The impact of predator exclosures on Snowy Plover nesting success: a seven-year study

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Nest predation has been identified as a major threat to ground-nesting birds, and predator exclosure cages have been used extensively to protect the nests of some shorebird species. Exclosures are generally effective at reducing egg predation but sometimes have unintended consequences, including nest abandonment and increased predation of incubating adults. We evaluated the effectiveness of exclosures at enhancing productivity of threatened Western Snowy Plovers *Charadrius alexandrinus nivosus* breeding in coastal northern California from 2001–2007. In coastal beach habitats, exclosed nests survived better than unexclosed nests, and exclosed beach nests survived as well or better than unexclosed nests in higher-quality habitat on riverine gravel bars. There was no significant difference in partial clutch survival or hatchability between exclosed and unexclosed beach nests, and there was no difference in fledging success for chicks that hatched from exclosed or unexclosed beach nests. Exclosed nests experienced significantly higher rates of nest abandonment than unexclosed nests. Although exclosures can greatly increase nest survival, this positive effect could be outweighed by increased nest abandonment or increased predation of incubating adults. Consequently, use of exclosures must be considered carefully, especially when dealing with threatened species or small, localized populations.

INTRODUCTION

Over the past 25 years, predator exclosure cages have been used frequently to protect the eggs of ground-nesting birds. Although some egg predation can still occur at exclosed nests (e.g. Isaksson *et al.* 2007, Johnson & Oring 2002, Mabee & Estelle 2000), this nonlethal method of predator control is generally effective at increasing hatching success (but see Mabee & Estelle 2000). Unfortunately, exclosures have occasionally been associated with increased mortality in incubating adults (Isaksson *et al.* 2007, Johnson & Oring 2002, Murphy *et al.* 2003, Neuman *et al.* 2004) and may also lead to an increase in nest abandonment (Isaksson *et al.* 2007, Neuman *et al.* 2004). Nevertheless, exclosures are still commonly used, and provide an alternative method of increasing nest survival rates when lethal predator control is not feasible.

Predator exclosures have been used extensively to manage various shorebird species, including sandpipers (Scolopacidae; Estelle *et al.* 1996, Isaksson *et al.* 2007, Niehaus *et al.* 2004) and, more commonly, plovers (Charadriidae; e.g. Johnson & Oring 2002, Murphy *et al.* 2003, Page *et al.* 1995). Several plover species are threatened either regionally or globally (IUCN 2007), and many populations suffer from high levels of egg predation (Grover & Knopf 1982, Haig 1992, Page *et al.* 1995). In North America, exclosures have been used to protect the nests of common, widespread species such as Killdeer *Charadrius vociferus* (Johnson & Oring 2002, Mabee & Estelle 2000, Nol & Brooks 1982) as well as threatened species such as Piping Plovers *C. melodus* (Melvin *et al.* 1992, Murphy *et al.* 2003, Rimmer & Deblinger 1990) and Snowy Plovers *C. alexandrinus* (Colwell *et al.* 2005, Page *et al.* 1995).

Predation of eggs and chicks poses a serious threat to the productivity of Snowy Plovers in California (Page *et al.* 1983) and Utah (Paton 1995). In 1993, following a significant population decline, the United States Fish and Wildlife Service (USFWS) listed the Pacific coast population of the Western Snowy Plover *C. a. nivosus* (hereafter plover) as threatened under the Endangered Species Act and identified predation of eggs by native and introduced predators as one of three factors that limit the population (USFWS 1993). Although some regions have achieved local recovery goals, the number of breeding plovers remains low in other areas (e.g. coastal northern California; Colwell *et al.* 2005).

