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Management and Conservation Article

Apparent Survival and Population Growth of Snowy Plovers in Coastal Northern California

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ABSTRACT An accurate understanding of factors influencing survival and how they affect population growth are required to determine the best conservation strategies for small populations, especially near the limit of a species' range. We estimated adult and juvenile survival for a small population of the threatened western snowy plover (*Charadrius alexandrinus nivosus*) in coastal northern California over 7 years (2001–2007). We also evaluated population structure and growth to determine the relative importance of immigration and local recruitment. Apparent survival for adult males ($\phi = 0.61 \pm 0.08$) was greater than that of adult females ($\phi = 0.50 \pm 0.11$), and survival of adults was greater than for juveniles ($\phi = 0.40 \pm 0.06$). An algebraic assessment of population growth (λ) revealed that fecundity and survival were insufficient to maintain the population ($\lambda = 0.66$–0.77), whereas estimates based on consecutive annual counts ($\lambda = 0.96 \pm 0.26$) and a Pradel model ($\lambda = 0.92 \pm 0.11$) suggested the population was more stable. These results, combined with annual variation in the number of newly marked plovers, indicate that the local population was maintained by immigration and can be classified as a sink. Management actions aimed at increasing fecundity, including predator control and greater restrictions on human activity, may be necessary to maintain this population; actions aimed at increasing adult survival are more challenging.

KEY WORDS apparent survival, *Charadrius alexandrinus nivosus*, demography, fecundity, immigration, mark–recapture, population growth, snowy plover.

In 1993, the United States Fish and Wildlife Service (USFWS) listed the Pacific Coast population of the western snowy plover (*Charadrius alexandrinus nivosus*) as threatened under the Endangered Species Act. The federal listing was based on a decline in the number of breeding locations and population size between 1977 and 1989 (Page et al. 1991). The species' recovery plan identified 3 factors that contributed to the population's threatened status via their negative effects on productivity (USFWS 1993, 2007). First, predation of eggs and chicks by growing populations of predators has limited recruitment of young at some breeding sites (Neuman et al. 2004). Second, human disturbance has been implicated as the cause of low chick survival at sites with high levels of human recreational activity (Ruhlen et al. 2003, Lafferty et al. 2006). Finally, the invasion and spread of introduced plants (e.g., *Ammophila arenaria*) has reduced the availability and quality of breeding habitat (USFWS 1993, 2007). The recovery plan contains little information or few management actions directed at plover survival.

Age-specific survival data are critical to perform even the simplest of population analyses (Sandercock 2003). Analysis of population viability and elasticity rely on accurate estimates of survivorship (Benton and Grant 1999, Larson et al. 2002). Recently, Sandercock (2003) proposed that adult survival had the greatest effect on rates of population change for shorebirds because of their longevity. For example, piping plover (*Charadrius melodus*) population viability models were most sensitive to variation in adult survivorship (Plissner and Haig 2000). Accordingly, accurate estimates from studies conducted across a species' range are valuable in honing estimates of population viability.

Several studies have estimated survival of snowy plovers. Stenzel et al. (2007) estimated juvenile and adult true survival at 0.46 and 0.69, respectively, based on a Barker analysis of a partially migrant population in central coastal California, USA. Paton (1994) estimated adult apparent survival of 0.69 for a migratory population breeding around the Great Salt Lake, Utah, USA. Sandercock et al. (2005) obtained a slightly lower estimate (0.64) for a population of Kentish plovers (*Charadrius alexandrinus alexandrinus*) breeding in Turkey. Estimates used in a population viability analysis as part of the species' recovery plan fall within this range of values (USFWS 2007).

We initiated a monitoring program in recovery unit 2 (RU2) in coastal northern California, one of 6 recovery units for the western snowy plover (USFWS 2007). This population is small (19–74 breeding ad; Colwell et al. 2009) and geographically remote from others along the Pacific coast. To understand local population growth, and relationships to other groups of plovers breeding elsewhere on the Pacific coast, we 1) estimated sex- and age-specific apparent survival of plovers; 2) described the population structure based on age, sex, and movement patterns; 3) estimated population growth rate using empirical estimates of survival and fecundity; and 4) evaluated whether this population is a source or sink.

STUDY AREA

We monitored a color-marked population of snowy plovers from 2001 to 2008 in Humboldt County, California, USA,

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Table 1. Annual population structure of snowy plovers, Humboldt County, California, USA, 2001–2008.

