeding plovers. Thirteen *a priori* models were developed based on these five covariates, representing independent hypotheses of the relationship between these variables and productivity. The same analyses undertaken using abundance rather than incidence measures gave near-identical model outputs; only models using incidence data are presented here, however, to simplify presentation of the results.

An information theoretic approach (Burnham & Anderson 2002) was used to evaluate relationships between predator activity and human activity (independent variables) and *per capita* fledging success (dependent variables) at the 19 breeding sites. Multiple linear regression models were evaluated using *a priori* parsimonious model selection and inference strategies based on Akaike's Information Criterion corrected for small sample size (AIC<sub>c</sub>) in programme R (R Development Core Team 2005; Burnham and Anderson 2002). Akaike weights ( $w_i$ ), based on the scaled-likelihoods for each model given the collection of models and dataset analysed, were derived for all candidate models (Burnham & Anderson 2002). There was no evidence of spatial autocorrelation among independent variables based on Moran's I (Burrell 2010).

Tests were conducted for model goodness-of-fit using residual standard

error, adjusted R-squared and *F*-tests for all candidate models. Comparisons of the differences in plover occupancy between beach and river habitats, as well as the cause of nest failure, were conducted using *t*-tests of untransformed data and Spearman's rank correlation. The estimates for all covariates used in models were obtained for all breeding sites in the last six years of the study (2004–2009; *i.e.* site-year). Plover breeding site-year was used as the sample unit and sample dispersion is represented with standard error (s.e.) for all analyses. We excluded all site-years in which predator exclosures were used. The relative importance of covariates of the individual predictor ( $x_k$ ) based on Akaike weight was estimated, derived from:  $(x_k) = \Sigma w_j$ , where  $x_k$  is in model  $j$ . Model averaging was applied to the most competitive models accounting for 90% of Akaike weights (Burnham & Anderson 2002), to derive unconditional beta coefficient estimates and associated 95% confidence intervals.