In 2001, the USFWS designated coastal northern California as a discrete management unit, Recovery Unit 2 (Humboldt, Mendocino, and Del Norte counties, hereafter RU2), and researchers began an intensive monitoring program. The plover population in RU2 is small (30–74 individuals annually) and apparently not self-sustaining; although there are some high-quality breeding sites in RU2, the breeding population appears to be maintained by immigration (Mullin *et al.* in review). Predation is the leading cause of nest failure, resulting in the loss of at least 7–27% of total nests annually. Many clutches that failed for "unknown" reasons were probably depredated as well. In this study, we summarize seven years of data to assess the impact of exclosures on plover nest survival, partial clutch loss, egg hatchability, nest abandonment, and fledging success on coastal beaches in RU2. Additionally, we calculated the expected number of chicks and fledglings produced by exclosed and unexclosed beach nests. We also present similar data for nests on riverine gravel bars to demonstrate how exclosed nests in low-quality beach habitat compare with unexclosed nests in high-quality river habitat (Colwell *et al.* 2005).

STUDY AREA AND METHODS

Study area

We conducted our study in RU2, using data collected from 2001–2007 as part of an intensive monitoring program which included color-marking adults and chicks (for a more thorough review of monitoring and management activities in RU2, refer to Colwell *et al.* 2005, 2007a). We conducted all research under permit (USFWS permit TE-823807-3; California Department of Fish and Game collecting permit #801059-03; Humboldt State University IACUC #04/05.W.17-A; USFWS Federal banding permit #22971).

Most breeding plovers in RU2 occurred in Humboldt County (Colwell *et al.* 2007a), and the most intensive monitoring efforts occurred there. Throughout the study area, most plovers nested on sandy ocean-fronting beaches where reproductive success was generally low. In Humboldt County, however, some plovers nested on gravel bars of the lower 14 km of the Eel River, near its confluence with the Pacific Ocean. The gravel bars can be considered high-quality breeding habitat. Apparent hatching success along the river is consistently higher than on beaches (Colwell *et al.* 2005), which can be attributed largely to the crypsis of eggs on gravel substrates (Meyer 2005). Furthermore, the daily survival rate of chicks is consistently higher on the river than on beaches (Colwell *et al.* 2007b), and fledging success on the river regularly exceeds the recovery goal of 1.0 fledglings per male determined by USFWS (2007).

Nest searching and monitoring

Each year, surveys for breeding plovers and nests were conducted in suitable habitat (i.e. sandy ocean-fronting beaches and riverine gravel bars) throughout the study area, beginning in mid-March and continuing into late August or early September. Surveys were usually conducted on foot, using spotting scopes and binoculars, but a vehicle was occasionally used on some of the longer stretches of beach. Survey efforts varied among years and study sites, but occupied sites were surveyed at least once a week. Known centers of breeding activity were surveyed more often, sometimes daily. Unoccupied sites with suitable breeding habitat were surveyed less frequently (generally at 7–10 day intervals). Following discovery of a complete clutch (i.e. three eggs), eggs were floated to determine their developmental stage and predict hatch dates (Liebezeit *et al.* 2007). Hatch dates for nests found with incomplete clutches were estimated based on the timing of clutch completion, and nests nearing their predicted hatch date were checked more frequently.

Predator exclosures

The principal nest predators in RU2 are corvids *Corvus corax* and *C. brachyrhynchos*, but gray foxes *Urocyon cinereoargenteus* and domestic dogs *Canis familiaris* also occasionally consume plover eggs. Consequently, exclosures were designed to exclude medium and large predators. Exclosures were 3–4 m square cages constructed of 5 cm × 10 cm wire mesh, centered over the nest and anchored at each corner by a steel fencepost driven into the sand. Additional posts were used as necessary to stabilize exclosures, and the bottom 10 cm of the mesh sides was buried in the substrate to deter digging predators. The top of each exclosure was either strung with closely-spaced lengths of twine (2001–2002) or covered with plastic netting (2002–2006) to discourage entry from above.

Predator exclosures were used in beach habitats from 2001–2006, and researchers made a concerted effort to exclose most beach nests after 15 April. Due to the increased risk of predation to adults incubating in exclosures, no nests were exclosed after June 2006 (see below). Exclosures were used primarily as a management tool, rather than as part of a controlled experiment. Consequently, exclosures were not assigned randomly to nests and no effort was made to obtain equal sample sizes of exclosed and unexclosed beach nests within any year. Nests along the Eel River were never exclosed, due in part to the difficulty of erecting exclosures on the firm, rocky substrate.