	M				F			
Yr	Returning ad[a]	Returning yearlings[b]	Immigrants[c]	Total	Returning ad[a]	Returning yearlings[b]	Immigrants[c]	Total
2001	14	6	8	28	11	2	16	29
2002	17	8	5	30	19	6	5	30
2003	23	4	1	28	18	5	6	29
2004	16	5	11	32	15	3	14	32
2005	17	9	7	33	17	4	11	32
2006	16	6	8	29	13	4	11	28
2007	10	2	4	16	8	2	4	14
2008	10	2	6	18	6	2	11	19
$\bar{x}$	15.4	5.3	6.3		13.4	3.5	9.8	

[a] Returning ad marked in the study area in a previous yr.
[b] Philopatric plover first marked as a chick and later recaptured and marked as a breeding ad.
[c] Unmarked ad captured as breeders and ad first marked at locations elsewhere along the Pacific coast and later breeding in the study area.

one of 3 coastal California counties that make up RU2 (Colwell et al. 2009). During the years we monitored plovers in RU2, >95% of breeding occurred at 19 sites in Humboldt County. Some plovers occasionally bred in Mendocino County during 4 of the 8 years; no plovers bred in Del Norte County during this interval. The geographic area we surveyed in Humboldt County extended roughly 70 km along the coast, much of which was suitable breeding habitat. We also surveyed for plovers along 15 km of the lower Eel River. Within each year, most individuals bred at just one site; however, a few plovers moved among sites, especially after breeding failure. The 19 breeding sites consisted of either linear stretches of ocean-fronting beach or gravel bars along the Eel River. On beaches, plovers nested and reared chicks amidst sparsely vegetated sand substrates dominated by European beach grass and native vegetation. Along the Eel River, plovers nested on gravel bars characterized by coarse substrates vegetated with white sweet clover (*Melilotus alba*) and sparse stands of willow (*Salix* spp.).

METHODS

We initiated a marking program in 2000 and began intensive resighting efforts in 2001. We captured most adult plovers using noose mats or walk-in traps during incubation or when plovers were tending newly hatched chicks. We captured chicks at or near their nest, usually within 24 hours of hatch. We marked adult plovers with a USFWS metal leg band wrapped with colored tape and 3 plastic bands, yielding a unique combination for each adult. We marked newly hatched chicks with a metal band wrapped with colored tape. When we recaptured chicks in subsequent years, we determined their identity and origin based on the USFWS band number and marked them with a unique adult band combination. During surveys, observers walked slowly along beaches and gravel bars and scanned habitat with binoculars and a spotting scope. When we observed a plover in the field, we recorded the band combination and used plumage (Page et al. 1995) and reproductive behaviors to categorize plovers as males or females. Fecundity measures, including fate of nests and chicks, were reported elsewhere (Colwell et al. 2005; 2007*a*, *b*; 2009).

The population we studied was small, geographically remote, and confined to a few breeding locations that we monitored intensively (Colwell et al. 2009). Observers surveyed suitable breeding habitats at 7–10-day intervals from mid-May through July, even when we failed to detect plovers. As a result, we surveyed most unoccupied but suitable breeding habitats approximately 10 times during the 4-month breeding season. When we observed plovers at a site, we increased the frequency of visits to 1–4-day intervals and continued to visit the site until chicks fledged or the brood failed. We assumed that chicks were dead when we observed the male without them for several consecutive days and he showed no signs of parental behavior. In some cases, observers surveyed a site into early September. Multiple observers often worked in a coordinated effort to find nests and record band combinations. Finally, except for the initial year of banding (2000), each year we marked nearly all adult plovers associated with a nest and we banded all chicks (Colwell et al. 2009). As a result, we are confident that our estimates and modeling represent a population in which we marked virtually all breeding individuals by the end of each breeding season.

Data Summary and Analysis

We maintained a database that consisted of detailed histories of individually marked males and females that bred in the population. Each year, we recorded philopatry and adult site fidelity of plovers marked in a previous year and we identified immigrants of 2 types (Table 1). One group consisted of plovers that were banded by researchers working elsewhere along the Pacific coast and that bred for the first time in RU2. A second group was unmarked birds of unknown origin that we subsequently marked with unique band combinations. We used chi-square tests to examine annual variation in the proportion of returning breeders and immigrants. We used capture and resighting data (over a 1-month interval from 15 May to 15 Jun) from 7 breeding seasons (2001–2007) to estimate local apparent survival. There was minor variation in the temporal distribution of recaptures due to capture effort between the first 2 years and

