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RESEARCH ARTICLE

Factors affecting Snowy Plover chick survival in a managed population

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ABSTRACT

Understanding survival of precocial chicks in the period immediately following hatching has important conservation implications because population growth is often sensitive to post-hatching survival. We studied federally threatened Western Snowy Plover (*Charadrius nivosus nivosus*) broods at the northern limit of their range in coastal Oregon ($n =$ 1,157) and Washington ($n = 84$) from 1991 to 2011 in an attempt to understand seasonal, annual, and spatial patterns of chick survival. In Oregon, plover chick survival increased with age, varied between sites, and was greater at sites with predator management. The mean probability of surviving from hatch to fledging at 28 days of age in Oregon was 0.57 (95% CI: 0.50, 0.63). In Washington, where predator management was not employed, we conducted separate analyses using individually banded and unbanded chicks and results indicated that survival generally increased with chick age. The mean estimated probability of surviving from hatch to fledging at 28 days of age in Washington was 0.27 (95% CI: 0.20, 0.35) for individually banded chicks when perfect detection was assumed. This probability increased to 0.67 (95% CI: 0.41, 0.83) when we analyzed unbanded chicks and included detection probability. Our findings confirm the importance of considering age effects in the survival of Snowy Plover chicks and raise questions about the validity of assuming perfect detection of plover chicks during brood checks. This work also highlights the benefit of predator management on chick survival.

Keywords: Charadrius nivosus, precocial species, chick survival, Oregon, Snowy Plover, Washington

Factores que afectan la supervivencia de polluelos de *Charadrius nivosus nivosus* en una población manejada para conservación

RESUMEN

Entender la supervivencia de los polluelos precoces en el periodo que sigue inmediatamente a la eclosión tiene implicaciones importantes para la conservación, porque el crecimiento poblacional frecuentemente es sensible a la supervivencia posterior a la eclosión. Estudiamos nidadas del ave federalmente amenazada *Charadrius nivosus nivosus* en el límite norte de su distribución geográfica en la costa de Oregon ($n = 1157$) y Washington ($n = 84$) entre 1991 y 2011, en un intento por entender los patrones estacionales, anuales y espaciales de supervivencia de los polluelos. En Oregon, la supervivencia de los polluelos se incrementó con la edad, varió entre sitios y fue mayor en sitios donde se controlan las poblaciones de sus depredadores. La probabilidad media de supervivencia desde la eclosión hasta el emplumamiento a los 28 días de edad en Oregon fue de 0.57 (IC del 95%: 0.50, 0.63). En Washington, donde no se controlan las poblaciones de los depredadores, hicimos análisis por separado usando polluelos anillados y no anillados y los resultados indicaron que la supervivencia generalmente se incrementó con la edad de los polluelos. La probabilidad media estimada de supervivencia desde la eclosión hasta el emplumamiento a los 28 días de edad en Washington fue 0.27 (IC del 95%: 0.20, 0.35) para los polluelos anillados cuando se supone que existe detección perfecta. La probabilidad se incrementó a 0.67 (IC del 95%: 0.41, 0.83) cuando analizamos los polluelos no anillados e incluimos la probabilidad de detección. Nuestros resultados confirman la importancia de considerar los efectos de la edad en la supervivencia de los polluelos de *C. n. nivosus* y generan preguntas sobre la validez de suponer que la detección de los polluelos durante los muestreos en las nidadas es perfecta. Este trabajo también resalta los beneficios del control de las poblaciones de depredadores para la supervivencia de los polluelos.

Palabras clave: Charadrius nivosus, especies nidífugas, Oregon, supervivencia de los polluelos, Washington

INTRODUCTION

Effective management for rare species requires knowledge of the species' vital rates, including chick survival from hatching to fledging. Such information is essential for targeting conservation actions on vital rates that are most likely to influence population growth (Lavers et al. 2010). During the first weeks after leaving the nest, juvenile birds face a high risk of mortality (Götmark 2002, Kershner et al. 2004, Low and Pärt 2009) because they are not fully developed physically, lack crucial life skills (Marchetti and Price 1989, Wheelwright and Templeton 2003), and are exposed to high predation rates (Naef-Daenzer et al. 2001). Understanding survival of precocial chicks during this period has important conservation implications because population growth is often extremely sensitive to changes in survival to fledging (Colwell et al. 2007). Many shorebird species demonstrate increased chick survival with age, including the Western Snowy Plover (*Charadrius nivosus nivosus*; Colwell et al. 2007), Mountain Plover (*C. montanus*; Dinsmore 2008), and Western Sandpiper (*Calidris mauri*; Ruthrauff and McCaffery 2005). Presumably, this relationship is driven by changes in a chick's ability to better thermoregulate, exploit habitats and food resources away from the nest site, and better avoid and escape predators as it ages.

