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Success of captive-rearing for a threatened shorebird

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ABSTRACT: Captive-breeding and -rearing programs have been widely used for the conservation and recovery of imperiled species, and the success of such programs should be rigorously evaluated. In this study, we assessed the success of captive-rearing for a threatened shorebird, the snowy plover *Charadrius nivosus*, by comparing the survival and reproductive success of captive-reared and wild-reared individuals on the central California coast from 2001 to 2010. We used mark-recapture analysis, implemented in the program MARK, to estimate apparent annual survival (φ) and encounter occasion detection probability (p) from capture and sighting data of marked plovers. We compared 3 measures of reproductive success (hatch rate, fledge rate and juveniles fledged per year) using stratified randomization tests based on individual breeding histories where captive- and wild-reared plovers were matched for age, sex and year. Captive- and wild-reared snowy plovers had similar apparent survival and reproductive rates and paired with mates of similar age in their first breeding year. The only exception was that captive males after their first breeding year had lower fledging rates than males from the overall population, but this did not affect the annual productivity rate. We conclude that releasing captive-reared individuals is a valuable part of ongoing efforts to restore the snowy plover population in California, and is also useful in cases where plover nests may need to be salvaged to protect them from oil contamination or other catastrophic events.

KEY WORDS: Shorebird · Snowy plover · Captive-rearing · Survival · Reproduction

INTRODUCTION

Captive-breeding, captive-rearing and reintroduction programs have been used extensively to support conservation efforts for a wide array of vertebrate taxa (Cade & Temple 1995, Seddon et al. 2007), but they are cost-, time- and infrastructure-intensive and often fail to result in the establishment of viable wild populations (Snyder et al. 1996), especially when key habitat-related threats are left unmitigated (Griffith et al. 1989, Lovegrove 1996). It is essential to determine the effectiveness of captive-rearing programs if effort is to be spent on them for the recovery of rare species. Assessing the post-release survival and reproductive parameters of captive-reared (hereafter captive) versus wild-reared (hereafter wild) individuals is an important measure of the effectiveness of captive-rearing programs (Scott & Carpenter 1987, Griffith et al. 1989).

In North America, shorebirds are an increasingly imperiled group of taxa, with many species in population decline (Howe et al. 1989, Page & Gill 1994,

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Bart et al. 2007). Two plover species are listed under the United States Endangered Species Act, the piping plover *Charadrius melodus* and the snowy plover *Charadrius nivosus*; *C. nivosus* was formerly treated as a conspecific of *C. alexandrinus* (Chesser et al. 2011), but the World Conservation Union (IUCN 2012) has not yet accepted this change or designated status for *C. nivosus*. Both the piping and snowy plover have recovery plans recommending captive-rearing programs to support conservation efforts (USFWS 2003, 2007). Plovers are ideal candidates for captive-rearing programs because their offspring develop rapidly and have limited need of parental care.

Captive-rearing programs for plovers have largely been ancillary to *in situ* conservation management or used on an emergency basis. Captive-rearing methods developed with killdeer *Charadrius vociferus* chicks (Powell & Cuthbert 1993, Powell et al. 1997) were applied to the Great Lakes population of the piping plover, but a subsequent analysis of this program found that the captive plovers had significantly lower apparent survival rates and breeding success than wild plovers (Roche et al. 2008). Similarly, Goossen et al. (2011) reported significantly lower return rates for captive versus wild piping plovers in Saskatchewan, Canada. The only study examining the success of captive-rearing of snowy plovers found no differences in return rates or reproductive success between captive and wild plovers (Page et al. 1989). However, the study was small (n = 22 plovers released), and it followed only a single year-cohort for 1 breeding year, so it may have lacked power to rigorously compare wild and captive birds. Here, we conducted a follow-up to the captive-rearing study conducted by Quinn (1989) by comparing survival and reproductive success of captive versus wild snowy plovers from central California over a subsequent and much longer (n = 10 yr) time period. We also discuss the implications of our findings for the snowy plover and other imperiled plover species.

MATERIALS AND METHODS

Study site

The study was conducted from 2001 to 2010 on the central California coast, in an area including 40 km of contiguous sandy beaches along Monterey Bay, in Monterey and Santa Cruz counties. Snowy-plover *Charadrius nivosus* (hereafter plover) nesting was concentrated in sandy beach habitat that was backed by low, sparsely vegetated foredunes and at retired salt ponds on the north shore of Elkhorn Slough. See Stenzel et al. (2007) for a more detailed description and map.