Nest survival

We calculated daily survival rates (DSR) and estimates of nesting success for the laying and incubation period (31 days) from daily nest histories using the method developed by Mayfield (1975) and modified by Johnson (1979). Eleven nests were discovered at hatch or after hatching, and one nest was already abandoned when it was found. Since the exposure period for these nests could not be determined, we excluded them from the analysis, resulting in a sample size of 420 nests over the seven years of study.

Within each year, we calculated separate estimates for exclosed beach nests (2001–2006 only), unexclosed beach nests, and nests along the Eel River. We considered a nest successful if at least one of the eggs hatched, and we considered a nest failed if (1) the parents abandoned the nest (i.e., eggs were left untended for extended periods or the parents were observed re-nesting elsewhere), (2) there was evidence of predation (e.g., all eggs missing or broken and predator tracks at the nest), (3) one or more eggs were damaged by another source (e.g., humans, vehicles, wind-driven sand, tidal overwash, or river flood) and the parents did not tend the nest afterwards, or (4) the clutch disappeared due to unknown causes. For most nests (97%), we used the "Last Active-A" approach (Manolis *et al.* 2000) to determine the number of exposure days, but nests that never progressed beyond the 1-egg stage and did not fail due to other causes were considered abandoned on the day following clutch initiation. Therefore, these nests (3%) received one exposure day each.

Partial clutch survival, hatchability, nest abandonment, and fledging success

We pooled data from all seven years of study and calculated DSR and rates of partial clutch survival, hatchability, and nest abandonment for exclosed and unexclosed beach nests and river nests. We then determined the expected reproductive value (i.e., the expected number of chicks hatching from a nest) for each group of nests using the method described by Arnold (1999):

$$R_{hatch} = C \times N \times PC \times H$$

where R_{hatch} = the expected number of chicks produced by a nest, C = clutch size (in this case, three eggs), N = the Mayfield estimate of nest success (DSR^{31}), PC = partial clutch survival (1 – the proportion of eggs that disappeared or were damaged before hatching), and H = hatchability (the proportion of eggs that hatched from all intact eggs that survived until the hatch date). In their study, Isaksson *et al.* (2007) modified Arnold's equation to include A (1 – the proportion of nests that were abandoned before hatching), but we did not follow their example since our Mayfield estimates already accounted for nests that failed due to abandonment and including A in our calculations would, in effect, penalize the estimate of R_{hatch} twice for each abandoned nest. However, since examining the effects of predator exclosures on hatching success while ignoring their impact on other life stages may lead to overly-optimistic conclusions about the effectiveness of management efforts (Neuman *et al.* 2004), we did modify Arnold's equation to include fledging success (where F = the proportion of chicks that survived until fledging) and calculated R_{fledge} values for all three groups (where R_{fledge} = the expected number of fledglings produced per nest).

In five cases (2004: four nests, 2005: one nest), we were unable to determine the number of eggs present at hatch. Therefore, we calculated PC, H, and both R values under two different scenarios: (1) assuming that the number of eggs present at hatch was equal to the number of eggs present at the last nest check before hatch, and (2) assuming that the number of eggs present at hatch was equal to the number of chicks known to have hatched from that nest. There were only minor differences in PC and H, and estimates of R were identical under both scenarios. The values we report here were calculated under the second scenario.

Statistical analysis

To evaluate the effectiveness of predator exclosures at increasing nest survival, we compared estimates of DSR for exclosed beach nests with estimates for unexclosed beach nests and river nests within each year (2001–2006) and tested for annual differences in DSR from 2001–2006 within each group using program CONTRAST (Sauer & Hines 1989). Using pooled data, we also compared partial clutch survival, hatchability, nest abandonment, and fledging success for exclosed and unexclosed beach nests using Fisher's exact test. Estimates for river nests are also included, although they were not compared statistically with either exclosed or unexclosed beach nests.

RESULTS

Mayfield estimates of nesting success and daily survival rates

In each of the first six years of study, Mayfield estimates of nesting success were higher for exclosed beach nests than for unexclosed beach nests and river nests (Table 1). However, success of exclosed nests varied greatly (47–93%), and there was no clear trend across years. Estimates for unexclosed beach nests were consistently low, ranging annually from approximately 0% to 8%. Nesting success on the river ranged from 15% to 48% over the first six years of study before increasing dramatically to 71% in 2007, and river nests were always more successful than unexclosed beach nests.