The Western Snowy Plover breeds along the Pacific Coast from Baja California Sur, Mexico, north to Washington, and at disjunct interior sites (Page et al. 1991). Populations within 50 miles of the coast were federally listed as threatened in 1993 (U.S. Fish and Wildlife Service 1993, 2006) because of threats to nesting habitat and documented long-term declines in breeding numbers. Our objectives here are to estimate survival of Snowy Plover chicks during the 28-day fledging period (immediately following hatching), identify variables that affect survival during this period, and compare survival estimates derived from individually banded and unbanded broods. During the course of this study, lethal predator control was implemented in Oregon, and we wanted to test whether this management action improved brood survival from hatching to fledging. We hypothesized that predator control would improve the survival of Snowy Plover chicks, consistent with other measures used to improve fledging success in shorebirds (Neuman et al. 2004, Dinsmore et al. 2014, Pearson et al. 2014). This represents the first summary of chick survival data from the northern portion of the species' Pacific Coast breeding range. It is also the first assessment of the influence of predator management on chick survival.

METHODS

Study Area

We studied breeding Snowy Plovers from 1991 to 2011 at 11 sites at the northern limit of the species' range along the Oregon and Washington coasts (Figure 1). Although plovers occasionally nested at other beaches ($n = 2$ during the course of this study), these sites include all regularly occupied habitat in Oregon and Washington. The sites represent habitats typical of nesting Snowy Plovers in this region, and include open ocean beaches, sand spits, ocean over-wash sites, sand dunes, estuarine sand flats, and several habitat restoration areas (HRAs). Dunes are dominated by nonnative, invasive American and European beachgrass (*Ammophila breviligulata* and *A. arenaria*, respectively). At HRAs, beachgrass is cleared and oyster shell spread to provide more open, sparsely vegetated habitat. Oyster shell helps stabilize drifting sand and is thought to improve nest crypsis (but see Pearson et al. 2014).

Sites varied in ownership, management activities, and predation and recreation pressures. Prior to 2002, predator management in Oregon was nonlethal and included harassment of individual predators, and trash and carcass removal to avoid attracting predators to nesting areas. In 2002 and 2003, an integrated predator management plan (U.S. Department of Agriculture and U.S. Department of Interior 2002) that included lethal control was instituted at Coos Bay North Spit, Bandon Beach, and New River to improve nest and fledging success (Dinsmore et al. 2014). Lethal predator management was conducted by USDA APHIS-Wildlife Services (APHIS-WS) in coordination with the Recovery Unit 1 Snowy Plover Working Team, and targeted American Crows (*Corvus brachyrhynchos*), Common Ravens (*Corvus corax),* nonnative red fox *(Vulpes vulpes),* and striped skunks (*Mephitis mephitis*). Other nontarget predators, including owls, falcons, coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and feral cats (*Felis catus*) were removed when they exhibited focused attention through regular presence or hunting on a nesting area, and nonlethal control measures proved ineffective. Predator control activities began before the plover nesting season (typically mid-February) each year and continued through August. Techniques included placement of chicken eggs tainted with the avicide DRC-1339, padded-jaw leg-hold traps, shooting, and cage traps. In 2002 and 2003, APHIS-WS provided one specialist to cover the 3 sites receiving lethal predator management. In 2004 and continuing through 2011, lethal predator management was extended to include all Oregon sites, and a second specialist was hired to cover predator management at these additional sites. Predator management efforts were approximately equal across sites and approximately 88% of the predators removed between 2002 and 2011 were crows and ravens and 5% were red fox (Table 1). Predator management was not conducted at Washington sites during this study.

Chick Capture and Monitoring

We located and monitored Snowy Plover nests weekly from early April through late September as described in Dinsmore et al. (2014) and used egg flotation to estimate hatch date (Westerskov 1950, Hays and LeCroy 1971, Dunn et al. 1979, Rizzolo and Schmutz 2007). In Oregon, most nest-tending adults were individually color-banded

