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Western Snowy Plovers *Charadrius alexandrinus nivosus* select nesting substrates that enhance egg crypsis and improve nest survival

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Predation is an important cause of nest failure for many birds and has shaped the life-history characteristics of many species, especially ground-nesting shorebirds. We examined nesting success, causes of clutch failure and nest survival in relation to variation in substrate characteristics in a colour-marked population of Western Snowy Plovers *Charadrius alexandrinus nivosus* breeding on riverine gravel bars in coastal northern California. Plovers experienced higher nesting success on gravel bars than on nearby beaches, which were characterized by more homogeneous, sandy substrates. On gravel bars, Plovers nested in habitats characterized by large, heterogeneous substrates, with more egg-sized stones, compared with random sites. Egg crypsis, as indexed by time required of a naïve observer to detect a nest, increased with number of egg-sized substrates. Nest survival correlated negatively with heterogeneity of substrates and positively with the number of egg-sized stones. Consistently high nesting success of Plovers on gravel bars indicates that this high-quality habitat deserves special management considerations given the species' threatened status.

Keywords: egg crypsis, habitat selection, nest survival, reproductive success, shorebird.

Predation strongly affects the productivity and demography of birds (Lack 1968, Martin 1993). Consequently, it has shaped the evolution of diverse life-history traits associated with breeding, including nest-site selection behaviours (Cody 1985), parental distraction displays (Gochfeld 1984) and egg coloration (Collias & Collias 1984, Underwood & Sealy 2002, Kilner 2006). Many ground-nesting birds build nests in vegetation that offers concealment to incubating adults and eggs, which may increase nest survival. Individuals of other species select nest-sites in sparsely vegetated habitats and rely on early detection of predators, adult departure from the nest and egg crypsis to enhance nest survival. This general behavioural dichotomy exists within two principal shorebird lineages (Van Tuinen *et al.* 2004), with sandpipers concealing nests in vegetation, and plovers, avocets/stilts and thick-knees nesting in open habitats (Colwell 2010). Females of both groups lay patterned eggs that enhance crypsis.

Visual crypsis of eggs is effective when egg appearance (size, colour and pattern) resembles the background such that detection by a predator is impaired (Endler 1978). Shorebird eggs are usually cryptically patterned, with a dull base colour and variable markings that disrupt the outline of the egg (Collias & Collias 1984). Egg coloration has been shown to influence crypsis and nest survival in at least one species of shorebird. Solis and de Lope (1995) showed that Stone-curlew *Burhinus oedicnemis* eggs survived better when

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their base colour matched background substrate. Habitat heterogeneity also may influence prey crypsis, as some backgrounds may be inherently more difficult for a predator to search. In support of this, search times of Great Tits *Parus major* increased when prey matched a larger, patterned background (Merilaita *et al.* 2001). Additionally, within-clutch variation in egg colour was positively related to nest survival in Namaqua Sandgrouse *Pterocles namaqua* (Lloyd *et al.* 2000), suggesting that varied egg coloration makes a nest more difficult to detect. For species that nest in open, sparsely vegetated habitats, the size and heterogeneity of substrates may confer added crypsis to eggs, but this relationship has rarely been addressed.

The Western Snowy Plover *Charadrius alexandrinus nivosus* is a threatened shorebird that breeds along the Pacific Coast of North America in sparsely vegetated habitats characterized by fine substrates and scattered debris (Page *et al.* 1995). Clutch predation is an important factor limiting population recovery (United States Fish & Wildlife Service 2007). In coastal northern California, Plovers nest in a unique habitat: large-grained, heterogeneous substrates on gravel bars of the lower Eel River. Since 2001, we have monitored reproductive success of a colour-marked population and shown that gravel bars are higher quality breeding habitats as evidenced by significantly higher per-capita fledgling success compared with ocean beaches (Colwell *et al.* 2005, 2010). We hypothesize that differences in substrates influence the ability of visual predators (principally Common Raven *Corvus corax*, and American Crow *Corvus brachyrhynchos*) to find eggs and chicks (Colwell *et al.* 2007). Specifically, on sandy beaches it may be easier for corvids to find nests for two reasons. First, comparatively large eggs contrast markedly with fine-grained substrates of beaches. Secondly, adult Plovers leave tracks in the sand leading to nests, which are easily detected by corvids. By contrast, nests on gravel bars occur in coarser substrates where Plovers rarely leave tracks. However, gravel bar substrate size, heterogeneity, and patchiness vary greatly and nests occur in a wide range of substrates from homogeneous sand or small pebbles (< 2 cm diameter) to heterogeneous mixes of sand, pebbles, stones (2–10 cm) and cobble (> 10 cm). Here, we present data on nesting success of gravel bar-nesting Plovers, compare substrates at nests with random sites to evaluate nest-site selection, examine the crypsis of river nests to a naïve human observer, and analyse nest survival in relation to variation in substrate size and heterogeneity.