DSR also varied greatly across the seven years of study. From 2001–2006, there were significant annual differences in DSR for both exclosed (χ^2 = 21.04, df = 5, p = 0.0008) and unexclosed beach nests (χ^2 = 24.89, df = 5, p = 0.0001), but not for river nests (χ^2 = 4.81, df = 5, p = 0.44). In 2007, when no exclosures were used, DSR was significantly higher than the 2001–2006 average for unexclosed beach nests (χ^2 = 16.16, df = 1, p = 0.0001). Furthermore, 2007 DSR for river nests was higher than the 2001–2006 river average (χ^2 = 5.21, df = 1, p = 0.02). During each year when exclosures were used, exclosed nests survived significantly better than unexclosed nests in beach habitats (7–43% higher DSR, $p \leq 0.04$ for each year) and DSR for exclosed beach nests was higher than or comparable to DSR for river nests within each year (Table 1).

Partial clutch survival, hatchability, nest abandonment, and fledging success

Partial clutch survival did not differ significantly between exclosed and unexclosed beach nests (Fisher's exact test, p = 1.0; n = 100 nests). Similarly, hatchability of eggs did not differ between exclosed and unexclosed nests (Fisher's exact test, p = 1.0; n = 100 nests). Exclosed nests, however, experienced a significantly higher rate of abandonment (16.8% versus 4.5%) than unexclosed nests (Fisher's exact test, p = 0.0013; n = 270 nests). Nevertheless, R_{hatch} for exclosed beach nests was still higher than R_{hatch} for river nests, and over 35 times greater than R_{hatch} for unexclosed nests (Table 2).

Although there was no significant difference in fledging success between exclosed and unexclosed beach nests (Fisher's exact test, p = 0.69; n = 100 nests), fledging success for chicks hatched from river nests was 2.35 times higher than for exclosed beach nests. Lastly, estimates of R_{fledge} showed a slightly different pattern than estimates of R_{hatch}: R_{fledge} for exclosed nests was 30.7 times higher than R_{fledge} for unexclosed nests, but only 77% of R_{fledge} for river nests (Table 3).

Predation of adults at exclosures

In June 2006, an unknown avian predator killed one incubating adult near a nest exclosure at one site (Clam Beach County Park/Little River State Beach). Seven other adults, all incubating exclosed nests, also disappeared from this site at around the same time; these losses were similar to the "episodic" predation events described by Murphy *et al.* (2003) and Neuman *et al.* (2004). To prevent further risk to adult plovers, we ceased using exclosures and no beach nests were exclosed in 2007.

DISCUSSION

Previous studies (e.g. Estelle *et al.* 1996, Johnson & Oring 2002, Melvin *et al.* 1992, Nol & Brooks 1982) showed that exclosing nests can be an effective means of increasing nesting success, and our results are in agreement with much of the published literature. In beach habitats, exclosed nests were more successful than unexclosed nests. Additionally, exclosed beach nests survived at least as well as nests on riverine gravel bars, further supporting the notion that nest exclosures can be a valuable management tool. Exclosures did not have a significant impact on partial clutch loss or hatchability of eggs, but greatly increased the frequency of nest abandonment. Neuman *et al.* (2004) also reported increased nest abandonment after initiating a predator management program including exclosure use. Furthermore, Isaksson *et al.* (2007) reported similar findings: in their study, there was a marginally significant (p = 0.052) increase in abandonment for exclosed Northern Lapwing *Vanellus vanellus* nests. Although predation is the leading known cause of nest failure in RU2, nest abandonment is also an important cause of nest failure, with 4–14% of nests abandoned each year. Regardless of increased nest abandonment, however, exclosed beach nests still produced more chicks (1.62 chicks per nest) than either unexclosed beach nests (0.046 chicks per nest) or nests on the Eel River (0.89 chicks per nest). Nevertheless, fledging success on beaches was still low, even for exclosed

Table 1. Daily survival rates (DSR), standard errors of DSR, and Mayfield estimates of nesting success across the laying and incubation period for exclosed beach nests, unexclosed beach nests, and nests in riverine gravel bar habitat.