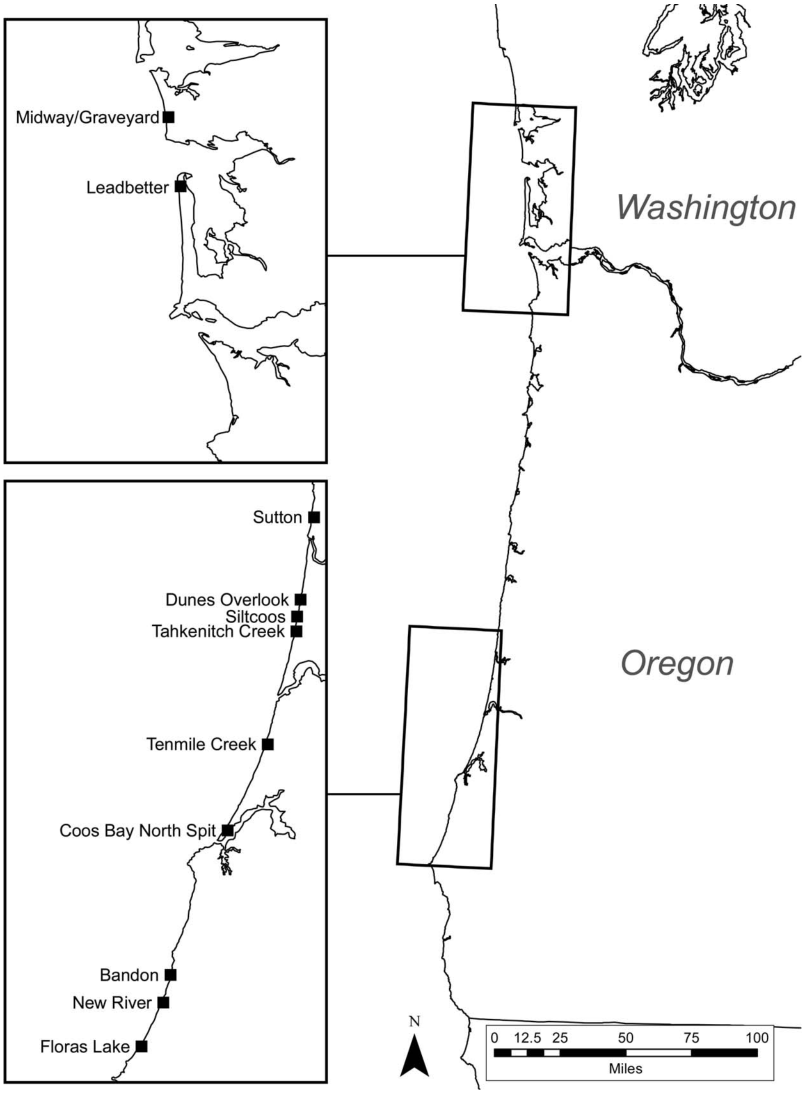

FIGURE 1. Sites along the Oregon and Washington coasts where nesting Snowy Plovers were monitored, 1991–2011.

to facilitate relocating broods during the fledging period. In Washington, approximately one-third of the adult population was marked. In both Oregon and Washington, there were some tending adults that were unbanded. These adults were still identifiable by association with their uniquely banded broods or chicks. In the few cases where neither the brood nor the tending adult was color-banded, we were able to identify "individual" broods by a combination of known hatch date, brood age (size), and geographic location. With relatively few unbanded birds, we could in nearly all cases accurately assign the identity of a specific brood to the nest from which the young hatched, and thus these birds were included in the analysis. Chicks were banded at or soon after hatching with brood-specific color combinations in Oregon, because the large number of broods prohibited individual combinations. All chicks of some broods were individually marked in Washington, where there were fewer total broods. We ran surveys to monitor broods 1–2 times per week. Early in the brood-rearing period plover chicks can be difficult to locate, and we often confirmed whether a brood was active based on adult behavior. We increased effort to relocate broods and count individual chicks as fledging age approached. We considered all hatch-year birds seen at any point after 28 days old as having fledged.

Chick Survival Modeling

We assessed survival over a 28-day period from egg hatching to independence, hereafter referred to as the fledging period (USFWS 2007). Because some chicks were individually banded in Washington, and because management differed between states, we used multiple analyses to

TABLE 1. The number of predators removed by species at Snowy Plover breeding locales in coastal Oregon, 2002–2011.

	Great Horned Owl[b]	Common Raven	American Crow	Virginia opossum[c]	Feral cat	Coyote	Red fox	Gray fox[d]	Raccoon	Striped skunk
2002[a]	0	12	14	1	1	0	6	2	12	5
2003[a]	0	150	38	1	1	0	12	2	8	6
2004	0	150	101	17	4	0	27	3	19	13
2005	0	82	132	3	2	0	15	0	0	3
2006	0	145	89	0	1	4	17	0	0	8
2007	1	65	144	0	0	0	13	3	2	7
2008	0	219	122	0	1	2	15	0	3	2
2009	0	151	169	0	4	2	10	2	3	4
2010	0	81	168	0	0	1	7	0	1	3
2011	1	95	178	0	0	0	15	0	0	6
Total	2	1,150	1,155	22	14	9	137	12	48	57

[a] Predator removal only occurred at 3 sites in 2002 and 2003.
[b] *Bubo virginianus*.
[c] *Didelphis virginiana*.
[d] *Urocyon cinereoargenteus*.

examine patterns in Snowy Plover chick survival. Below, we outline the specific approaches for each state separately and then comment on our approach to interpreting the collective findings.