METHODS

Study area and field methods

We studied Plovers in Humboldt County, California, on gravel bars of the lower 15 km of the Eel River, near its confluence with the Pacific Ocean. Gravel bar substrates varied in size from fine sediments of clay and silt to large stones. Breeding habitats were mostly unvegetated, although sparse stands of willow *Salix* spp. and White Sweet Clover *Melilotus alba* occurred throughout the study area. Colwell *et al.* (2010) provide a detailed description of the study area.

We monitored a population of colour-marked Plovers from 2001 to 2009 under permit (United States Fish & Wildlife Service permit TE-823807-3; California Department of Fish & Game collecting permit 801059-03; Humboldt State University IACUC 00/01.W.83.A; USFWS Federal banding permit 22971). Observers surveyed Plovers from mid-March to early September, recording colour band combinations and searching for nests. We found most nests by observing courting and incubating adults. Nest age was determined by observing dates of clutch completion, back-dating 31 days from the date of hatch (Page *et al.* 1995), or floating completed clutches (Alberico 1995). We monitored nests one to four times a week by observing incubating adults or, if no adult bird was present, by approaching nests to verify the presence of eggs. A nest was categorized as successful if at least one egg hatched. Failed nests were of several types: those in which (1) eggs were left unattended by adults for prolonged periods and parents were absent or observed breeding elsewhere (abandoned), (2) damaged eggs, dried yolk or eggshell fragments were observed in the nest cup and recent vehicle tracks were present near the nest (vehicle), (3) eggs disappeared after high water in the river washed over nest-sites (flooding), (4) eggs disappeared since a recent visit and prior to predicted hatch date, and direct observation or tracks indicated a predator consumed the eggs (predation), and (5) nest cups were empty but a long interval had transpired such that we could not confidently assign the nest to any category (unknown).

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Habitat measures

In 2001–2004, we measured substrate characteristics at all nests that we found by centring over the nest (or paired random site) a 1-m^2 plastic sampling frame subdivided by cord at 20-cm intervals, such that crossing lines created 16 sampling points. Using callipers, we measured (to the nearest 0.1 mm) the greatest exposed axis of the substrate lying under each sampling point. In 2001, however, an observer collected data by categorizing substrates into 10 pre-defined size classes (Meyer 2005). We converted these ordinal measures to continuous data using the middle value of each category. The largest category had no upper limit, hence we used the average rock size for substrates larger than 100 mm from subsequent years. To minimize disturbance and reduce the risk of leading predators to nests, we measured habitat after eggs hatched or failed. We selected paired random sites by generating a random compass bearing and distance (< 50 m; average distance to nearest neighbouring nest = 72 ± 32 m, n = 67); we chose this random distance to yield samples that represented substrates in the area where Plovers selected the nest-site.

Nest detectability

After the nest hatched or failed, we evaluated egg crypsis in relation to substrate characteristics using the following protocol. J.J.M. recorded the time(s) it took M.A.C. (naïve to the location of each nest but experienced in nest searching) to find a nest. J.J.M. simulated a nest by placing three Plover eggs at the actual nest-site. To standardize the area searched by the observer, he placed a circular plot (~4 m diameter) on the ground around the site to define a search area; plot placement varied such that nest location within the plot was unpredictable. Substrates were hard enough such that tracks were not left during this procedure, which might have influenced M.A.C. in his search for the eggs. Next, J.J.M. positioned M.A.C. (with eyes closed) on the edge of the plot, instructed him to open his eyes, and timed how long it took to find the nest. We used the same protocol at paired random sites, with eggs placed at a random location. J.J.M. randomly varied the order in which M.A.C. visited the nest or random site, and did not inform M.A.C. of this decision.