Captive-rearing program

Between 2000 and 2009, a small number of abandoned eggs (n = 52) and chicks (n = 22) from the Monterey Bay population were salvaged and reared at the Monterey Bay Aquarium. Eggs and chicks were salvaged only if biologists determined that they had been abandoned by attending parents or were picked up off the beach by members of the general public. Once in captivity, eggs aged 1 to 25 d were incubated in a Brinsea Octagon 20 w/Autoturn cradle (Brinsea Products) at 37.6 to 37.8°C, with a relative humidity of 40 to 50%. From an egg-age of 26 d to hatch, the relative humidity was raised to 65% and recorded vocalizations of adult snowy plovers were played to the eggs. After hatching, chicks were held indoors in 1.5 m long × 0.5 m wide × 0.5 m high holding tanks, with supplemental heat at 35°C in one corner. They were fed krill, mealworms, tubifex and fly larvae coated in Nekton-R powdered vitamin supplement for birds (Gunter Enderle), and powdered calcium carbonate. When chicks reached at least 10 d of age and a minimum weight of 13 g, they were placed into a 5.3 m long × 1.7 m wide × 3.3 m high outdoor flight cage where they remained until they reached an age of 35 d, weight of 30 g and wing chord of 100 mm, and were capable of flying. Captive chicks were reared with conspecifics (often broodmates), with conspecifics and an adult snowy plover, alone with an adult snowy plover, or with killdeer chicks. Forty-one captive chicks that reached the final body condition and flight benchmarks received unique 4-color leg band combinations before release into the wild on Monterey Bay (n = 39) or Half Moon Bay beaches (n = 2), where their subsequent survival and reproductive success was monitored. The majority (80%) were released after 1 July and before 30 September (range: first week of June to third week of October). This range of release dates was consistent with mid- to late-season fledging dates of wild plovers (Page et al. 2009), and fledge date has been determined to have no effect on first year survival (Stenzel et al. 2007). The release method was considered a 'hard' release; captive fledglings were released directly onto beaches where conspecifics were present, with no acclimatization to the environment prior to release. Captive fledglings were often observed in these flocks following release.

Demographic monitoring

We have intensively monitored demographic rates of snowy plovers in the Monterey Bay area since the late 1970s (Warriner et al. 1986, Neuman et al. 2004, Stenzel et al. 2007, 2011) by uniquely color-banding the majority of birds in the breeding population and monitoring their survival and breeding success (n > 1000 each for banded females and banded males, 1984 to 2010). We attempted to locate every nest and visited nesting areas as frequently as necessary to monitor the activities of breeding pairs and the status of their nests (usually 3 to 4 times per week, but at some locations as infrequently as once a week or as frequently as daily). A nesting attempt was defined as a clutch of eggs that was incubated until it hatched successfully or failed. Hatch dates were projected from egg-laying dates or from floating eggs found after clutch completion (Hays & LeCroy 1971). As the estimated hatch date approached, the estimate was refined by examining eggs for signs of imminent hatching. Newly hatched chicks were banded with a unique 3- or 4-color leg band combination. Broods were monitored by directly observing chicks or adult display behaviors throughout the chick-rearing period. Young birds seen at ≥28 d of age were considered fledged. Methods are described in greater detail in Warriner et al. (1986), Neuman et al. (2004) and Stenzel et al. (2007, 2011).

Statistical analysis

Survival

We compared annual survival of 41 captive snowy plovers released at Monterey Bay and nearby beaches with that of 205 uniquely banded, wild plovers that fledged on Monterey Bay beaches. To control for a potential effect of release date on subsequent survival, we selected 5 wild plovers at random from those that fledged from 5 d before to 5 d after the release of each of the 41 captive plovers. We had to extend the early limit by several days for 2 late-season releases in order to obtain an adequate sample of wild fledglings for comparison.

We used mark-recapture analysis, implemented in the program MARK (White & Burnham 1999), to estimate apparent annual survival (φ) and encounter occasion detection probability (*p*) from capture and sighting data of marked plovers. Apparent annual survival is a product of the probabilities of true annual survival and fidelity to the study area. Our encounter occasion was June through September. We constructed recapture-only encounter histories with 11 encounter occasions (11 yr) and specified 2 groups (rearing mode: wild- or captive-reared). We used a time-since-marking form of a Cormack-Jolly-Seber model, since hatching-year (Age 1 yr) survival is known to be lower than after-hatching-year (Age 2 yr and older, hereafter 2+ yr) survival for this population (Stenzel et al. 2007, 2011). Further, if captive-rearing were to lower survival of fledged young, we suspect that increased mortality would most likely occur in the first year. Consequently, our most general model included rearing mode (our variable of interest), and time (year) for apparent survival and time for detection, since inter-year variability in both survival and detection has been demonstrated to be important for this population (Stenzel et al. 2007). We used a logit link function and constructed our models with design matrices. Survival estimates for Age 1 yr in 2005, a year in which no captive plovers were released, were fixed at 0.