Oregon Chick Survival

The Oregon dataset consisted of 1,157 plover broods (2,925 chicks); the number of broods per year generally increased throughout the study period (Table 2). We used the chick survival from marked adults model (Lukacs et al. 2004) in Program MARK (White and Burnham 1999) to model the survival of chicks with a uniquely identifiable parent (usually a male). The encounter histories included counts of brood size throughout the 28-day fledging period. For this analysis we used only known chick counts, omitting those where the brood was known to be present but no chick count was possible. This is a conservative approach and avoids the need to make assumptions about the number of chicks present on days when we did not record an actual count. We used a hierarchical approach to model effects on survival (no effect [.], linear [age], quadratic [age^2], and cubic [age^3] age effects, hatch date, year, and site differences) and detection probability (no effect [.], and linear [T] and quadratic [TT] time trends across years) separately, and then combined these effects additively to get a best model (Pagano and Arnold 2009). An earlier nest survival analysis (Dinsmore et al. 2014) supported a strong benefit of predator management to nest survival, and we were interested in seeing if those benefits extended to dependent chicks. Thus, we added a single covariate to each brood that coded for whether or not it was at a site that received predator management. We added the predator management covariate to the best model from the process described earlier to see if there was a change in model support.

Washington Chick Survival

Washington chick data were available across a 6-year period (2006–2011) and our modeling approach was similar to that used with the Oregon data. However, unlike Oregon, some Snowy Plover chicks were individually marked in Washington, making it possible to estimate chick survival using 2 approaches: (1) for banded chicks we used a variation of a known fate model (the nest survival model; Dinsmore et al. 2002) under the assumption of perfect detection of chicks; (2) for unbanded chicks we used the Lukacs et al. (2004) chick survival model using just the chick counts on each visit.

Washington banded chicks. We used data from 132 individually banded chicks from 51 broods monitored during a 4-year period (2007–2010) to model daily chick survival. Banded chicks were from Midway and Leadbetter beaches and included 36 broods of 3, 9 broods of 2, and 6 broods of 1 chick. We used a hierarchical approach to model effects on daily survival (no effect [.], linear [age], quadratic [age^2], and cubic [age^3] age effects, site differences, year, and hatch date) and then combined competitive effects additively as we did for Oregon chicks (see above). We used the nest survival model in Program MARK to model chick survival under the assumption of perfect detection probability. This assumption may be reasonable given the small population, intensity of brood checks, and because it was rare to miss chicks on brood checks (thus, when a chick was not detected it was usually deceased). We assessed the fit of the nest survival model to the chick survival data using a chi-square test of

TABLE 2. Number of Snowy Plover broods included in chick-survival analyses, by year and site, in coastal Oregon, 1991–2011. Sites are Sutton Beach (SU), Siltcoos River estuary (SI), Dunes Overlook (OV), Tahkenitch Creek estuary (TA), Tenmile Creek estuary (TM), Coos Bay North Spit (CBNS), Bandon Beach (BB), New River (NR), and Floras Lake (FL).

Year	SU	SI	OV	TA	TM	CBNS	BB	NR	FL	Total
1991						5	2	3	2	12
1992					7	8	3	2	4	24
1993					7	8	4		9	28
1994		2		3	1	16	5	5	5	37
1995		2		4	4	14	2	5	5	36
1996		1		9	2	20	1	15	2	50
1997	4	2		4	1	14		14	6	45
1998	4	4		4	3	8		21		44
1999	1	8	2	1	3	13	1	15		44
2000	3	7	3	2	5	8		6	4	38
2001	1	1	4	8	5	9	2	9		39
2002		3	5	7	6	8		9	1	39
2003	1	2	3	7	9	12	2	10		46
2004		7	6	6	11	16	13	13		72
2005		8	7	6	7	15	13	13		69
2006		8	6	3	11	20	7	13		68
2007		8	7	2	18	20	10	19		84
2008		10	2		10	27	3	16		68
2009		11	5	2	12	23	5	20		78
2010		13	16	3	18	16	11	15		92
2011		16	32	14	7	47	13	15		144

independence of the fates of chicks within broods as a function of brood size (Dinsmore and Knopf 2005).