Data summary and analyses

We examined nest-site selection by comparing substrate characteristics between 100 nests and paired random sites sampled over 4 years. For each nest and random site, we used the sample of 16 measures to characterize mean size (mm) and heterogeneity (sd) of substrates, and the number of egg-sized substrates (20–40 mm), which brackets Plover egg size (31.3 ± 1.0 mm; Page *et al.* 1995). We compared substrates between nests and random sites using two-tailed paired t-tests because substrate size (r = 0.60, P < 0.01) and heterogeneity (r = 0.48, P < 0.01) were positively correlated between nests and random sites across samples. We omitted a small number of nests (10) from the nest-site selection and survival analyses (see below) because substrates had changed since a Plover's original selection of the site. At one nest, fine sediments had settled over substrates after river flooding, which altered habitat from that selected by the Plovers. At nine other nests that were damaged by vehicles, disturbance altered substrate size (i.e. it brought smaller substrates to the surface).

In the crypsis experiment, search times were not normally distributed. Consequently, we used a Wilcoxon matched-pairs signed-ranks test to compare search times at nests with paired random sites. We used stepwise multiple linear regression to investigate relationships between substrate variables and search time. We included all the näive observer trials (at nests and random sites) in this regression.

We used program MARK to estimate daily survival rates (DSRs) of nests in two separate analyses. First, we examined annual and seasonal (linear and quadratic time trends) variation in DSR for 165 nests monitored over 9 years. In a second analysis using program MARK, we examined the effects of substrate characteristics on nest DSR sampled over the first 4 years (2001–2004) (Dinsmore *et al.* 2002, Rotella *et al.* 2004). In 2002, one nest hatched a few days after being abandoned by both parents; we considered this nest successful (for the nest survival analysis) because it had survived the entire laying and incubation period. We treated substrate and temporal variables (year, Julian date) as two subsets, and initially modelled them separately. Within the subsets we modelled the variables alone and in combinations. Then we combined the best substrate model with the best temporal model. We evaluated models using

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Akaike's information criterion corrected for small sample sizes (AIC_c; Akaike 1973, Burnham & Anderson 2002), and present beta estimates with standard errors and confidence intervals (CIs). We did not adjust for overdispersion because program MARK does not include a goodness-of-fit bootstrap simulation for the nest survival models.

RESULTS

Nesting success

We monitored 165 nests over 9 years (Table 1). Over this interval, apparent annual nesting success was 55 ± 22% averaged across years and more than half of all nests across years (52%) hatched. Predation was the most common cause of nest failure, with eggs disappearing from (combined categories of predation and unknown) an average of 30 ± 13% of nests. Failures owing to vehicles (n = 11) and flooding (n = 7) were the next most common causes of nest failure. Although apparent nesting success varied annually (Table 1) there was only a weak annual effect on DSR (ΔAIC_c = 4.13). The top model included a linear time trend ($\hat{\beta}_T = 0.008$, 95% CI −0.0002, 0.017), suggesting that nests survived better as the season progressed (Fig. 1).

Nest-site selection

Plovers nested in larger, more heterogeneous substrates, amidst more egg-sized stones compared with random sites (Table 2). However, substrate measures were correlated. Large stones were interspersed with patches of finer substrates, which resulted in a significant positive correlation between substrate size and heterogeneity (r^2 = 0.70, $P < 0.001$). The number of egg-sized substrates was weakly correlated with size (r^2 = 0.05, P = 0.001) but not with heterogeneity (r^2 = 0.003, $P < 0.38$).

Egg crypsis

We used 44 paired nests and random sites to examine relationships between substrate characteristics and egg crypsis, excluding one outlier (sd = 7.8) where search time was high. Search time was similar (z = 1.46, P = 0.14) at nests ($\bar{x}$ = 8.1 ± 10.0) and random sites ($\bar{x}$ = 10.2 ± 11.9 s). Therefore, we combined data to investi-

Table 1. Annual variation (%) in apparent nesting success, causes of clutch failure and daily survival rate (DSR) for Snowy Plover nests on gravel bars of the Eel River, Humboldt County, CA.