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the last 3 years (Mullin 2006). We used Cormack–Jolly–Seber models for live-encounter data to estimate annual apparent survival (ϕ) and resighting probability (p) of this demographically open population of snowy plovers using Program MARK (White and Burnham 1999). We summarized banding and resighting data into encounter histories for individual plovers. We included juveniles in the survival analysis if they survived 28 days after hatch; survival of chicks was reported elsewhere (Colwell et al. 2007*a*). We modeled juvenile and adult survival jointly and included effects of sex (ad only; we could not sex fledglings in the field) and annual variation (yr-specific and as linear and quadratic trends across years). Sandercock et al. (2005) reported differences in survival among age classes of the Kentish plover and studies of closely related plover species often find that age and year are important predictors of annual survival (Dinsmore 2008, Roche et al. 2008). For adults the starting global model was $\phi_{age\times sex(ad\ only)\times t}$, $p_{sex\times t}$, which allows for a sex by time interaction for adults and time only for juveniles and sex by time interaction for capture probability independent of age class. We constructed reduced-parameter models for adults and juveniles where we constrained the effects of time or sex or both.

We used Program RELEASE (Burnham et al. 1987) to assess model fit by pooling the results of tests 2 and 3, which is a commonly used goodness-of-fit test for Cormack–Jolly–Seber survival analyses (Dinsmore et al. 2003). We also checked the data for over-dispersion (Burnham and Anderson 2002) and estimated a variance inflation factor ($\hat{c}$) using the median $\hat{c}$ procedure in MARK. We used Program U-CARE (v2.02, <ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR/>, accessed 10 Jan 2005) to run additional goodness-of-fit tests to check for behavioral responses to marking and transience in the encounter histories (Mullin 2006), using procedures outlined in Choquet et al. (2003). Estimates of median $\hat{c}$ in Program MARK were slightly <1 for both age classes, so we did not adjust $\hat{c}$ in MARK (Cooch and White 2009). We used Akaike's Information Criterion, adjusted for small samples (AIC_c), to select among competing models (Burnham and Anderson 2002). We ranked models by ΔAIC_c values, included models with $\Delta AIC_c \leq 3$, and used normalized Akaike weights (w_i) and ratios of Akaike weights (w_i/w_j) to determine relative support for a given model. We evaluated the best model as the one with the greatest weight (w_i). We report model-averaged estimates of apparent survival and capture probability ($\pm$SE) to account for model-selection uncertainty (Burnham and Anderson 2002).

In a separate analysis, we used Program MARK to estimate realized population growth rate using Pradel models (Pradel 1996). This analysis uses the same encounter histories (birds marked as adults and those marked as juveniles and subsequently resighted as adults in the following year) as the Cormack–Jolly–Seber model. However, it looks backward in time using the concept of seniority to estimate population growth rate. Specifically, the Pradel model uses a parameter (γ) defined as the probability that an individual alive and in the population at time i was also alive and in the population at time $i - 1$. The realized growth rate is the observed rate of change of the adult age class between successive years, which we estimated in Program MARK as the following:

$$\lambda_t = \phi_t / \gamma_{t+1}$$

where λ = the population growth rate, and ϕ_t and γ_t represent forward and backward probabilities of survival and seniority, respectively. Here, we retained the same model structure for apparent survival and capture probability of adults that we obtained in the Cormack–Jolly–Seber analysis (see above). All key assumptions of Pradel modeling were met including equal capture probability between banded and unbanded birds and retention of a consistent study area.

To understand the contribution of immigration to population growth, we estimated λ in 2 additional ways. First, we algebraically calculated λ from our estimates of adult and juvenile survival (see above) combined with annual productivity of the population derived from the reproductive histories of plovers. We determined the algebraic estimate (annual growth rate) with the following equation:

$$\lambda = b\phi_{juveniles} + \phi_{adults}$$

where ϕ_{adults} = apparent adult survival estimated in Program MARK, $\phi_{juveniles}$ = apparent juvenile survival estimated in Program MARK, and b = fecundity (F fledglings/breeding F per yr) estimates for this population. We assumed an equal sex ratio and that fecundity was similar across age classes. We also estimated λ using the ratio of consecutive annual counts (n_{t+1}/n_t) of breeding plovers in the study area. Finally, we evaluated source–sink threshold for the population and determined the amount of recruitment required to yield a stable population without immigration (Ricklefs 1973, Trine 1998) as the following:

$$\text{Source} - \text{sink threshold} = 2(\text{ad mortality})/(1 - \text{juv mortality}).$$

If recruitment is below the threshold, the population is a sink, whereas greater recruitment indicates a source.

RESULTS

We captured and marked 287 plovers during the first 7 years of the study, including 182 fledged chicks and 105 individuals first marked as adults. The proportion of site-faithful adults, philopatric yearlings, and immigrants in the population varied annually ($\chi^2 = 23.3$, df = 10, $P = 0.01$), although the total number of birds varied little in the first 6 years and sex ratio was stable (Table 1). The average number of immigrants in the population ($\bar{x} = 16 \pm 8$) exceeded the number of yearlings ($\bar{x} = 9 \pm 3$) returning to breed locally.