Washington unbanded chicks. We used the Lukacs et al. (2004) model in Program MARK to model survival for 33 unbanded Washington broods during the 28-day fledging period in 2006–2011. Broods were from Midway (15), Leadbetter (13), and Graveyard (5) beaches. Because the banded group did not contain chicks from Graveyard, we ran an additional analysis with data from 28 broods at Midway and Leadbetter beaches (omitting Graveyard broods) to allow comparison of methods used to estimate survival. In both cases, we used a hierarchical approach to model effects on daily survival and detection probability (no effect [.], linear [age], quadratic [age^2], and cubic [age^3] age effects, and hatch date) and then used the same approach for model building and inference as with banded Washington chicks.

Model Selection

For each analysis described above we used model selection by Akaike's Information Criterion corrected for small sample size (AIC_c; Akaike 1973) and the general approach of Burnham and Anderson (2002) to evaluate competing models and their effects. For Oregon, we make inferences about model effects based on a single best model with all support. For individually banded birds in Washington we make inferences based on the top 3 competitive models (combined AIC_c weight [w_i] of 0.98). For unbanded Washington chicks, the top model (including broods from Graveyard) comprised 0.55 of all support, and was 2.6% more likely than the next model, which differed only in the detection probability (p). When we analyzed the unbanded broods without data from Graveyard, the top model did not change, though support declined slightly ($w_i = 0.48$). Because the inclusion of birds from Graveyard did not appear to change model results, we report results from all broods.

RESULTS

Oregon Chick Survival

From the 1,157 Oregon broods monitored, 1,259 chicks were observed at or beyond 28 days. Our analysis revealed that a single model with additive effects of chick age, site, and predator management on apparent survival and a quadratic trend across age on detection probability had all model weight (Table 3). The second-best model ($\Delta AIC_c = 15.14$) was missing the effect of predator management. Plover chick survival increased as the birds aged ($\beta_{Age} = 0.13$, SE = 0.018, 95% CI: 0.09, 0.16). There was also strong evidence supporting site differences in chick survival. Most of the estimated daily survival rates across all Oregon sites were >0.95 (range: 0.936–0.997). We calculated the probability (and 95% CI) that a chick would survive the 28-day fledging period for each of the 9 sites (Figure 2). Survival to fledging was greatest at Coos Bay North Spit and lowest at Sutton Beach; mean survival across all sites was 0.53 (SE = 0.04, 95% CI: 0.45, 0.60). Lastly, there was a strong positive benefit of predator management on chick survival ($\beta_{PredatorMgmt} = 0.33$, SE = 0.08, 95% CI: 0.17, 0.48).

TABLE 3. Model selection results for the daily survival of Snowy Plover chicks in coastal Oregon 1991–2011 and Washington 2006–2011. The model name shows effects on annual survival (ϕ) and detection probability (p); models are ranked by ascending ΔAIC_c values with the model weight (w_i), number of parameters (K), and model deviance. Final parameters included linear, quadratic (^2), and cubic (^3) effects of age; site; predator management (PM); and year for survival and linear (T) and quadratic (TT) time trends for detection probability. Only models with a non-zero model weight are shown. Results are shown for coastal Oregon (A), individually banded Washington chicks (B), and unbanded Washington chicks with (C) and without (D) Graveyard broods.

Model	ΔAIC_c[a]	w_i	K	Deviance
(A)				
ϕ (Age+Site+PM) p(TT)	0.00	1.00	14	5364.25
(B)				
Age	0.00	0.46	2	499.20
Age^3	0.56	0.35	4	495.75
Age^2	1.99	0.17	3	499.19
Year	7.33	0.01	4	502.52
(C)				
ϕ (Age^2) p(T)	0.00	0.55	5	287.26
ϕ (Age^2) p(TT)	1.98	0.21	6	287.10
ϕ (Age^2) p(.)	2.42	0.16	4	291.79
ϕ (.) p(T)	5.20	0.04	3	296.67
ϕ (.) p(TT)	5.69	0.03	4	295.07
(D)				
ϕ (Age^2) p(T)	0.00	0.48	5	249.35
ϕ (Age^2) p(.)	1.23	0.26	4	252.70
ϕ (Age^2) p(TT)	1.98	0.18	6	249.18
ϕ (Age) p(.)	3.86	0.07	3	257.44

[a] The AIC_c value of the best model was 5392.42 for model set (A), 503.52 for (B), 297.60 for (C), and 259.72 for (D).

To illustrate this effect, we predicted the age-specific daily survival rates for Snowy Plover chicks at a single site, Coos Bay North Spit (CBNS), with and without predator management (Figure 3). No other effects, including year and hatch date, appeared to influence estimates of chick daily survival. Detection probability was nonlinear as a function of chick age; it was 0.79 at age 1 day, dropped to ~0.62 at ages 10–13 days, and then rose to a peak of 0.90 by age 28 days. This pattern is best explained by variable effort to relocate chicks during the fledging period. As the chicks approach fledging age, effort to relocate them increases, resulting in higher estimates of detection probability. Likewise, higher detection probability at day 1 reflects increased effort to band newly hatched broods.