We used Akaike's Information Criterion (AIC) to select the most parsimonious models to estimate parameters (Burnham & Anderson 2002). AIC values provide a comparative measure of the fit of different models to a data set, penalizing for increased model complexity (or increased numbers of parameters). The fit of our most general model was tested with the bootstrap goodness-of-fit procedure implemented in the program MARK, and $\hat{c}$, an estimate of the over-dispersion of the data, was estimated using both the $\hat{c}$ and deviance methods. We used the larger of the 2 $\hat{c}$ estimates (1.083) to adjust our AIC model values and variance estimates. We compared the adjusted or quasi ($QAIC_c$) values, corrected for small sample size, for models and considered models whose $QAIC_c$ values differed by <2 from the best-supported model (that with the lowest $QAIC_c$ value) to be equally parsimonious with the best-supported model. We reduced our most general model by first simplifying the parameterization of *p*, then φ, removing the time effect, then the rearing mode effect, first on the Age 2+ yr cohort and then on the Age 1 yr cohort.

Reproduction

We compared 3 measures of reproductive success in the wild: (1) egg hatching rate (proportion of eggs that hatched), (2) chick fledging rate (proportion of chicks that survived to 28 d of age) and (3) juveniles fledged per year for 15 captive snowy plovers that entered the Monterey Bay breeding population with 213 wild snowy plovers from the same population using individual-based breeding histories. Because most plovers nested more than once a year, we first calculated annual arithmetic means for egg hatching rate and chick fledging rate and then averaged the values for all years. For juveniles fledged per year, the number of fledglings was summed over all nesting attempts for each year and then averaged by the number of years. Nests protected from predators by exclosures (Neuman et al. 2004) were excluded from analyses of hatch rate, but not from other analyses. Small sample sizes precluded comparisons of reproductive rates among chick groups reared with different methods.

To remove the effects of year and age on reproductive success, we selected wild plovers that exactly matched the age (in years) and breeding year distribution of the captive plovers and grouped them by sex so that for each captive plover, the number of matching wild plovers varied from 3 to 51. Cases of wild plovers nesting with captive plovers were excluded from the wild sample, as were cases of either wild or captive plovers nesting with plovers that had been oiled during the 'Cosco Busan' oil spill, which took place during the study period, because we did not want any possible oil-related deficiencies to affect the results. The one case of 2 captive plovers nesting together was not excluded because the tests were grouped by sex.

For each reproductive parameter, we used a 1-tailed, stratified random permutation test coded in MATLAB (MathWorks). In each case, we tested whether the value of interest was lower for captive birds than for wild and captive birds combined, with a null hypothesis of no difference. Data were grouped into categories corresponding to each captive bird; each category included data for 1 captive bird and all wild birds of corresponding sex, age and years in the breeding population. In 10 000 randomizations, 1 bird from each category was chosen without replacement, and the mean and standard deviation of the value of interest (egg hatching rate, chick fledging rate, or juveniles fledged per year) was calculated for this random sample. A distribution of mean random values from the combined captive and wild plover population was generated, and the mean value of interest for the captive population was considered to be significant if it was <0.05 (i.e. <500 out of 10 000) of the mean values for the combined population. In other words, does the observed mean value for the captive plovers differ from a random sample from the combined population? We estimated standard deviation of the random samples as the mean of the standard deviations calculated in each permutation. The same method was used to compare chick-fledging rate between captive and wild males for the Age 1 and Age 2+ yr age classes. We used a 1-tailed Fisher exact test to examine if the age distribution (either Age 1 or Age 2+ yr) of first mates chosen by Age 1 yr snowy plovers differed between captive (n = 6 males and 5 females, sexes pooled) and wild groups.

RESULTS

Survival

In our best-supported model, apparent survival of snowy plovers at Age 1 yr was constant and lower than that at Age 2+ yr, which was also constant. Our overall estimate of apparent survival from the top ranked model at Age 1 yr was 0.357 (SE = 0.032) and at Age 2+ yr was 0.684 (SE = 0.033). There was much less support for an effect of rearing mode on apparent survival (Table 1). Apparent survival was a function of rearing mode for both age classes in the second and third ranked models. In the second ranked model, with slightly more than a third the support of the top ranked model, the difference between captive and wild plover apparent survival rates for Age 1 yr birds paralleled those for Age 2+ yr birds. Age 1 yr apparent survival for wild plovers was 0.354 (SE = 0.034) and for captive plovers 0.369 (SE = 0.062); Age 2+ yr apparent survival for wild plovers was 0.682 (SE = 0.035) and for captive plovers 0.696 (SE = 0.057). In the third ranked model, with negligible support, the difference between captive

Table 1. *Charadrius nivosus*. Top 3 models for apparent annual survival of snowy plovers fledged or captive-reared and released on Monterey Bay beaches between 2000 and 2009, with $\hat{c}$ = 1.083. $QAIC_c$: quasi-Akaike's information criterion, corrected for small sample size; φ1: apparent survival of plovers of Age 1 yr; φ2+: apparent survival of plovers of Age 2 yr or older; *p*: encounter occasion detection probability; c: constant; r: rearing mode

Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	No. of parameters
{φ1(c) φ2+(c)} *p*(c)	608.06	0.00	0.66	3
{φ1(r) + φ2+(r)} *p*(c)	610.03	1.98	0.24	4
{φ1(r) × φ2+(r)} *p*(c)	612.07	4.01	0.09	5

and wild plover survival rates for Age 1 yr birds did not parallel those for Age 2+ yr birds, allowing the difference between wild and captive apparent survival rates to increase slightly for Age 1 yr plovers and to decrease slightly for Age 2+ yr plovers. Detection probability at 0.946 (SE = 0.019) was constant for the top 3 models.