The global model of apparent survival was a good fit to the data ($\chi^2_{13} = 11.30$, $P = 0.67$) with no evidence of lack of fit detected by goodness-of-fit tests (Program U-CARE; $P = 0.89$). The best model included a sex difference in survival (Table 2); in this model, male survival was greater than female survival ($\hat{\beta}_M = 0.48$, 95% CI = -0.03 to 0.93). Model-averaged estimates of apparent survival were greater

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Table 2. Competing Cormack–Jolly–Seber models we used to estimate apparent survival (ϕ) and recapture rates (p) for adult and juvenile snowy plovers, Humboldt County, California, USA, 2001–2007. Models in the set allow survival and recapture rates to vary across years and in a linear (T) and quadratic (TT) manner.

Model structure				Model statistics			
Ad ϕ	Juv ϕ	Ad p	Juv p	ΔAIC_c[a]	w_i	K	Deviance
Sex + TT	Constant	T	Constant	0.00	0.25	8	326.61
Sex + TT	Constant	Sex	Constant	0.01	0.25	8	326.62
Sex + T	Constant	Sex	Constant	0.13	0.24	7	328.81
Sex + TT	Constant	Sex + T	Constant	2.07	0.09	9	326.61
Sex + yr	Constant	T	Constant	2.77	0.06	11	323.13
Sex + yr	Constant	Sex	Constant	2.78	0.06	11	323.14
Constant	Constant	Constant	Constant	8.54	0.00	4	343.36

[a] Akaike's Information Criterion for small sample sizes (AIC_c) for the best model was 717.90. We show only models with ΔAIC_c values <4, except for a model with constant age-specific effects on each parameter (shown for comparison). w_i = Akaike wt. K = no. of parameters.

for males than females (Table 3). The 3 top models also included annual variation in survival, with a quadratic trend across years receiving slightly more support than a model with a linear trend ($\Delta AIC_c = 0.13$). There was weak evidence for differences in capture probability as explained by a linear trend across years ($\hat{\beta}_T = 0.03$, 95% CI = −0.66 to 0.72) or by sex ($\hat{\beta}_M = -0.05$, 95% CI = −1.87 to 1.78), but neither was a strong effect. All competitive models suggested that juvenile survival and capture probability were constant across years (Table 2). Consequently, model-averaged estimates of juvenile survival were the same (ϕ = 0.40 ± 0.06) across years.

To derive estimates of population growth rate, we used a model with the additive effects of sex and a quadratic time trend across years on apparent survival and a linear time trend across years on capture probability. The best estimate of growth rate for the breeding adult population based on encounter histories (Pradel model) was λ = 0.92 (± 0.11). An average estimate derived from consecutive annual censuses (0.96 ± 0.26) was slightly higher. Both these estimates were substantially greater than estimates of λ based on fecundity and survival estimates (Table 4). Evaluation of source–sink threshold using average survival estimates of adult males and juveniles indicates that ≥2.7 fledglings per adult would be required for a stable population without immigration.

DISCUSSION

Apparent Survival

Our estimates of adult survival were low compared with other studies of plovers (Sandercock 2003). Stenzel et al. (2007) estimated true survival at 0.69 for adult snowy plovers in a partially migratory population in central coastal California, approximately 400 km south of our study area and connected via dispersal to our population (Colwell et al. 2007*b*, Stenzel et al. 2007). Apparent adult survival of Kentish plovers in Turkey (0.64; Sandercock et al. 2005) and the Netherlands (M: 0.65; F: 0.61; Foppen et al. 2006) was slightly higher than the population we studied. However, our estimate of apparent adult survival was similar to other recently published accounts. Paton and Edwards (1996) reported comparable survival estimates (M: 0.58; F: 0.51) for a migratory population of snowy plovers breeding around the Great Salt Lake, Utah. A migratory population of semipalmated plovers (*Charadrius semipalmatus*) breeding in the subarctic was lower (M: 0.60; F: 0.41, Flynn et al. 1999). Apparent survival of adult ringed plovers (*Charadrius hiaticula*; M and F combined) averaged 0.74 over 3 years. Atlantic Coast and Great Plains populations of piping plover averaged 0.70 and 0.74, respectively (Larson et al. 2000, Cohen et al. 2006).