## Results

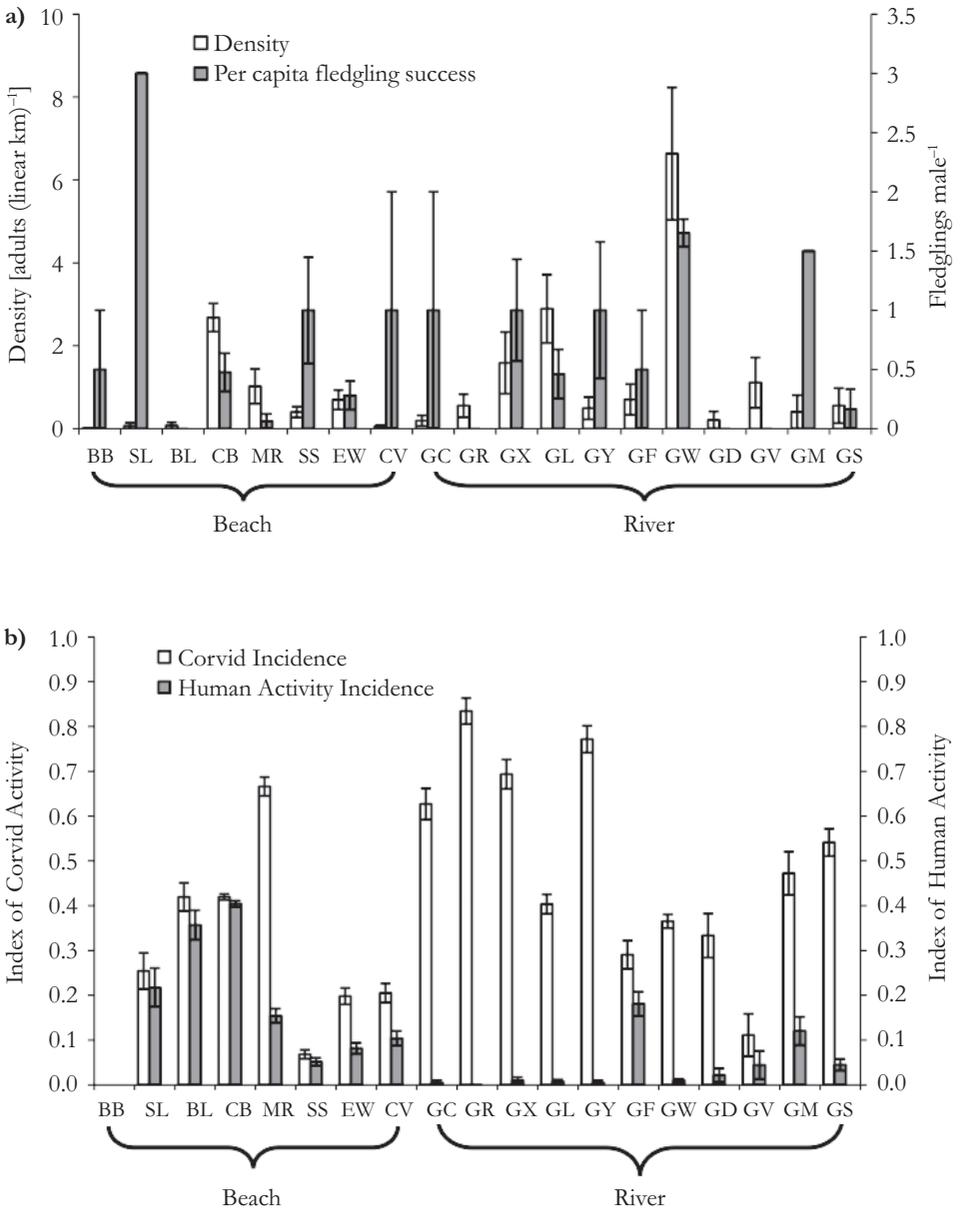
Plover breeding activity varied greatly among the 19 sites (Appendix 1). Two sites (CB and GW) were occupied consistently by breeding plovers and these locations had the highest breeding densities (plovers per km). Overall, occupancy correlated positively with breeding density ( $r^2_{17} = 0.52$ ,  $P < 0.01$ ). On average, breeding density was lower on beaches ( $0.75 \pm 0.04$ ) than on gravel bars ( $1.64 \pm 0.27$ ), but this difference did not reach statistical significance ( $t_{15} = 2.07$ ,  $P = 0.06$ , n.s.; Fig. 2a).

Observers detected corvids on 40% of 10,745 point counts (Appendix 1), with an average of  $1.41 \pm 0.06$  corvids per observation. Most (87%) observations were of Common Ravens. Human activity (*i.e.* pedestrian, dog, vehicle, horse) occurred on a quarter of all point counts (Fig. 2b; Appendix 1).

## Plover productivity and activity of humans and corvids

*Per capita* fledging success varied greatly among sites (Appendix 1). The best-fitting model, accounting for 37.4% of corrected Akaike weights, had fledging success correlate negatively with *ravens* and positively with *crows* (Table 1). The most competitive model performed well on goodness-of-fit tests, with a comparatively low residual standard error (0.80), a significant *F*-test ( $F_{27} = 6.94$ ,  $P = 0.004$ ) and an adjusted  $R^2_{27} = 0.31$ . Estimates for the beta coefficients indicate that *per capita* fledging success correlated negatively with *raven* incidence ( $-2.40 \pm 1.59$ ) and positively with *crow* incidence ( $3.41 \pm 3.63$ ), although the 95% CI for *crows* overlapped with zero.

The covariate *ravens* occurred in the top five competitive models and had the highest importance (0.88) based on corrected-Akaike weights. The covariate *crows*, which appeared in two of the six most-competitive models, had comparatively low covariate importance (0.26). Four of the top six models, accounting for the top 90% of all Akaike weights, included covariates *vehicles*, *dogs* or *pedestrians*, but the 95% confidence intervals all broadly overlapped zero. The top six models all had relatively good



**Figure 2.** a) Variation in average ( $\pm$  s.e.) density and *per capita* fledging success (2001–2009) and, b) average ( $\pm$  s.e.) incidence of corvid and human (*i.e.* pedestrians, dogs, vehicles, horses) activity detected on 500 m point counts at 19 Snowy Plover breeding sites in Humboldt County, California (2004–2009). Two-letter codes represent breeding sites.