Washington Chick Survival

Banded chicks. Of the 132 banded chicks ($n = 51$ broods) that were monitored, 35 (27%) were known to reach the fledging age of 28 days. The nest survival model fit the chick survival data well ($\chi^2 = 7.12$, df $= 8$, $P = 0.52$) and the estimate of over-dispersion was $\hat{c} = 0.89$ (it was kept at 1.0 for all analyses). Survival was driven by strong age effects, best explained by a linear age model with competitive cubic ($\Delta AIC_c = 0.56$) and quadratic ($\Delta AIC_c = 1.99$) models (Table 3). In the best model, the age effect was positive ($\beta_{Age} = 0.06$, SE $= 0.017$, 95% CI: 0.03, 0.09) and closely matched the pattern from Oregon chick data. The estimates of daily survival increased with age (Figure 4A) and the probability of surviving the 28-day fledging period was 0.27 (SE = 0.04, 95% CI: 0.20, 0.35) when perfect detection was assumed. As in Oregon, year and hatch date did not appear to influence estimates of chick daily survival. We did not find differences in survival between the 2 Washington sites, but sample sizes at these sites were small.

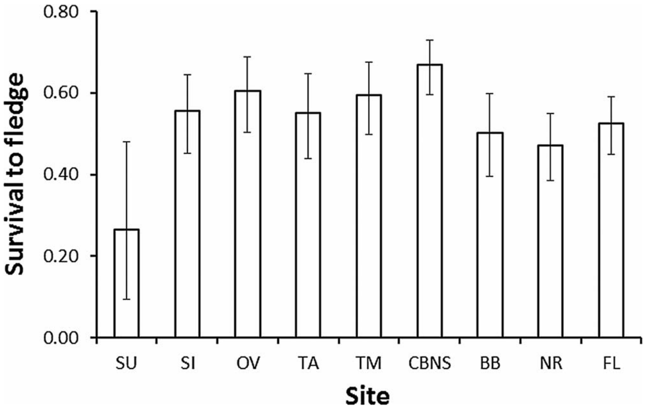

FIGURE 2. Probability of surviving the 28-day fledging period (95% CI) for Snowy Plover chicks banded at 9 sites in coastal Oregon, 1991–2011. Sites are Sutton Beach (SU), Siltcoos River estuary (SI), Dunes Overlook (OV), Tahkenitch Creek estuary (TA), Tenmile Creek estuary (TM), Coos Bay North Spit (CBNS), Bandon Beach (BB), New River (NR), and Floras Lake (FL).

Unbanded chicks. Of the 64 unbanded chicks ($n = 28$ broods) monitored, 43 survived to fledging age of 28 days.

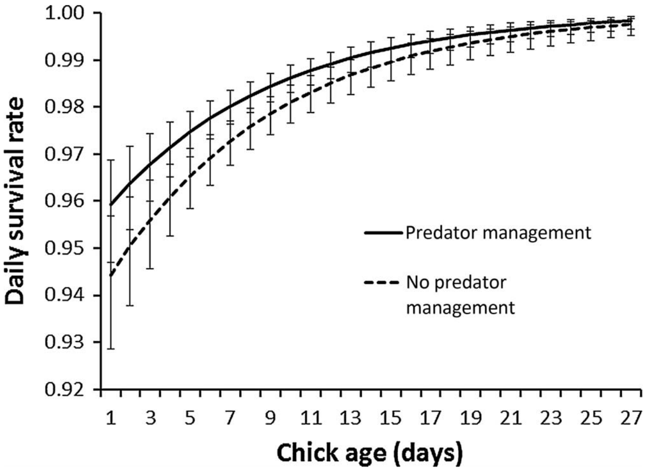

FIGURE 3. Daily survival probabilities (mean and 95% CI) of Snowy Plover chicks with and without predator management at Coos Bay North Spit, Oregon, 1991–2011.