Sex differences in apparent survival, a finding reported by others (see Sandercock 2003), may be attributed to greater dispersal of females (Stenzel et al. 1994, 2007). Because of a long breeding season (approx. 120 days) and the capability of breeding successfully up to 3 times in a year (Page et al. 1995), female snowy plovers often disperse within a year, occasionally moving several hundred kilometers between breeding sites (Stenzel et al. 1994, 2007; Colwell et al. 2007*b*). With the capability of breeding at multiple locations, females may select higher quality habitats elsewhere and not return to those of lower quality. Compared with most other studies of shorebirds (Sandercock 2003), slightly lower adult survival estimates may stem from permanent emigration of failed breeders from our study area, which may be related to frequent reproductive failure and the tendency for failed breeders to disperse widely along the Pacific coast (Stenzel et al. 1994, Colwell et al. 2007*b*).

Although apparent survival differed between the sexes, there was no evidence for a male-biased sex ratio in the local breeding population (Table 1). Fewer returning females were balanced with a female-biased immigration rate. This corroborates findings from elsewhere along the Pacific coast showing greater female dispersal (Stenzel et al. 1994, 2007). Other studies, however, reported male-biased sex ratios.

Table 3. Model-averaged estimates of annual apparent survival (ϕ) and capture probability (p) for snowy plovers, Humboldt County, California, USA, 2001–2007.

	M (n = 73)				F (n = 91)			
	ϕ		p		ϕ		p	
Yr	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
2001–2002	0.70	0.07	0.94	0.04	0.59	0.07	0.94	0.04
2002–2003	0.71	0.05	0.94	0.03	0.61	0.06	0.94	0.04
2003–2004	0.66	0.06	0.94	0.03	0.55	0.06	0.95	0.04
2004–2005	0.63	0.06	0.94	0.04	0.51	0.06	0.94	0.04
2005–2006	0.55	0.05	0.95	0.04	0.43	0.06	0.95	0.04
2006–2007	0.43	0.11	0.94	0.09	0.33	0.13	0.94	0.09
$\bar{x}$	0.61	0.11	0.94	0.004	0.50	0.11	0.93	0.01

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Table 4. Estimates of population growth (λ) for snowy plovers breeding in Humboldt County, California, USA, 2001–2007, based on consecutive annual counts, model-averaged estimates from Pradel models, and algebraic calculations based on survival and productivity estimates.

		Pradel models[a]		Algebraic estimate[b]	
Yr	Consecutive yr counts	$\bar{x}$	SE	ϕ_M	ϕ_F
2001–2002	1.03	1.00	0.12	0.95	0.84
2002–2003	0.97	0.98	0.10	0.83	0.73
2003–2004	1.34	1.01	0.11	0.82	0.71
2004–2005	0.80	1.00	0.11	0.80	0.68
2005–2006	0.89	0.92	0.11	0.68	0.56
2006–2007	0.54	0.58	0.10	0.53	0.43
$\bar{x}$ ± SE	0.96 ± 0.26	0.92	0.11	0.77 ± 0.14	0.66 ± 0.14

[a] Pradel model structure: $\phi_{age\times sex(ad\ only)\times t}$, $p_{sex\times t}$.
[b] We based algebraic estimates on annual data on the average no. of young fledged per M.

Sandercock et al. (2005) found a male-biased sex ratio in Kentish plover in Turkey, which they attributed to sex differences in encounter rates. Previous studies observed differences in encounter rates for snowy plover ($p_M = 0.68$ and $p_F = 0.52$; Paton 1994) and Kentish plover ($p_M = 0.84$ and $p_F = 0.74$; Sandercock et al. 2005). We did not observe differences in encounter rates, which suggests that there was a nearly equal annual sex ratio.

Estimated survival for plovers during their first year (0.40) was lower than that of adults (M: 0.61; F: 0.50), which is typical of many shorebird species (Evans and Pienkowski 1984, Sandercock 2003). Our estimate of juvenile apparent survival was low but overlapped those reported for other populations of snowy plover along the Pacific coast, including southern (0.42 ± 0.16; USFWS 2007) and central coastal California (0.46 ± 0.12; Stenzel et al. 2007) and Oregon, USA (0.44 ± 0.65; USFWS 2007). Additionally, return rates of yearling plovers in Humboldt County were lower (approx. 26%) than in these other areas (e.g., 46% in OR; Lauten et al. 2006), which suggests that young plovers in coastal northern California may experience higher mortality or disperse more often compared with plovers elsewhere along the Pacific coast. Lower survival of plovers in their first year may be the result of 2 factors: age-related differences in mortality and greater natal dispersal. Support for the effect of dispersal comes from higher estimates of survival owing to inclusion of dispersed juveniles from the entire Pacific coast as reported by Stenzel et al. (2007). However, juvenile shorebirds suffer greater mortality than adults (Evans and Pienkowski 1984), which is thought to be linked to their inexperience with predation, environmental conditions, and locating food sources (Page et al. 1983, Kus et al. 1984).