**Table 1.** Model covariates, parameters ( $k$ ), adjusted  $R^2$ ,  $\Delta\text{AIC}_c$ , and Akaike weights for the six most competitive candidate linear regression models predicting *per capita* fledging success of male Snowy Plovers in Humboldt County, California (2004–2009).

Model covariates	$k$	Adjusted $R^2$	$\Delta\text{AIC}_c^a$	Akaike weights
<i>Ravens + crows</i>	3	0.31	–	0.37
<i>Ravens</i>	2	0.24	1.05	0.22
<i>Ravens + vehicles</i>	3	0.25	2.05	0.13
<i>Ravens + dogs</i>	3	0.23	2.86	0.09
<i>Ravens + pedestrians</i>	3	0.21	3.48	0.07
<i>Crows + dogs</i>	3	0.19	4.40	0.04
Null model	1	–	7.52	0.01

<sup>a</sup> Change in  $\text{AIC}_c$  from the most competitive, best-fitting model.

model fit based on significant  $F$  tests, low residual standard errors and a moderately high adjusted  $R^2$ . To obtain unconditional beta estimates, we averaged the top six most competitive models, which accounted for 92.53% of Akaike weights (Table 2), and found that the covariate *ravens* ( $-1.77 \pm 0.08$ ) was negatively correlated with fledging success.

### Evidence from video cameras

Video cameras monitored 25 nests over two years (Appendix 2). Cameras operated successfully at 21 nests, 7 in 2008 and 14 in 2009, which represented 18% and 56% of nests each year, respectively, at Clam Beach. Nests monitored by camera were initiated by at least 14 different birds (6 males and 8 females; see Appendix 2). Four cameras did not record video evidence at the time of

clutch failure because the system failed ( $n = 3$ ) or the camera system was vandalised ( $n = 1$ ).

Cameras provided conclusive evidence of two main causes of clutch failure at 20 nests (Appendix 2), with Common Ravens depredating eggs at 14 (70%) of the nests. Ravens ate eggs at an average of 12 ( $\pm 2.82$  s.e.) days after clutch initiation (*i.e.* within a week of the start of incubation), which was similar in duration ( $t_{17} = 0.58$ ,  $P = 0.57$ , n.s.) to six nests that failed for other reasons ( $\pm 2.12$  s.e.). Humans (or dogs) destroyed four (20%) clutches; two additional nests failed because a high tide washed over the nest or wind-driven sand buried eggs prior to clutch completion and the start of incubation.

Each year, field observers often categorised the cause of failure as

**Table 2.** Unconditional  $\beta$  estimates with 95% confidence intervals and covariate weights based on corrected-Akaike (AIC<sub>c</sub>) weights for models examining relationships between corvid and human occurrence and *per capita* fledging success of Snowy Plovers.

Covariate	$w_i$	Estimate	Model averages	
			95% CI	
			Lower	Upper
Intercept	–	1.1125	0.9931	1.2319
<i>Ravens</i>	0.8840	–1.7660	–1.8464	–1.6856
<i>Crows</i>	0.2645	1.5746	–0.0624	3.2116
<i>Dogs</i>	0.1944	–0.3210	–0.8610	0.2190
<i>Pedestrians</i>	0.1127	–0.0251	–0.2003	0.1501
<i>Vehicles</i>	0.0781	–0.6148	–1.6352	0.4056