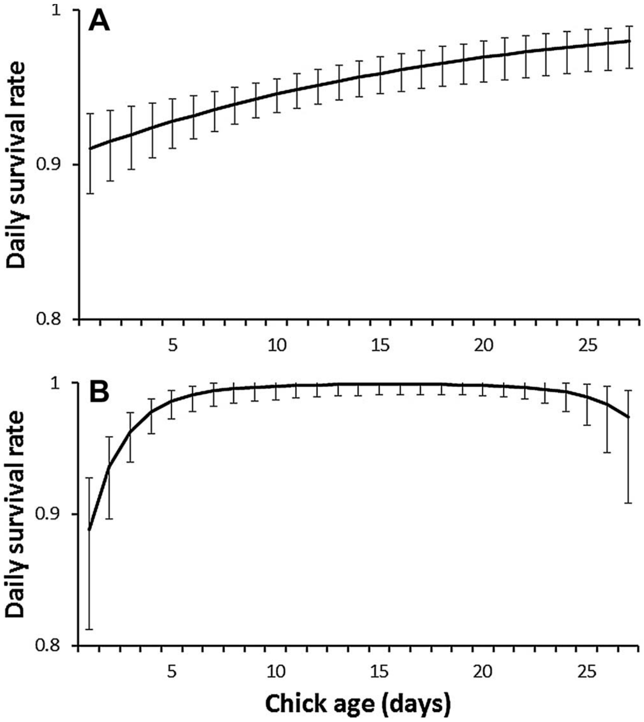

FIGURE 4. Daily survival probabilities (95% CI) as a function of chick age for Snowy Plover chicks banded in coastal Washington, 2007–2011. Patterns of daily survival are shown for chicks that were individually banded **(A)** and those that were unbanded **(B)**.

Survival in the unbanded population was mostly driven by strong age effects, best explained by a quadratic age model where survival increased through about age 15 days and then decreased slightly until age 28 days (Table 3 and Figure 4B); other age models and hatch date were not important predictors of survival. Detection probability was explained by a linear trend that increased with age ($\beta_T = 0.07$, SE = 0.034, 95% CI: 0.01, 0.14). The estimates of detection probability from these data were relatively high (range: 0.84–0.97). The probability of surviving the 28-day fledging period under this model was 0.69 (SE = 0.06, 95% CI: 0.56, 0.80). Year, hatch date, and site were not important predictors of survival.

When we removed the Graveyard broods from the analysis to facilitate comparison with the banded data, which did not include Graveyard, the top 3 models were competitive (combined w_i of 0.93). The top model was identical to the full analysis, but the AIC_c weight was lower. All models showed a strong age effect and varied only in detection probability.

DISCUSSION

These results advance our knowledge of dependent young shorebird survival patterns, document an important vital rate (chick survival) of a federally listed species at the northern extent of its range, and complement the results of an earlier study that found a positive effect of predator management on nest survival (Dinsmore et al. 2014). Our results closely mirror results from studies of this (Ruhlen et al. 2003, Colwell et al. 2007) and other shorebird species (Ruthrauff and McCaffery 2005, Dinsmore 2008, Ackerman et al. 2014, Catlin et al. 2015). For example, in all our analyses, Snowy Plover chick survival generally improved with age, especially during the first 10 days. This is because newly hatched chicks are less able to thermoregulate and must gradually learn to forage and evade predators, which translates into lowered survival during this stage (Powell 1992, Visser and Ricklefs 1993, Colwell et al. 2007). However, we believe the unusual and statistically insignificant decline observed in Washington unbanded chick survival after day 15 is an artifact of small sample size. As in other studies, we found strong evidence for spatial variability in Snowy Plover chick survival and believe this is related to variation in recreation pressure and predator communities between sites (e.g., Colwell et al. 2007). Our comparison of chick survival estimation approaches revealed that an assumption of perfect detection may cause survival estimates to be severely biased low, even when chick detection probability during brood checks is relatively high (>0.84). Our survival estimates are the first for Snowy Plover chicks along the northern Pacific Coast (recovery Unit 1; USFWS 2007). Our findings have implications not only for conservation actions specific to this species but also for the methods used to estimate dependent chick survival in shorebirds generally.

Comparison of Methods to Estimate Snowy Plover Chick Survival

In Washington we had an opportunity to compare survival estimates derived from 2 approaches: (1) assuming perfect detection of individually banded chicks, or (2) estimating detection probability from unbanded broods associated with a banded adult. Survival estimates varied widely between these 2 approaches. Hatching and fledging rates for birds at Graveyard are higher than at other Washington sites (S. F. Pearson personal communication), making it difficult to compare survival from banded (no Graveyard broods) and unbanded broods. However, removing the Graveyard broods from the analysis did not appreciably alter chick survival estimates.

A prevailing assumption in the analysis of the banded broods is that chick detection during brood checks is very close to 100%. Our analyses with the Washington data suggest that this is not a valid assumption. In our model using unbanded chicks where we did not assume perfect detection, detection probability increased with age and ranged from 0.84 to 0.97, but never reached 1.0 despite a small population and intense monitoring efforts. Likewise, detection probability of the Oregon broods was high (range: 0.63–0.90), but did not reach 1.0. Thus, there is a need to incorporate detection probability into survival estimates. Because detection appears imperfect, we believe the estimate of chick survival using unbanded chicks in Washington (0.69) is more robust than the much lower estimate that used individually banded chicks (0.27) and assumed perfect detection. In addition, the survival estimate from unbanded chicks is comparable to estimates from the much larger Oregon population, where survival to fledging averaged 0.53 across all sites (range: 0.27–0.67).