Apparent survival was considerably lower in the last year of study (0.44 and 0.38 for M and F, respectively), which resulted from 2 episodes of mortality. First, ≥8 adults disappeared during a 3-week interval of the 2006 breeding season when their nests were protected by a predator exclosure cage used to reduce egg predation (Hardy and Colwell 2008). We suspect that a raptor depredated these plovers near the exclosures, a finding reported for other species of shorebird (Isaksson et al. 2007). Second, approximately 50% of marked adults disappeared from a wintering flock (approx. 45 birds) after an unusually cold January (2007). Several of these birds were permanent residents that had not left the study area for several consecutive years, suggesting that these individuals had died.

Population Growth

Separate estimates of λ produced contradictory results regarding local population growth. Estimates derived from Pradel models (0.92 ± 0.11) and ratios based on counts of breeding plovers in consecutive years (0.96 ± 0.26) suggested that the population was nearly stable. By contrast, algebraic calculations of λ based on estimates of survival and observed productivity showed a declining population (F: 0.66 ± 0.14; M: 0.77 ± 0.14). These latter estimates, however, are influenced by the use of apparent survival estimates, which fail to account for permanent emigration. Nevertheless, when we included higher survival estimates ($\phi_{ad} = 0.75$, $\phi_{juv} = 0.45$; USFWS 2007) in the Pradel model, the population breeding in Humboldt County would still be expected to decline. Our estimate was lower than that for the Monterey, California, population before ($\lambda = 0.89$) and after ($\lambda = 1.07$) lethal predator control (Stenzel et al. 2007), suggesting that management actions need to address the low productivity of plovers in our study area. Low productivity of plovers breeding in Humboldt County is associated with high predation rates of eggs and chicks (Colwell et al. 2007*a*, 2009). Our findings also highlight that low survival may compromise management actions directed at recovering the population solely through efforts directed at increasing productivity.

It was not possible to separate immigration from local recruitment in the Pradel models. Therefore, the population growth rates estimated in Program MARK included all sources (local recruitment and true immigration) of new birds entering the population. Calculating population growth algebraically allowed for the separation of immigration and juvenile recruitment, providing a quantitative value for immigration. We justified the use of this equation because there was no evidence for an unequal sex ratio in either the population (Table 1) or in resighting probability.

Except for a sharp decrease in 2007, the number of plovers breeding in the Humboldt County population varied little over time; there were, however, interesting changes in the composition of the population. Immigration became increasingly important in the population. Our knowledge

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of the origin of the immigrants is limited because of the many unmarked individuals. However, some immigrants were marked at other sites along the Pacific coast (20% of total immigrant birds, 12 of 23 from OR). Over the 8 years, the number of marked immigrants from Oregon and Monterey increased (Colwell et al. 2009). Given that the number of breeding adults in the Humboldt County population was stable, we conclude that immigration, rather than recruitment of locally hatched plovers, maintained the population, as evidenced by consistently low and declining productivity for the population (Colwell et al. 2009).

Source–sink threshold equations are used to determine the amount of recruitment that would be required to provide a stable population without immigration (Ricklefs 1973, Trine 1998). Even with the greatest output of fledglings observed in our study area (1.8/ad M; Colwell et al. 2009), the minimum recruitment of young will not be met. Thus, our data suggest that the Humboldt County population of western snowy plovers is a sink population, although plovers that breed in gravel bar habitats consistently have high reproductive success (Colwell et al. 2010).

MANAGEMENT IMPLICATIONS

For threatened taxa such as the Pacific coast population of the snowy plover, projecting persistence over long periods of time is difficult due to uncertainties in environmental policies and continued changes in factors that limit the population (e.g., predator populations, human disturbance, and habitat degradation). Our data highlight that management locally and elsewhere within the range of the listed population segment is critical to recovering the population. For instance, a proposal (4[d] rule) under the Endangered Species Act (United States Department of the Interior 2006) would have provided less protection in counties such as Monterey County, California, where plover populations surpassed local recovery objectives. But, it is this very population that provides immigrants that partly sustain the Humboldt County population. Consequently, loosening regulations elsewhere in the species' range where habitat quality is high and plovers are productive will have negative consequences for sink populations. The low productivity of plovers in our study area (Colwell et al. 2009) contrasts with high productivity in Oregon (D. J. Lauten, OR Department of Fish and Wildlife, unpublished report) and Monterey, California (Neuman et al. 2004), where lethal and nonlethal predator control is practiced. Because it is difficult to alter overwinter survival of adults through management actions directed at predators and food, it may be necessary to expand efforts to increase productivity throughout the range of the listed population segment by increasing efforts to boost productivity by enhancing habitats, managing predators, and restricting human access to plover breeding areas.