Reproduction

Fifteen of the 41 captive snowy plovers returned and bred in the Monterey Bay area in the year following their release. Egg-hatching rate, chick-fledging rate and juveniles fledged per year were not significantly lower for captive female snowy plovers (Table 2). For males, there were no differences in hatching success or juveniles fledged per year, but captive males fledged a lower proportion of their chicks than males sampled from the overall population ($p = 0.04$; Table 2). Chick-fledging rates of first-year captive males were not lower ($p = 0.31$), but fledging rates of Age 2+ yr captive males were lower than for wild males ($p = 0.03$; Table 2). The age distribution of first mates did not differ between captive and wild plovers (Fisher Exact 1-tailed test, $p = 0.18$). Captive plovers that reached breeding age in this study successfully fledged 46 juveniles over the 10 yr study. Assuming a true juvenile survival rate of about 46% (Stenzel et al. 2007), the direct contribution of this captive-rearing program to the Pacific coast population over 10 yr was approximately 21 adult plovers, in addition to the original 15 captive birds that recruited into the breeding population. This does not include the additional indirect contribution of the offspring of the 21 returning captive plovers to the population.

DISCUSSION

The Monterey Bay captive-rearing program was initiated to test the usefulness of this technique to augment the productivity of coastal nesting snowy plovers in the region. After an initial assessment of the program found no differences between reproductive success of captive and wild plovers (Page et al. 1989), the program was continued as part of an ongoing conservation management plan. The follow-up assessment we present here provides further evidence that captive-rearing is a viable method to support conservation of the species in the region.

Survival

We did not find evidence that survival of captive snowy plovers was lower than survival of wild plovers. Captive animals may be especially vulnerable in the period immediately following release because they lack crucial behavioral skills such as predator avoidance (Lockwood et al. 2005). There is evidence that anti-predator behavior has both innate and learned components (McLean et al. 1999, Griffin et al. 2000, Galbraith et al. 2007, Saunders et al. 2013), and, consequently, pre-release predator recognition training can improve survival rates of captive-reared animals (van Heezik et al. 1999, White et al. 2005). In this study, captive plovers survived as well as wild plovers, even without the benefit of pre-release conditioning to commonly occurring avian predators, such as owls, hawks and falcons.

Captive animals may also have impaired foraging skills. Aikman (1999) noted that some recently reintroduced shore plovers *Thinornis novaeseelandiae* on Motuora Island, New Zealand, succumbed to starvation, and White et al. (2012) report that supple-

Table 2. *Charadrius nivosus*. Results of randomization tests for reproductive success of captive-reared snowy plovers relative to a control population on Monterey Bay beaches between 2001 and 2010. See 'Materials and methods' for details of matching. N: number of randomization tests; *: significant results at $p < 0.05$

Group	Parameter	Captive			Wild + Captive			p-value	No. of wild matched histories (range)
		Mean	SD	N	Mean	SD	N		
Females	Hatch rate	0.48	0.33	6	0.61	0.28	88	0.15	6–32
	Fledge rate	0.54	0.35	6	0.45	0.28	81	0.78	6–27
	Juveniles (yr^{-1})	1.46	1.35	6	1.61	1.05	89	0.39	6–32
Males	Hatch rate	0.68	0.28	9	0.64	0.28	139	0.66	3–51
	Fledge rate	0.22	0.18	9	0.38	0.30	117	0.04*	3–45
	Juveniles (yr^{-1})	0.84	0.90	9	1.11	0.87	140	0.15	3–51
Males by age	Fledge rate (Age 1 yr)	0.29	0.37	7	0.37	0.36	61	0.31	3–22
	Fledge rate (Age 2+ yr)	0.21	0.12	6	0.40	0.26	77	0.03*	3–45