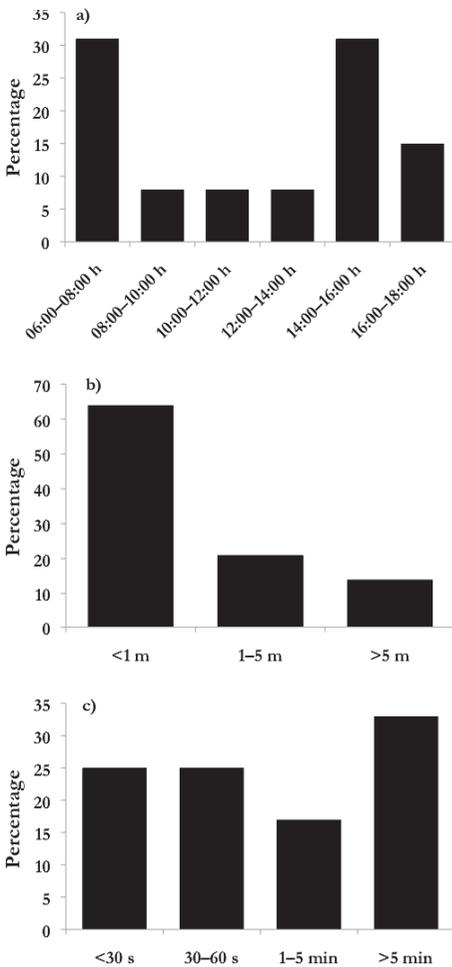
<sup>a</sup> Covariate weight ( $x_k$ ) =  $\sum w_p$ , where  $x_k$  is in model.

“unknown” (Appendix 2), including 69% and 24% of nests in 2008 and 2009, respectively. For the 20 failed nests that were monitored by cameras, 10 (77%) of the 13 “unknowns” resulted from raven predation; three additional “unknowns” failed due to human activity. In one noteworthy case, eggs disappeared from a plover nest and an absence of tracks and other evidence led field observers to classify the cause of failure as “unknown”, but video recordings showed that two humans removed the eggs from the nest. At another nest, eventually destroyed by high tide, a woman flushed the incubating adult, manipulated eggs, and photographed the nest. Unleashed dogs destroyed two incomplete clutches when they stepped on nests. Field observers

correctly labelled one nest destroyed by tide, but they did not determine that wind-driven sand had buried another nest.

### Behaviour of corvids

Common Ravens were the only nest predator detected by cameras. Most predation (31%) occurred shortly after sunrise or later in the afternoon (44%) (Fig. 3a). In 50% of losses to ravens, it appeared that departure of an incubating adult plover from the nest prompted predation by a raven flying nearby. This was based on the observation that in 64% of predation events, ravens landed within 1 m of the nest (Fig. 3b) and that 50% walked directly to the nest within 1 min of landing (Fig. 3c). In two instances, the



**Figure 3.** Percentage of Common Ravens preying on Snowy Plover nests ( $n = 20$ ): a) across all daylight hours, b) on landing near the nest, and c) on walking to the nest relative to the departure of the incubating plover.

plovers had already left the nest when ravens landed and took the eggs, illustrated by the long ( $> 10$  min) intervals between departure of the incubating adult and arrival of a raven.

## Discussion

Our results offer important insights for correlative studies investigating variation in the reproductive success of waders, and have strong management implications for the threatened Snowy Plover population. Plovers in northern California generally have experienced low reproductive success attributable to predation, although at some sites plovers are occasionally highly successful (Burrell 2010; Colwell *et al.* 2010, 2011). This variation has been linked to Common Raven abundance, and ravens were also suspected as being the most important nest predator in our study area and elsewhere (USFWS 2007; Demers & Robinson-Nilsen 2012). The video evidence gives strong evidence for this association at the most important breeding site in our study area, and provides a foundation for implementing more effective management measures to control predation of Snowy Plover eggs by ravens and other predators (MacDonald & Bolton 2008).

### Variation in reproductive success

MacDonald and Bolton (2008) reviewed an extensive literature on European waders to show that nesting success (*i.e.* daily predation rate; DPR) was highly variable across species, years and habitats. Similarly, our results demonstrate that Snowy Plovers exhibited considerable variation in *per capita* fledging success (which correlated strongly and produced nearly identical modelling results as DPR of nests; Burrell 2010) among sites and across years. Interestingly, DPR for Snowy Plover nests at the one site (Clam Beach), occupied consistently by a

large proportion of the population in northern California (Burrell 2010; Mark A. Colwell, unpubl. data), is much higher than values reported for nearly all waders with the exception of the closely related Kentish Plover *Charadrius alexandrinus*, which also breeds on coastal beaches (MacDonald & Bolton 2008).