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LITERATURE CITED

Benton, T. G., and A. Grant. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. Trends in Ecology and Evolution 14:467–471.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph 5, Bethesda, Maryland, USA.

Choquet, R., A. M. Reboulet, R. Pradel, O. Gimenez, and J. D. Lebreton. 2003. User's manual for U-CARE. CEFE/CNRS, Montpellier, France.

Cohen, J. B., J. D. Fraser, and D. H. Caitlin. 2006. Survival and site fidelity of piping plovers on Long Island, New York. Journal of Field Ornithology 77:409–417.

Colwell, M. A., N. S. Burrell, M. A. Hardy, K. Kayano, J. J. Muir, W. J. Pearson, S. A. Peterson, and K. A. Sesser. 2010. Arrival times, laying dates and reproductive success of snowy plovers in two habitats in coastal northern California. Journal of Field Ornithology 81:in press.

Colwell, M. A., N. S. Burrell, M. A. Hardy, K. Kayano, J. J. Muir, W. J. Pearson, S. A. Peterson, K. A. Sesser, and R. R. Thiem. 2009. Final Report: 2009 snowy plover breeding in coastal northern California, Recovery Unit 2. Submitted to MRB Research, Inc. <http://www.fws.gov/arcata/es/birds/WSP/plover.html>. Accessed 23 Aug 2010.

Colwell, M. A., S. J. Hurley, J. N. Hall, and S. J. Dinsmore. 2007*a*. Age-related survival and behavior of snowy plover chicks. Condor 109:638–647.

Colwell, M. A., S. E. McAllister, C. B. Millett, A. N. Transou, S. M. Mullin, and R. R. LeValley. 2007*b*. Philopatry and natal dispersal of western snowy plovers. Wilson Journal of Ornithology 119:378–385.

Colwell, M. A., C. B. Millett, J. J. Meyer, J. N. Hall, S. J. Hurley, S. E. McAllister, A. N. Transou, and R. R. LeValley. 2005. Snowy plover reproductive success in beach and river habitats. Journal of Field Ornithology 76:373–382.

Cooch, E., and G. C. White. 2009. Program MARK—a gentle introduction. Fifth edition. <http://www.phidot.org/software/mark/docs/book/>. Accessed 7 Feb 2009.

Dinsmore, S. J. 2008. Influence of drought on annual survival of the mountain plover in Montana. Condor 110:45–54.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2003. Annual survival and population estimates of mountain plovers in southern Phillips County, Montana. Ecological Applications 13:1013–1026.

Evans, P. R., and M. W. Pienkowski. 1984. Population dynamics of shorebirds. Pages 83–123 *in* J. Burger and B. L. Olla, editors. Behaviour of marine animals, current perspectives in research. Plenum Press, New York, New York, USA.

Flynn, L., E. Nol, and Y. Zharikov. 1999. Philopatry, nest-site tenacity, and mate fidelity of semipalmated plovers. Journal of Avian Biology 30:47–55.

Foppen, R. P. B., F. A. Majoor, F. J. Willems, P. L. Meininger, G. C. Van Houwelingen, and P. A. Wolf. 2006. Survival and emigration rates in