Conservation Implications

The negative influence of expanding predator populations on vulnerable bird species has made predator management an important issue for avian conservation (Lavers et al. 2010, Smith et al. 2010). Predation of nests and chicks, particularly by corvids, has negative effects on Snowy Plover nest and chick survival throughout its range (Page et al. 1983, Colwell et al. 2005, 2010, Pearson et al. 2014) and plover fledging success negatively correlates with raven activity (Burrell and Colwell 2012). To reduce predation rates, managers can use techniques that change predator behavior, reduce their numbers, or prevent them from accessing nests, chicks, and/or adults (table 1 in Pearson et al. 2014). Initially, predator management throughout much of the Snowy Plover's range focused on wire cages placed around nests (exclosures) with positive effects on hatching rates (e.g., Neuman et al. 2004, Dinsmore et al. 2014, Pearson et al. 2014) but in some cases, exclosures had apparent negative effects on adult survival (Neuman et al. 2004, Hardy and Colwell 2008, Mullin et al. 2010). Recently, predator management in Oregon has focused on harassment, culling, and translocation of predators, but with an emphasis on the individual predators responsible for the observed predation events. Our results indicate that these recent management activities have benefitted chick survival in Oregon. During the past 2 years predator management has been implemented in Washington, and very preliminary findings indicate a nest success and fledging success response similar to that seen in Oregon (S. F. Pearson personal communication). Other sites with declining populations may find predator management an effective tool in improving reproductive success (but see Stenzel et al. 2007). Among the recovery criteria identified in the Western Snowy Plover Pacific Coast Recovery Plan (USFWS 2007) is an average desired yearly productivity of 1.00 chicks fledged per breeding male. In Oregon, prior to lethal predator control, productivity across all sites averaged 1.06 chicks fledged per breeding male. Between 2004 and 2011 (years when all sites had predator control), productivity averaged 1.32 chicks per male, which was a significant improvement ($t_{16} = 2.38$, $P = 0.03$).

Survival varied across sites in Oregon, and was lowest at Sutton and New River. Colwell et al. (2007) found variable survival across habitat types, mirroring a portion of the site differences we found. Likewise, Brudney et al. (2013) found strong differences in survival of Piping Plover chicks across sites. All Oregon sites possess roughly similar habitat (ocean beach and estuary), but spatial variability in survival is likely caused by subtle differences in habitat quality, management, recreation, predator assemblages, and predation pressure. For example, red fox are only predators at the southern-most sites in our study area, crows are more common at the central sites, and ravens are much more numerous at New River than at other sites. These site differences have conservation implications; emphasizing conservation resources on sites with large populations and high survival and productivity is critical to maintaining population growth but may further concentrate a small population. Management to improve survival at poorly performing sites is likely to have a smaller impact on overall productivity, but will increase the suite of active sites.

We did not find an effect of hatch date in our analyses: broods that hatched earlier in the season had no survival advantage. In other Piping and Snowy plover studies, early broods were found to be more likely to fledge than late broods (Colwell et al. 2007, Brudney et al. 2013, Saunders et al. 2014, Catlin et al. 2015). It is possible, especially at the north end of the range, that the expected effect of hatch date is influenced by occasional early-season storms that reduce survival of the earliest broods and by seasonally changing predator populations, especially in Oregon, where cumulative effects of predator control across the season may have benefited later broods.

Summary

One of the challenges in working with species at risk is that little information is available on vital rates, population ecology, and mechanisms of decline. At the same time, at-risk species require immediate conservation attention to reverse declining trends (Lavers et al. 2010, Martin et al. 2012). By modeling a single life stage, chick survival to fledging, we demonstrate the effectiveness of predator management (primarily culling and harassment). This analysis, coupled with a previous examination of nest survival (Dinsmore et al. 2014, Pearson et al. 2014), highlights the importance of predator management in recovering Snowy Plovers at the northern end of their range. We also demonstrate the importance of including detection probabilities when estimating survival in future modelling efforts. Moreover, the information gained from our life-stage specific model can now be incorporated in an overall population model using either age- or stage-based matrix models (Caswell 2001, Fieberg and Ellner 2001) or Life-Stage Simulation Analysis (Wisdom and Mills 1997, Wisdom et al. 2000, Camfield et al. 2011) to evaluate the relative importance of different vital rates on population growth. Ultimately this will allow us to identify vital rates most responsive to management and determine where efforts may be best directed to decrease or reverse population declines.

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