mental feeding enhanced the survival of parrots in the period immediately following release. In the present study, the lack of difference in survival rate between captive and wild plovers suggests that foraging skills of recently released plovers were unimpaired. Furthermore, behavioral deficits from the rearing environment that impaired foraging efficiency or predator recognition should have been most evident in the first winter, and this was not the case. In fact, there was limited evidence from the second ranked model that apparent survival rates for the captive plovers were slightly higher than for the wild plovers. For the Age 1 yr survival interval, this result may have been due to a minor methodological bias: captive plovers were released at or after Age 35 d and after acquiring flight ability, whereas wild plovers were considered fledged at Age 28 d. Recently fledged plovers are more obvious due to their conspicuously unskilled flight, and avian predators may be adept at spotting this behavioral anomaly. If this is the case, the initial days of acquiring flight ability for wild plovers may be a period of elevated mortality due to extra vulnerability to predators. Although younger shorebirds may be more susceptible to predation (Kus et al. 1984), assessing age-related mortality in the period immediately following fledging is extremely difficult because juveniles rapidly disperse away from natal areas. Although we lack information on survival of wild plovers during this critical post-fledging period, any differential survival during this period should only affect the Year 1 apparent survival, and, in the second ranked model, captive plover apparent survival rates were still slightly greater than those of wild plovers in subsequent years. We have no hypotheses as to what might cause survival to be higher for captive than for wild plovers in subsequent years. However, apparent survival is the product of true survival and annual fidelity, and differences between the groups in their propensity to disperse away from natal areas could also be responsible for this result, particularly if captive plovers were less likely to venture away from the Monterey Bay area.

The apparent survival and detection rates we observed for both wild and captive snowy plovers were consistent with estimates obtained in other west coast studies of the species. Previously obtained true survival and site fidelity rate estimates from the larger Monterey Bay population were 0.46 for first-year survival and 0.77 for fidelity (Stenzel et al. 2007). The product of these rates (true survival × site fidelity) yields an Age 1 yr apparent survival of approximately 0.35 during the previous study at Monterey Bay. In northern California, Mullin et al. (2010) estimated apparent survival of first-year snowy plovers at 0.40. The estimates of Age 1 yr apparent survival in this study of 0.36 overall, 0.35 for wild plovers and 0.37 for captive plovers are well within the range of the previous estimates. Stenzel et al. (2011) estimated Age 2+ yr survival at 0.69 for females and 0.73 for males for the Monterey Bay area population. Fidelity of locally nesting birds of local natal origin was 1.0, except for females the year after first breeding, the fidelity of which was 0.95. Mullin et al. (2010) estimated Age 2+ yr apparent survival at 0.61 for males and at 0.50 for females, but many of these breeders were likely not of local origin. As immigrants, these breeders may have had lower site fidelity than the Monterey Bay area plovers, and lower fidelity would have reduced the apparent survival rate observed by Mullin et al. (2010), accounting for the difference between northern California and Monterey Bay. Similar to the comparison for Age 1 yr birds, the Age 2+ yr survival estimate of 0.68 in the present study was well within the range of previous estimates for the west coast populations.

Most published reports of the success of captive-rearing for shorebirds have centered on recovery efforts for the federally endangered piping plover. Goossen et al. (2011) report very low resighting rates for captive versus wild piping plovers on the breeding grounds in Saskatchewan (0.18 versus 0.52) and coastal Texas wintering grounds (0.09 versus 0.30). Roche et al. (2008) report an apparent Age 1 yr survival rate of 0.08 for captive piping plovers, which was significantly lower than that of wild plovers from the Great Lakes, but low site fidelity likely was an important factor in this very low apparent survival estimate. Thus, both studies reported much lower apparent survival or return rates for captive than for wild plovers, in contrast to our results for Pacific coast snowy plovers. There are key ecological and population characteristics that differ between piping and snowy plovers that may underlie the divergent results of captive-rearing efforts. Inland piping plover populations are highly migratory, travelling hundreds of kilometers, probably nonstop, from northern inland breeding areas to southern Atlantic and Gulf coast wintering areas (Elliott-Smith & Haig 2004). The Pacific coast snowy plover population is partially resident year round and partially migratory (Warriner et al. 1986, Page et al. 2009), and coastal sandy beach habitat is mostly contiguous, allowing migrating birds to stop over at many sites (Page et al. 1986, 2009). The snowy plover population at our release site was fairly large (mean = 337 breeding adults, SD = 58, n = 10 yr;

Point Blue unpubl. data), and newly reared plovers were released onto beaches where many conspecifics were present and likely to remain through winter. This provided ample opportunity for newly released plovers to acquire information about the release location, and they also had the option of migrating or remaining in the area through winter. In contrast, the Great Lakes piping plover breeding population is small (<100 individuals; Haig et al. 2005), and a lower number of conspecifics present at releases may limit the ability of newly released plovers to acquire information prior to undertaking an energetically expensive and obligatory post-breeding migration.

When compared with inland captive piping plovers, recently released Pacific coast snowy plovers may have a greater opportunity to acquire behavioral skills that facilitate optimal habitat selection, foraging and predator avoidance. Pacific coast snowy plovers are probably less constrained by the timing and physiological costs of migration; they move over smaller distances, have access to contiguous habitat, and migration is not obligatory. Cumulatively, these factors may enhance survival of captive Pacific coast snowy plovers relative to inland piping plovers in the first year after release.