19372817, 2010, 8, Downloaded from https://wildlife.onlinelibrary.wiley.com/doi/10.2193/2009-503 by Iowa State University Library, Wiley Online Library on [11/03/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Kentish *Charadrius alexandrinus* and ringed plovers *Ch. hiaticula* in the Delta area, SW-Netherlands. Ardea 94:159–173.
Hardy, M. A., and M. A. Colwell. 2008. The impact of nest exclosures on snowy plover nesting success: a seven-year study. Wader Study Group Bulletin 115:161–166.
Isaksson, D., J. Wallander, and M. Larsson. 2007. Managing predation on ground-nesting birds: the effectiveness of nest exclosures. Biological Conservation 136:136–142.
Kus, B. E., P. Ashman, G. W. Page, and L. E. Stenzel. 1984. Age-related mortality in a wintering population of dunlin. Auk 101:69–73.
Lafferty, K. D., D. Goodman, and C. P. Sandoval. 2006. Restoration of breeding by snowy plovers following protection from disturbance. Biodiversity and Conservation 15:2217–1130.
Larson, M. A., M. R. Ryan, and R. K. Murphy. 2002. Population viability of piping plovers: effects of predator exclusion. Journal of Wildlife Management 66:361–371.
Larson, M. A., M. R. Ryan, and B. G. Root. 2000. Piping plover survival in the Great Plains: an updated analysis. Journal of Field Ornithology 71:721–729.
Mullin, S. M. 2006. Apparent survival and population growth of western snowy plovers (*Charadrius alexandrinus nivosus*) in Humboldt County, CA. Thesis, Humboldt State University, Arcata, California, USA.
Neuman, K. K, G. W. Page, L. E. Stenzel, J. C. Warriner, and J. S. Warriner. 2004. Effect of mammalian predator management on snowy plover breeding success. Waterbirds 27:257–263.
Page, G. W., L. E. Stenzel, W. D. Shuford, and C. R. Bruce. 1991. Distribution and abundance of the snowy plover on its western North American breeding grounds. Journal of Field Ornithology 62:245–255.
Page, G. W., L. E. Stenzel, D. W. Winkler, and C. W. Swarth. 1983. Spacing out at Mono Lake: breeding success, nest density, and predation in the snowy plover. Auk 100:13–24.
Page, G. W., J. S. Warriner, J. C. Warriner, and P. W. C. Paton. 1995. Snowy plover (*Charadrius alexandrinus*). Account 154 *in* A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.
Paton, P. W. C. 1994. Survival estimates for snowy plovers breeding at Great Salt Lake, Utah. Condor 96:1106–1109.
Paton, P. W. C., and T. C. Edwards, Jr. 1996. Factors affecting interannual movements of snowy plovers. Auk 113:534–543.
Plissner, J. H., and S. M. Haig. 2000. Viability of piping plover *Charadrius melodus* metapopulations. Biological Conservation 92:163–173.
Pradel, R. 1996. Utilization of capture–mark–recapture for the study of recruitment and population growth rate. Biometrics 52:703–709.
Ricklefs, R. E. 1973. Fecundity, mortality, and avian demography. Pages 366–434 *in* D. S. Farnon, editor. Breeding biology of birds. National Academy of Sciences, Washington, D.C., USA.
Roche, E. A., F. J. Cuthbert, and T. W. Arnold. 2008. Relative fitness of wild and captive-reared piping plovers: does egg salvage contribute to recovery of the endangered Great Lakes population? Biological Conservation 141:3079–3088.
Ruhlen, T. D., S. Abbott, L. E. Stenzel, and G. W. Page. 2003. Evidence that human disturbance reduces snowy plover chick survival. Journal of Field Ornithology 74:300–304.
Sandercock, B. K. 2003. Estimation of survival rates for wader populations: a review of mark–recapture methods. Wader Study Group Bulletin 100:163–173.
Sandercock, B. K., T. Székely, and A. Kosztolányi. 2005. The effects of age and sex on the apparent survival of Kentish plovers breeding in southern Turkey. Condor 107:582–595.
Stenzel, L. E., G. W. Page, J. C. Warriner, J. S. Warriner, D. E George, C. R. Eyster, B. A. Ramer, and K. K. Neuman. 2007. Survival and natal dispersal of juvenile snowy plovers in central coastal California. Auk 124:1023–1036.
Stenzel, L. E., J. C. Warriner, J. S. Warriner, K. S. Wilson, F. C. Bidstrup, and G. W. Page. 1994. Long-distance breeding dispersal of snowy plovers in western North America. Journal of Animal Ecology 63:887–902.
Trine, C. L. 1998. Wood thrush population sinks and implications for the scale of regional conservation strategies. Conservation Biology 12:576–585.
United States Department of the Interior. 2006. Endangered and threatened wildlife and plants: proposed special rule pursuant to Section 4(d) of the Endangered Species Act for the Pacific coast distinct population of the Western Snowy Plover. Federal Register 58:12864–20636.
United States Fish and Wildlife Service [USFWS]. 1993. Threatened status for the Pacific coast population of the western snowy plover. Federal Register 58:12864–12874.
United States Fish and Wildlife Service [USFWS]. 2007. Western snowy plover (*Charadrius alexandrinus nivosus*) Pacific coast population recovery plan. USFWS, Portland, Oregon, USA.
Warriner, J. S., J. C. Warriner, G. W. Page, and L. E. Stenzel. 1986. Mating system and reproductive success of a small population of polygamous Snowy Plovers. Wilson Bulletin 98:15–37.
White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from population of marked animals. Bird Study 46:120–138.

Associate Editor: Arnold.

19372817, 2010, 8, Downloaded from https://wildlife.onlinelibrary.wiley.com/doi/10.2193/2009-503 by Iowa State University Library, Wiley Online Library on [11/03/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License