Predation has been implicated as a cause of low nesting success and a principal driver of declining wader populations worldwide (MacDonald & Bolton 2008), and for some threatened and endangered taxa. In Europe, evidence suggests that many wader populations have experienced unsustainably high nest losses to predators. In a large sample ( $n = 544$  site-years sampled across 57 studies), MacDonald and Bolton (2008) reported that >50% of nests were depredated in 55% of site-years or studies reviewed. Moreover, population viability analyses suggest a linkage between chronically high nest failure and population declines in Temminck's Stint *Calidris temminckii* (Rönkä *et al.* 2006) and Northern Lapwing *Vanellus vanellus* (MacDonald & Bolton 2008). Extending this reasoning, several authors have suggested that the southern extent of breeding range for Palearctic waders may be limited by predation (Pienkowski 1984; Koivula & Rönkä 1998). Waders with low population size and at the limits of their range may be especially vulnerable to the effects of predation. Interestingly, it is widely recognised that high rates of nest predation continue to limit recovery of the listed Snowy Plover population (Neuman *et al.* 2004; USFWS 2007; Colwell *et al.* 2010, 2011).

Snowy Plovers have experienced chronically low nesting success in our study area, averaging 0.71 ( $\pm 0.28$  s.e.) fledged young per breeding male per year ( $n = 9$  years ending 2009; M. Colwell, unpubl. data), with predators causing the majority of nest failures. Adult numbers are sustained by immigration of birds from sites elsewhere along the Pacific coast of North America (Mullin *et al.* 2010). The negative correlation between plover productivity and Common Raven occurrence across multiple breeding sites and multiple years adds further evidence for the detrimental effects of ravens, as abundant, synanthropic omnivores (Perry & Henry 2010). Video camera evidence collected over two years where Common Ravens were strongly suspected to be a significant nest predator reinforced this view, with ravens consuming eggs at nearly all nests where observers classed the cause of failure as "unknown" (*i.e.* eggs had disappeared from the nest cup and there was no clear sign to indicate that a predator had visited the nest).

### Predation by ravens

Our videos showing that Common Ravens were the only nest predator at the site where plovers have experienced chronically low breeding success contrasts with evidence from European studies (MacDonald & Bolton 2008) and for the listed population of the Snowy Plover (USFWS 2007). In Europe, nest predation is commonly attributed to mammals, with occasional mention of corvids and gulls (MacDonald & Bolton 2008). For Snowy Plovers, a diversity of predators has been suspected as the cause of poor reproductive success,

resulting in occasional lethal control (Neuman *et al.* 2004). In the San Francisco Bay area, where corvid populations have grown rapidly (Kelly *et al.* 2002), a raven was one of five species of bird detected by video cameras eating plover eggs (Demers & Robinson-Nilsen 2012). After more than a decade of studying plovers in northern California, we have only rarely observed or determined (*e.g.* based on tracks at nest) that other species (American Crow *Corvus brachyrhynchos*, Ring-billed Gull *Larus delawarensis* and Grey Fox *Urocyon cinereoargenteus*) have caused reproductive failure by eating plover eggs and occasionally chicks.

*Per capita* fledging success was inversely correlated with an index of raven abundance, which was the only covariate of importance in the analyses. Moreover, at the most important breeding site (*i.e.* Clam Beach, where >50% of the local population has bred in recent years, albeit with consistently low success; Colwell *et al.* 2010), video cameras showed that ravens caused 70% of nest failures, and that most (77%) of the “unknown” causes of nest loss were attributable to ravens. Additional evidence supports this interpretation. For instance, apparent nesting success in the population has varied annually between 14–68%, although success has decreased with time ( $r_8 = -0.89$ ) coincident with a shift in the population away from high quality riverine gravel bars (Colwell *et al.* 2011) to ocean beaches (Colwell *et al.* 2010). On gravel bars, survival of nests and chicks is significantly higher than on ocean beaches because rocky substrates afford greater crypsis (Colwell *et al.* 2011). Collectively, these observations

strongly indicate that egg predation by Common Ravens is a major cause of low plover productivity in our study area.