Recruitment

The establishment of viable populations can be hampered when captive-reared individuals fail to recruit into the breeding population (Maxwell & Jamieson 1997, Lockwood et al. 2005, Brown et al. 2006). For highly social shorebird species, presence of conspecifics at release appears to strongly influence recruitment of captive individuals into wild populations. Captive-bred black stilts *Himantopus novaezelandiae* were more likely to remain at their release site when more conspecifics were present at release (van Heezik et al. 2009). Retention rates of captive shore plovers released on Motuora Island in New Zealand were low because many individuals dispersed back to the mainland (Aikman 1999), possibly because there was no existing plover population on the island. In the present study, 88% of captive snowy plovers that survived their first winter recruited into the breeding population at the Monterey Bay release site. This recruitment rate is markedly greater than estimates of 59 and 74% for male and female plovers, respectively, from the larger Monterey Bay population (Stenzel et al. 2007). We believe this enhanced recruitment rate was due in part to the presence of large numbers of wild plovers in the area at release.

Reproduction

Even when recruitment rates are adequate, low reproductive success of captive-reared animals may be related to behavioral deficits from the captive-rearing environment. Roche et al. (2008) posited that a deficit in behaviorally transmitted skills may cause lower reproductive success of captive piping plovers. In the present study, the lower proportion of chicks fledged by Age 2+ yr captive males may have been related to behavioral deficits from the captive environment. If males reared as chicks in captivity had less opportunity to learn behaviorally transmitted skills, such as predator avoidance and selection of optimal habitat, this deficit might be reflected in lower reproductive success. Male snowy plovers typically rear chicks (Warriner et al. 1986, Page et al. 2009), so a failure to learn these aforementioned skills would most likely be reflected in male fledging rates. It is somewhat surprising that a difference in fledge rates between captive and wild males is not apparent in the first year but becomes apparent in the second breeding year, possibly because all first-year males are learning a difficult and novel task, and the demands of this novel task may have swamped any differences between groups. Nonetheless, because captive males hatched a slightly greater proportion of chicks than wild males, these differences in overall male fledge rate and the fledge rate for Age 2+ yr did not affect individual annual productivity (i.e. juveniles fledged per year per male). Female snowy plovers typically do not rear chicks (Warriner et al. 1986, Page et al. 2009) and so would be less affected by behavioral deficits from the captive environment that may affect chick rearing, explaining why fledging success of nesting attempts involving captive females was unaffected.

Poor reproductive performance of captive animals after release can also be caused by low habitat quality at the release site (Tweed et al. 2006, Martínez-Abraín et al. 2011, White et al. 2012), and management of predators can play a significant role in improving habitat quality (Hegg et al. 2012). During our study, the Monterey Bay area had active habitat and predator management programs and a population monitoring program that allowed managers to identify limiting factors and develop management actions. For example, when predator exclosures were determined to cause an increased chance of adult mortality (Neuman et al. 2004), their use was greatly restricted. This adaptive management program has resulted in a measurable increase in plover breeding numbers during the time frame of this study (from about 220 in 2001 to about 385 in 2010), and these efforts likely benefitted captive plovers as much as wild plovers.

Implications for other imperiled plover species

We believe there are several key factors why the captive-rearing program discussed here was successful and that consideration of these points may be of assistance in planning captive-rearing efforts to sustain other imperiled plover populations.

(1) Sociality — Plovers are highly social species on both nesting and wintering grounds. We believe that the presence of large numbers of conspecifics at release sites allows for efficient transfer of information about the 'assigned' natal site and may increase the degree of fidelity to the site in the future. When the natural tendency for juveniles to disperse is compounded by a small or non-existent population at the release site, captive projects may be more prone to failure. This is particularly evident where animals are reintroduced into environments (often islands) where there is no existing population of the target species (Aikman 1999). To combat this, social attraction has been proposed for highly imperiled shorebirds (Dowding & Murphy 2001) and has been used with some success in recruiting Pacific coast snowy plovers to unoccupied sites (A. Transou pers. comm.).

(2) Migratory pattern — Species that are highly migratory, such as the inland piping plover, may be at a disadvantage because time at the assigned natal site after release is limited. For highly migratory species, if breeding populations are known to segregate on wintering grounds, as is the case with the piping plover (Gratto-Trevor et al. 2012), a viable option may be to release captive birds in early fall on wintering grounds where there are large groups of conspecifics, to potentially limit the physiological stress of their first migration. Captive-reared birds could then associate with conspecifics that would eventually migrate back to the target breeding area.

(3) Habitat and predator management — Even when all the population and demographic factors have been addressed as well as possible, captive projects will be more likely to fail if habitat threats are left unmitigated. We believe a large part of the success of the snowy plover captive program was due to the managed environment at Monterey Bay. Even with some evidence of behavioral deficits in captive males, there was no strong evidence of reduced fitness for captive plovers. In an unmanaged environment these deficits might become more apparent.