	Year									
Nest fate	2001	2002	2003	2004	2005	2006	2007	2008	2009	
Successful	66	53	42	48	38	38	75	100	33	
Predated	8	10	11	32	8	0	0	0	33	
Human-caused	3	10	8	4	0	15	0	0	33	
Abandoned	3	7	3	4	8	0	0	0	0	
Inundated by river	0	0	14	0	23	0	0	0	0	
Unknown	20	20	22	12	23	47	25	0	0	
DSR (se)	0.979 (0.006)	0.976 (0.006)	0.963 (0.008)	0.970 (0.008)	0.961 (0.013)	0.954 (0.018)	0.989 (0.011)	1.000 (0.000)	0.966 (0.9024)	
Total nests	38	30	36	25	13	13	4	3	3	

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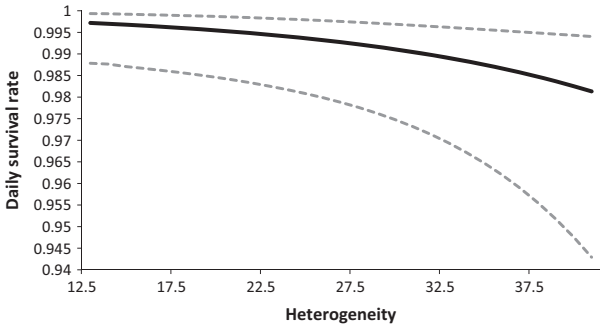

Figure 1. Daily survival rates of Snowy Plover nests declined with increasing heterogeneity of substrate size (as indexed by the standard deviation of mean substrate size) on gravel bars of the Eel River, Humboldt County, CA. Ninety-five per cent confidence intervals shown.

Table 2. Characteristics of substrate measures taken at Snowy Plover nests and paired random sites along gravel bars of the lower Eel River, Humboldt County, CA, 2001–2004.

		Nest	Random	
Year	*n*	Mean ± sd	Mean ± sd	*P*
Substrate size (mm)				
2001	30	26.3 ± 12.7	20.7 ± 13.6	0.02
2002	25	29.9 ± 15.3	23.9 ± 19.6	0.14
2003	26	24.6 ± 12.8	23.9 ± 16.7	0.60
2004	19	34.1 ± 16.9	29.3 ± 17.4	0.04
Total	100	28.3 ± 14.4	24.0 ± 16.7	< 0.001
Heterogeneity of substrate size				
2001	30	21.8 ± 10.9	18.2 ± 8.5	0.06
2002	25	29.0 ± 16.2	19.7 ± 14.3	0.04
2003	26	23.7 ± 11.7	21.9 ± 12.2	0.35
2004	19	30.3 ± 11.8	24.4 ± 12.4	0.01
Total	100	25.7 ± 13.1	20.7 ± 11.9	< 0.001
Number of egg-sized stones				
2001	30	4.0 ± 1.5	2.9 ± 1.9	0.01
2002	25	4.0 ± 2.1	3.0 ± 2.2	0.05
2003	26	3.5 ± 1.8	3.1 ± 2.3	0.14
2004	19	3.5 ± 2.5	3.6 ± 2.3	0.84
Total	100	3.8 ± 1.9	3.1 ± 2.1	0.001

gate relationships between search time and substrates (Table 3). Detection time increased with number of egg-sized stones ($r^2 = 0.10$, $P = 0.002$; Fig. 2); there was no significant relationship between detection time and substrate size or heterogeneity.

Nest survival

Models with substrate measures ranked higher than the constant survival model, and yearly and seasonal time variation models ranked lowest. The top four models had similar AIC_c weights ranging from 0.15 to 0.22, so no single model was clearly the best (Table 4). The top five models each included a negative relationship between heterogeneity and nest survival; the 95% CI on the beta for heterogeneity did not include zero in any of these models. In the best model, the heterogeneity effect ($\beta = -0.07$, se = 0.03, 95% CI −0.12, −0.01) suggested that nests placed in more homogeneous substrates (e.g. lower variation in substrate size) had greater survival than nests placed in more heterogeneous substrates. There was weak evidence for a positive relationship between mean substrate size and nest survival, although the 95% CIs for this effect in the two competitive models containing it included zero. The linear trend model had the lowest AIC_c score among the temporal models, although the effect for this trend in all competitive models was non-significant and 95% CIs included zero.

Table 3. Results of multiple linear regression examining relationship between search time(s) of a naïve human observer and substrate characteristics at Snowy Plover nests and random sites on gravel bars of the Eel River, Humboldt County, CA, 2001–2004.