Overall, our results underestimated the impact of corvids as egg predators for several reasons related to field methods. First, our classification of causes of nest failure included an “unknown” category, which accounted for the majority of failed nests (*e.g.* Colwell *et al.* 2011). These “unknowns” occurred when eggs disappeared prior to the predicted hatch date for a clutch and observers lacked clear evidence (*e.g.* corvid tracks in the sand) at the nest cup to determine the cause of failure. Video cameras showed that 77% of these “unknowns” failed owing to corvid predation. A second reason why our data from early in the study (2001–2006) underestimate the importance of egg predation is because we used exclosures to protect many nests, especially at sites with high raven activity. As a result, apparent nesting success was artificially high. After 2006, when we ceased using exclosures owing to an episode of high predation on incubating adults by an unknown avian predator, nesting success and *per capita* fledging success dropped to the lowest values recorded in 11 years (Colwell *et al.* 2011).

We used cameras to monitor nests at Clam Beach because this site had the majority of breeding plovers (Appendix 1) that experienced low nest survival and fledging success (Hardy & Colwell 2008; Colwell *et al.* 2010); it was also the location where corvid activity was relatively high (see Appendix 1). In most cases, ravens depredated eggs by landing near the nest

shortly after departure of an incubating adult. This suggests that the initial cue possibly used by ravens to find a nest was the movement of the incubating adult. However, without detailed information on the behaviour of ravens (both those that did and did not depredate eggs) as they moved about the study area, it is difficult to ascertain conclusively the circumstances that led to nest predation events. Only a detailed study of the behaviour of ravens foraging in the vicinity of plover nests will increase our understanding of how predators detect nests. At this same site, variation in survival of plover nests was not enhanced by varying degrees of crypsis afforded to eggs by natural habitat features in the vicinity of the nest (Hardy & Colwell 2012). Collectively, these observations suggest that abundant corvids overwhelmed the capacity of the physical habitat to sustain plover reproductive success. Moreover, if this phenomenon is widespread, then some management practices (*e.g.* spreading shell hash; Colwell 2010) intended to ameliorate high predation rates by enhancing the crypsis of nesting substrates are likely to fail.

### Human disturbance

Worldwide, waders frequenting ocean beaches are subject to high levels of disturbance owing close proximity to centres of human population that favour coastal habitats for recreation and development (Brown *et al.* 2001). Human disturbance is one of three main factors affecting the threatened status of the plover. In our study area, reproductive success was weakly correlated with human activity. Most

models that included vehicles, dogs or pedestrians contributed little to improving model fit. This probably resulted from the comparatively low percentage of nest or brood failure that was caused by humans compared to losses inflicted by corvids (Colwell *et al.* 2010, 2011). Nevertheless, videos showed that humans did cause reproductive failure at Clam Beach (20% of nest attempts videoed) where human recreational activity was highest, either directly (*e.g.* eggs stolen, vehicle strike) or indirectly (dogs taking the eggs or chicks) (Fig. 2b; Appendix 2). On riverine gravel bars, vehicle strikes accounted for 14% of nest losses during 2001–2009 (Colwell *et al.* 2011). These observations: 1) show that plover reproductive success may be compromised at some sites by human activity, and 2) argue that some types of recreational use are incompatible with plover conservation goals and require active management. Finally, it is noteworthy that we conducted our study in a region of low human population size and often at remote sites not often frequented by humans. Elsewhere in the species' range data suggest that restrictions (*e.g.* fencing that provides a refuge for breeding plovers in areas of high human use) on recreational activity in close proximity to plovers can promote breeding (Lafferty *et al.* 2006). Furthermore, in our study area, use of fencing resulted in an increase in breeding success at the site with highest human activity (Wilson & Colwell 2010).