CONCLUSIONS

The IUCN recommends consideration of captive-breeding for vertebrate species with populations that have fallen below 1000 individuals (Ebenhard 1995), yet there is well-founded concern that establishment of captive breeding programs shifts the focus away from the primary concerns of habitat conservation that facilitate successful reintroduction of species to the wild (Snyder et al. 1996). Rangewide breeding season surveys from 2005 to 2011 indicate that the Pacific Coast population of the snowy plover (not including Mexico) numbers approximately 1500 to 2000 individuals (USFWS 2012), a number well above the IUCN threshold. We believe that evidence presented here demonstrates that captive-rearing is a valuable tool in support of ongoing conservation efforts to restore the federally threatened Pacific coast snowy plover population, but that it should not replace traditional efforts at conserving or managing the species throughout the range. We also believe this technique would be reliable in the event that nests need to be salvaged due to catastrophic events (such as oils spills).

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LITERATURE CITED

Aikman H (1999) Attempts to establish shore plover (*Thinornis novaeseelandiae*) on Motuora Island, Hauraki Gulf. Notornis 46:195–205

Bart J, Brown S, Harrington B, Morrison RIG (2007) Survey trends of North American shorebirds: population declines or shifting distributions. J Avian Biol 38:73–82

Brown J, Collopy MW, Gott EJ, Juergens PW, Montoya AB, Hunt WG (2006) Wild-reared aplomado falcons survive and recruit at higher rates than hacked falcons in a common environment. Biol Conserv 131:453–458

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York, NY

Cade TJ, Temple SA (1995) Management of threatened bird species: evaluation of the hands-on approach. Ibis 137: 161–172

Chesser RT, Banks RC, Barker K, Cicero C and others (2011) Fifty-second supplement to the American Ornithologists' Union check-list of North American birds. Auk 128: 600–613

Dowding JE, Murphy EC (2001) The impact of predation by introduced mammals on endemic shorebirds in New Zealand: a conservation perspective. Biol Conserv 99:47–64

Ebenhard T (1995) Conservation breeding as a tool for saving animal species from extinction. Trends Ecol Evol 10: 438–443

Elliott-Smith E, Haig SM (2004) Piping plover (*Charadrius melodus*). In: Poole A (ed) The birds of North America online. Cornell Laboratory of Ornithology, Ithaca, NY

Galbraith J, Sancha S, Maloney R, Hauber M (2007) Alarm responses are maintained during captive rearing in chicks of endangered kaki. Anim Conserv 10:103–109

Goossen JP, Vander Lee R, Kruse C, Gratto-Trevor CL, Westworth SM (2011) Resightings of captive-reared and wild piping plovers from Saskatchewan, Canada. Wader Study Grp Bull 118:1–9

Gratto-Trevor C, Amirault-Langlais D, Catlin D, Cuthbert F and others (2012) Connectivity in piping plovers: Do breeding populations have distinct winter distributions? J Wildl Manag 76:348–355

Griffin AS, Blumstein DT, Evans CS (2000) Training captive-bred or translocated animals to avoid predators. Conserv Biol 14:1317–1326

Griffith B, Scott JM, Carpenter JW, Reed C (1989) Translocation as a species conservation tool: status and strategy. Science 245:477–480

Haig SM, Ferland CL, Cuthbert FJ, Dingledine J, Goossen JP, Hecht A, McPhillips N (2005) A complete species census and evidence for regional declines in piping plovers. J Wildl Manag 69:160–173

Hays H, LeCroy M (1971) Field criteria for determining incubation stage of the common tern. Wilson Bull 83:425–429

Hegg D, Greaves G, Maxwell JM, MacKenzie DI, Jamieson IG (2012) Demography of takahe (*Porphyrio hochstetteri*) in Fiordland: environmental factors and management affect survival and breeding success. N Z J Ecol 36:75–89

Howe MA, Geissler PH, Harrington BA (1989) Population trends of North American shorebirds based on the international shorebird survey. Biol Conserv 49:185–199

IUCN (International Union for the Conservation of Nature) (2012) IUCN Red List of Threatened Species, Version 2012.2. www.iucnredlist.org (accessed 24 June 2013)

Kus BE, Ashman P, Page GW, Stenzel LE (1984) Age-related mortality in a wintering population of Dunlin. Auk 101: 69–73

Lockwood MA, Griffin CP, Morrow ME, Randel CJ, Silvy NJ (2005) Survival, movements, and reproduction of released captive-reared Attwater's prairie chicken. J Wildl Manag 69:1251–1258

Lovegrove TG (1996) Island releases of saddlebacks *Philesturnus carunculatus* in New Zealand. Biol Conserv 77: 151–157

Martínez-Abraín A, Regan HM, Viedma C, Villuendas E, Bartolomé MA, Gómez JA, Oro D (2011) Cost-effectiveness of translocation options for a threatened waterbird. Conserv Biol 25:726–735

Maxwell JM, Jamieson IG (1997) Survival and recruitment of captive-reared and wild-reared takahe in Fiordland, New Zealand. Conserv Biol 11:683–691