Substrate variable	β coefficient	se	*P*
Intercept	2.6617	3.2452	0.414
Number of egg-sized stones	1.742	0.6382	0.007
Mean substrate size	0.1918	0.1484	0.199
Substrate heterogeneity	−0.174	0.1865	0.353

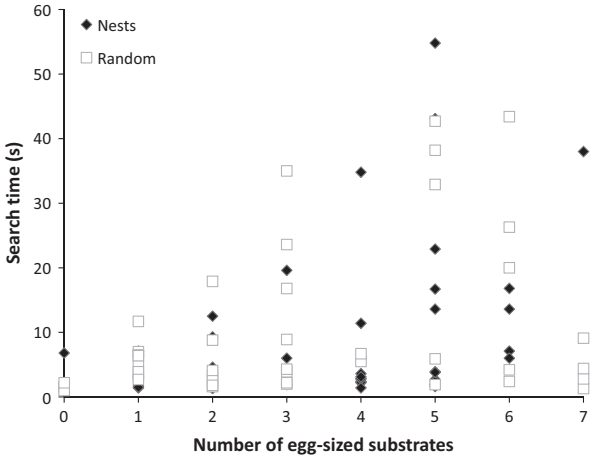

Figure 2. The time required for a naïve observer to detect a three-egg Snowy Plover clutch increased with the number of egg-sized substrates at nests and random sites.

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Table 4. Summary of competing models evaluating relationships between Snowy Plover nest survival, substrate characteristics and temporal variables. Models are ranked by ascending ΔAIC_c values with the number of parameters (*K*), model deviance and Akaike weights.

Model	*K*	ΔAIC_c[a]	Deviance	w_i
T + heterogeneity + mean substrate size	4	0.00	230.06	0.22
T + heterogeneity	3	0.23	232.30	0.20
Heterogeneity	2	0.52	234.60	0.17
Heterogeneity + mean substrate size	3	0.80	232.87	0.15
T + heterogeneity + egg-sized stones	4	2.23	232.30	0.07
Constant survival	1	3.72	239.80	0.03

T, a linear time trend across the breeding season.
[a]The AIC value for the best model was 238.09.

DISCUSSION

Several important results emerge from our study. First, Snowy Plovers selected nest-sites where heterogeneous substrates with more egg-sized stones conferred greater crypsis to eggs. Secondly, nest survival decreased as large-grained substrates became more heterogeneous. Finally, reproductive success of Plovers on gravel bars was consistently high compared with nearby beach habitats where predators had a stronger impact on egg and chick survival.

Nesting success of Snowy Plovers on gravel bars varied annually (55 ± 22%; range: 33–100%); when combined with cases when eggs disappeared from nests (unknown cause of failure, but likely to be predation), predation was the most common cause of nest failure. This finding is similar to many other reports for temperate and Arctic breeding shorebirds (Colwell 2010). Nesting success was slightly higher than estimates for other conspecific populations elsewhere in North America (Wilson-Jacobs & Meslow 1984, Page *et al.* 1985, Warriner *et al.* 1986, Paton 1995, Neuman *et al.* 2004) and much higher than on ocean-fronting beaches in our study area (Hardy & Colwell 2008, Colwell *et al.* 2010). This observation, and the comparatively high chick survival (Colwell *et al.* 2007), indicate that gravel bars are high-quality habitats based on consistently high per-capita reproductive success of individuals occupying this habitat (Colwell *et al.* 2010).

On gravel bars, Plovers selectively nested in large-grained, heterogeneous substrates with a greater number of egg-sized stones compared with surrounding habitats. A growing body of literature has shown that shorebirds, and plovers in particular, select nest-sites with characteristics that confer greater camouflage for eggs and incubating adults, or facilitate early detection of approaching predators. Eurasian Golden Plovers *Pluvialis apricaria* selected flat or gently sloping habitats for nesting, which may facilitate early detection of predators (Whittingham *et al.* 2002). Snowy Plovers selected nest-sites that were in more open, sparsely vegetated habitats (Wilson-Jacobs & Meslow 1984, Page *et al.* 1985, Powell 2001, Hood & Dinsmore 2007, Muir & Colwell 2010). Similarly, Piping Plovers *Charadrius melodus* preferred to nest on sparsely vegetated beaches with more coarse substrates compared with surrounding habitats (Burger 1987, Prindiville-Gaines & Ryan 1988, Flemming *et al.* 1992, Espie *et al.* 1996, Cohen *et al.* 2008). In the subarctic, Semipalmated Plovers *Charadrius semipalmatus* preferentially nested at sites with more pebbles and less bare ground than surrounding habitats (Nguyen *et al.* 2003). In most cases, however, it is unclear how these habitat choices affected nest survival.