### Management implications

The results show that Common Ravens are the most important factor influencing

reproductive success of plovers in our study area. This result is not universal within the range of the listed population (Demers & Robinson-Nilsen 2012). The population of plovers in northern California is a demographic sink plagued by low reproductive rates (Colwell *et al.* 2010; Mullin *et al.* 2010) and sustained by immigration (Mullin *et al.* 2010). As a result, we suggest that enhanced predator management should be considered for our study area. Plovers initially (2001–2006) had higher *per capita* reproductive success in our study area when: 1) a larger proportion of birds nested amidst gravel substrates that offered camouflage for eggs and chicks (Colwell *et al.* 2011), and 2) nest exclosures were used to boost hatching success at sites where ravens were especially problematic (Hardy & Colwell 2008). We stopped using exclosures after an episode of high adult mortality in 2006 (Mullin *et al.* 2010; Hardy & Colwell 2008). In the subsequent 6 years, exclosures were used to protect only two of 250+ nests. As a result, *per capita* fledging success has continued to decline to a low of 0.45 fledged chicks per male in 2011. Renewed interest in predator management is therefore warranted, with the aim of boosting plover productivity and facilitating population recovery in northern California and elsewhere in the species' range.

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**Appendix 1.** Number of years that each site was occupied, estimates of average density and *per capita* fledgling success with associated standard error (s.e.) for Snowy Plover breeding locations in Humboldt County over a nine year study (2001–2009). Incidence of corvid and human recreational activity based on 500 m point counts conducted at Snowy Plover breeding locations in Humboldt County (2004–2009).

Site <sup>a</sup>	Occupancy	Density	Fledging success <sup>b</sup>	Corvid incidence <sup>c</sup>						Human activity incidence <sup>d</sup>							
				2004	2005	2006	2007	2008	2009	2004	2005	2006	2007	2008	2009		
BB	2	0.01 ± 0.01	0.50 ± 0.50	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SL	1	0.07 ± 0.07	3.00 ± 0.00	–	–	0.12	0.62	0.18	0.22	–	–	–	–	–	0.10	0.30	0.19
BL	1	0.08 ± 0.08	0.00 ± 0.00	–	–	0.33	0.51	0.42	0.32	–	–	–	–	0.00	0.35	0.34	0.51
CB	9	2.68 ± 0.34	0.48 ± 0.16	0.26	0.41	0.41	0.50	0.48	0.47	0.29	0.39	0.40	0.50	0.36	0.36	0.48	0.48
MR	4	1.02 ± 0.42	0.06 ± 0.06	–	–	–	0.69	0.69	0.62	–	–	–	–	–	0.22	0.13	0.12
SS	6	0.40 ± 0.13	1.00 ± 0.45	0.05	–	–	0.18	0.02	0.20	0.04	–	–	–	0.09	0.04	0.00	0.00
EW	7	0.70 ± 0.24	0.28 ± 0.12	0.16	–	0.11	0.11	0.24	0.27	0.02	–	0.17	0.06	0.09	0.09	0.09	0.09
CV	2	0.05 ± 0.03	1.00 ± 1.00	0.09	–	0.32	0.37	0.15	0.14	0.00	–	–	0.04	0.14	0.16	0.06	0.06
GC	2	0.19 ± 0.13	1.00 ± 1.00	0.24	0.29	0.64	0.76	0.75	0.75	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00
GR	3	0.56 ± 0.28	0.00 ± 0.00	0.55	–	1.00	0.97	0.96	0.88	0.00	–	–	0.00	0.00	0.00	0.00	0.00

Appendix 1 (continued)

Site <sup>a</sup>	Occupancy	Density	Fledging success <sup>b</sup>	Corvid incidences <sup>c</sup>					Human activity incidences <sup>d</sup>						
				2004	2005	2006	2007	2008	2009	2004	2005	2006	2007	2008	2009
BGX	4	1.59 ± 0.74	1.00 ± 0.43	0.34	–	0.82	0.88	0.71	0.77	–	0.00	0.00	0.00	0.02	0.03
GL	6	2.89 ± 0.82	0.46 ± 0.21	0.20	0.44	0.43	0.70	0.60	0.58	0.00	0.00	0.03	0.00	0.00	0.04
GY	3	0.49 ± 0.27	1.00 ± 0.58	0.48	0.72	0.88	0.92	0.91	0.93	0.00	0.00	0.00	0.00	0.02	0.00
GF	3	0.70 ± 0.37	0.50 ± 0.50	0.19	0.14	0.33	0.32	0.22	0.41	0.13	0.00	0.08	0.19	0.32	0.12
GW	9	6.63 ± 1.6	1.65 ± 0.12	0.25	0.27	0.38	0.50	0.44	0.38	0.00	0.03	0.01	0.01	0.01	0.01
GD	1	0.21 ± 0.21	0.00 ± 0.00	0.27	–	0.40	0.48	0.31	0.29	0.00	–	0.00	0.05	0.04	0.00
GV	3	1.11 ± 0.61	0.00 ± 0.00	0.08	–	0.25	–	–	–	0.00	–	0.25	–	–	–
GM	1	0.40 ± 0.40	1.50 ± 0.00	0.40	–	0.00	0.59	0.50	0.42	0.10	–	0.00	0.19	0.13	0.08
GS	2	0.56 ± 0.42	0.17 ± 0.17	0.20	0.25	0.52	0.74	0.69	0.42	0.00	0.00	0.00	0.02	0.06	0.12