McLean IG, Holzer C, Studholme BJS (1999) Teaching predator recognition to a naïve bird: implications for management. Biol Conserv 87:123–130

Mullin SM, Colwell MA, McAllister SE, Dinsmore SJ (2010) Apparent survival and population growth of snowy plovers in coastal northern California. J Wildl Manag 74: 1792–1798

Neuman KK, Page GW, Stenzel LE, Warriner JC, Warriner JS (2004) Effect of mammalian predator management on snowy plover breeding success. Waterbirds 27: 257–263

Page GW, Gill RE Jr (1994) Shorebirds in western North America: late 1800s to late 1900s. Stud Avian Biol 15: 147–160

Page GW, Bidstrup FC, Ramer RJ, Stenzel LE (1986) Distribution of wintering snowy plovers in California and adjacent states. West Birds 17:145–170

Page GW, Quinn PL, Warriner JC (1989) Comparison of the breeding of hand- and wild-reared snowy plovers. Conserv Biol 3:198–201

Page GW, Stenzel LE, Page GW, Warriner JS, Warriner JC, Paton PW (2009) Snowy plover (*Charadrius nivosus*). In: Poole A (ed) The birds of North America online. Cornell Laboratory of Ornithology, Ithaca, NY

Powell AN, Cuthbert FC (1993) Augmenting small populations of plovers: an assessment of cross-fostering and captive-rearing. Conserv Biol 7:160–168

Powell AN, Cuthbert FJ, Wemmer LC, Doolittle AW, Feirer ST (1997) Captive-rearing piping plovers: developing techniques to augment wild populations. Zoo Biol 16: 461–477

Roche EA, Cuthbert FJ, Arnold TW (2008) Relative fitness of wild and captive-reared piping plovers: Does egg salvage contribute to recovery of the endangered Great Lakes population? Biol Conserv 141:3079–3088

Saunders SP, Ying Ong TW, Cuthbert FJ (2013) Auditory and visual threat recognition in captive-reared Great Lakes piping plovers (*Charadrius melodus*). Appl Anim Behav Sci 144:153–162

Scott JM, Carpenter JW (1987) Release of captive-reared or translocated endangered birds: What do we need to know? Auk 104:544–545

Seddon PJ, Armstrong DP, Maloney RF (2007) Developing the science of reintroduction biology. Conserv Biol 21: 303–312

Snyder NF, Derrickson SR, Beissinger SR, Wiley JW, Smith TB, Toone WD, Miller B (1996) Limitations of captive breeding in endangered species recovery. Conserv Biol 10:338–348

Stenzel LE, Page GW, Warriner JC, Warriner JS and others (2007) Survival and natal dispersal of juvenile snowy plovers (*Charadrius alexandrinus*) in central coastal California. Auk 124:1023–1036

Stenzel LE, Page GW, Warriner JC, Warriner JS and others (2011) Adult survival, sex ratio, mating opportunity, and site-fidelity in the snowy plover. Ibis 153:312–322

Tweed EJ, Foster JT, Woodworth BL, Monahan WB, Kellerman JL, Leiberman A (2006) Breeding biology and success of a reintroduced population of the critically endangered puaiohi (*Myadestes palmeri*). Auk 123:753–763

USFWS (US Fish and Wildlife Service) (2003) Recovery plan for the Great Lakes piping plover (*Charadrius melodus*). USFWS, Ft. Snelling, MN

USFWS (US Fish and Wildlife Service) (2007) Recovery plan for the Pacific coast population of the western snowy plover (*Charadrius alexandrinus nivosus*). USFWS, Sacramento, CA

USFWS (US Fish and Wildlife Service) (2012) Results of the 2011 rangewide breeding survey for western snowy plovers. Available at www.fws.gov/arcata/es/birds/WSP/plover.html (accessed 7 November 2013)

van Heezik Y, Seddon PJ, Maloney RF (1999) Helping reintroduced houbara bustards avoid predation: effective anti-predator training and the predictive value of pre-release behavior. Anim Conserv 2:155–163

van Heezik YR, Maloney F, Seddon PJ (2009) Movements of translocated captive-bred and released critically endangered kaki (black stilts) *Himantopus novaezelandiae* and the value of long-term post-release monitoring. Oryx 43: 639–647

Warriner JS, Warriner JC, Page GW, Stenzel LE (1986) Mating system and reproductive success of a small population of polygamous snowy plovers. Wilson Bull 98:15–37

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46(Suppl):120–139

White TH Jr, Collazo JA, Villela FJ (2005) Survival of captive-reared Puerto Rican parrots released in the Caribbean National Forest. Condor 107:424–434

White TH Jr, Collar NJ, Moorhouse RJ, Sanz V, Stolen ED, Brightsmith DJ (2012) Psittacine reintroductions: common denominators of success. Biol Conserv 148:106–115

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