Substrate characteristics, especially the number of egg-sized stones, positively influenced egg crypsis (as indexed by the time required for a naïve human observer to find a nest). This finding is consistent with observations that crypsis: (1) is enhanced by matching the background (i.e. more egg-sized substrates) and (2) increases with grain size (i.e. larger substrates) (Merilaita *et al.* 2001). However, despite evidence that Plovers nested in cryptic substrates, we found relatively weak evidence that differences in substrate composition influenced nest survival. In addition, the strongest pattern, a negative relationship between nest survival and heterogeneity, appears to contradict literature showing that habitat heterogeneity enhances crypsis (Endler 1978, Merilaita *et al.* 2001) and nest survival. In coastal Texas, Snowy Plover nests survived better when located near a conspicuous object (Hood & Dinsmore 2007). Piping Plover eggs had a higher chance of hatching in sand than in a mixture of sand, shell and stones, but this relationship only held at one of two study sites (Patterson *et al.* 1991). In other cases, nest survival was enhanced by the similarity between eggs and substrates. For example, Stone-curlew nests survived better when the base colour of eggs matched background substrates (Solis & de Lope 1995).

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Several factors may explain the lack of a strong relationship between nest-site characteristics and Plover nest survival. First, we limited analyses to gravel bar nests only. We did not measure substrate at nests on sandy, ocean-fronting beaches, where nest survival is lower (Hardy & Colwell 2008). Sand comprised < 15% of substrates on gravel bars compared with 99% of beaches (Colwell *et al.* 2010). As a result, only two of 86 nests that we measured occurred in small substrates (< 5 mm). Had we measured beach nests and included them in our analysis (M.A. Colwell unpubl. data), we are confident that we would have obtained a much stronger relationship. Secondly, we did not analyse variation in substrate colour, which may have enhanced egg crypsis (Solis & de Lope 1995).

Thirdly, we assumed that egg crypsis deterred visual predators (e.g. corvids), which were the main cause of egg loss in our study area (Colwell *et al.* 2010). However, we do not fully understand the mechanisms by which corvids find nests. If an over-flying corvid detects the movement of an incubating adult Plover that leaves a nest upon close approach of the predator, then nest survival is likely to be less affected by egg crypsis and more strongly influenced by the crypsis of the adults' plumage and the tendency to sit tight or depart a nest when a predator passes nearby. Evidence from video cameras monitoring Plover nests in our study area (albeit on beaches) suggests that predation by Common Ravens is often prompted by the movement of the incubating Plover leaving the nest. We conclude this because most Ravens landed within 1 m of the nest-site shortly after the departure of the Plover (M.A. Colwell *et al.* in prep.). However, a thorough understanding of the means by which corvids find Plover nests is desirable and would benefit greatly our understanding of the role of adult behaviour and egg patterning in influencing nest survival. Moreover, relationships between substrate characteristics and nest survival may be weakened by a greater role played by mammalian predators, which tend to use both olfaction and vision to locate nests.

Finally, we only characterized physical features of nest-sites and neglected to include the behaviour of incubating adults, which can influence nest survival. For example, Smith *et al.* (2007) compared nest success in five Arctic shorebirds and offered preliminary support that frequency of incubation recess negatively affected nest survival. More importantly, Koivula and Rönkä (1998) showed that nest departure behaviour of incubating Temminck's Stints *Calidris temminckii* influenced nest survival. Stints that nested in sparser vegetation detected predators early and quietly left their nests, which increased nest survival. In Snowy Plovers, individual females (which incubate during the day and thus are encountered more often by observers) differ in response to an approaching human (Muir & Colwell 2010). Females vary in: (1) distance at which they leave a nest, (2) type and intensity of distraction display and (3) time required to resume incubation (M.A. Colwell unpubl. data). We suspect that this variation may interact with physical features to influence nest survival (Koivula & Rönkä 1998, Whittingham *et al.* 2002), given that most predation in our study area occurs during daylight hours by corvids (M.A. Colwell *et al.* in prep.). We urge others to include behavioural measures of incubating adults in future analyses of nest survival.

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