<sup>a</sup> Two-letter codes represent breeding locations (*i.e.* sites); they are listed north to south (beaches) and down- to upstream (gravel bars; *i.e.* those codes beginning with a “G”).

<sup>b</sup> *Per capita* fledging success (fledged chicks male<sup>-1</sup>).

<sup>c</sup> Incidence (proportion) of all point counts in which corvids were detected within a 500 m radius of an observer.

<sup>d</sup> Incidence (proportion) of all point counts in which pedestrians, dogs, vehicles and/or horses were detected within a 500 m radius of an observer. (–) indicates site was not surveyed in given season.

**Appendix 2.** Summary of video-monitored Snowy Plover nests at Clam Beach, Humboldt County, California (2008–2009).

Year	Nest Identity	Male	Female	Clutch initiated	Date		Determined outcome of nest attempt	
					Camera installed	Failed or hatched	Field observation	Video camera
2008	CN06	GV:GB	VW:GW	25-Apr	26-Apr	1-May	Unknown	Common Raven
	CS07	OR:RY	VW:YY	28-Apr	2-May	2-May	Unknown	Common Raven
	CS13	GV:GB	BP:OG	9-May	22-May	29-May	Unknown	Common Raven
	CS18	VW:OW	GL:WO	25-May	7-Jun	23-Jun	Unknown	Common Raven
	CS19	OR:YR	WW:YG	26-May	30-May	1-Jun	Unknown	Common Raven
	CS26	OR:YR	RY:YW	27-Jun	30-Jun	20 & 29 Jul	Vehicle <sup>a</sup>	Vehicle <sup>a</sup>
	CS27	VW:OW	GL:WO	30-Jun	30-Jun	21-Jul	Unknown	Common Raven
2009	CN02	OR:YR	OR:RR	17-Mar	20-Mar	21-Mar	Unknown	Dog
	CN03	Unknown	Unknown	20-Mar	24-Mar	24-Mar	Common Raven	Common Raven
	CN04	VW:BR	VW:GW	23-Mar	24-Mar	25-Mar	Unknown	Common Raven
	CN09	WW:YB	BP:OG	29-May	29-May	30-May	Common Raven	Dog
	CN10	WW:YB	BP:OG	6-Jun	12-Jun	26-Jun	Tidal overwash	Tidal overwash
	CN11	WW:YB	BP:OG	5-Jul	8-Jul	15-Jul	Common Raven	Common Raven
	CN12	VW:BR	VW:YY	11-Jul	16-Jul	1-Aug	Unknown	Common Raven
	CS04	OR:YR	OR:RR	17-Apr	19-Apr	3-May	Unknown	Common Raven
	CS05	VW:OW	VW:YY	25-Apr	2-May	29-May	Hatched	Hatched
	CS07	VW:BR	VW:GW	2-May	8-May	9-May	Unknown	Human
	CS08	WW:YB	BP:OG	12-May	15-May	17-May	Common Raven	Common Raven
	CS10	GV:GB	X:R	17-May	18-May	20-May	Unknown	Buried by sand
CS11	VW:BR	VW:YY	5-Jun	8-Jun	9-Jun	Common Raven	Common Raven	
CS12	VW:BR	VW:YY	13-Jun	16-Jun	2-Jul	Unknown	Common Raven	

<sup>a</sup> Truck crushed 2 eggs; 3rd egg hatched.