	Exclosed nests				Unexclosed nests						River nests					
Year	**n**	**DSR**	**SE**	**Mayfield**[a]	**n**	**DSR**	**SE**	**Mayfield**[a]	**Difference**[b]	p^c	**n**	**DSR**	**SE**	**Mayfield**[a]	**Difference**[b]	p^c
2001	15	0.998	0.002	0.929	4	0.881	0.056	0.019	13%	0.0369	36	0.976	0.006	0.476	13%	0.002
2002	25	0.976	0.007	0.465	20	0.795	0.042	0.001	23%	<0.0001	26	0.969	0.008	0.382	1%	0.5595
2003	23	0.981	0.006	0.555	15	0.725	0.060	0.000	35%	<0.0001	36	0.962	0.008	0.301	2%	0.0563
2004	28	0.982	0.005	0.565	16	0.684	0.067	0.000	43%	<0.0001	22	0.960	0.011	0.283	2%	0.072
2005	27	0.990	0.004	0.734	16	0.873	0.032	0.015	13%	0.0002	13	0.961	0.014	0.288	3%	0.0374
2006	19	0.982	0.006	0.566	25	0.920	0.017	0.075	7%	0.0005	13	0.941	0.020	0.153	4%	0.0537
2007	–	–	–	–	37	0.913	0.015	0.060	–	–	4	0.989	0.011	0.710	–	–

[a] Mayfield estimate = DSR^{31}
[b] Difference in DSR between unexclosed beach nests or river nests and exclosed beach nests
[c] DSR compared using program CONTRAST (df = 1)

Table 2. Clutch size (C), daily survival rate (DSR), Mayfield estimate ($N = DSR^{31}$), partial clutch survival (PC), hatchability (H), and the expected number of eggs hatching from each clutch ($R_{hatch} = C \times N \times PC \times H$), assuming a high rate of partial clutch loss. Results for unexclosed beach nests, exclosed beach nests, and nests in riverine gravel bar habitat (pooled data from 2001–2007) are presented.

Nests	**C**	**DSR**	**N**	**PC**	**H**	R_{hatch}
Unexclosed	3	0.876	0.016	0.976	0.95	0.046
Exclosed	3	0.985	0.617	0.948	0.924	1.622
River	3	0.966	0.346	0.972	0.883	0.89

nests, and the expected number of fledglings produced was considerably lower for exclosed beach nests (0.43 fledglings per nest) than for river nests (0.56 fledglings per nest). Clearly, factors other than nest survival must also be taken into consideration in order to draw sound conclusions regarding the cumulative impact of exclosures on plover productivity. Specifically, the trade-off between enhancing hatching success and increasing nest abandonment must be considered carefully.

In their review of predator exclosure studies, Mabee & Estelle (2000) found that results were often confounded by one or more factors and offered suggestions to improve future study designs. The widespread use of predator exclosures from 2001–2006 in RU2 was not part of a controlled experiment; it was a management action specifically intended to protect as many nests as possible in habitats where nest loss due to predation was high. Since we did not set out to experimentally test the effectiveness of exclosures, and we only analyzed the impacts of exclosures retrospectively, we did not follow Mabee & Estelle's recommendations regarding experimental design. Therefore, this analysis suffers from unequal sample sizes between exclosed and unexclosed nests within years, and lacks the random assignment of exclosures to nests that could control for several confounding factors (e.g. time of season).

Moreover, many unexclosed nests were only left unexclosed because they failed before biologists could protect them with exclosures. As a result, 2001–2006 estimates for unexclosed beach nests are almost certainly biased low by nests that failed early during laying or incubation; this is supported by the finding that DSR was significantly higher in 2007. DSR and Mayfield estimates for exclosed nests and river nests should not suffer from this same bias. Admittedly, biased estimates of DSR for unexclosed nests will confound comparisons between exclosed and unexclosed nests. However, while it may not be possible to accurately quantify the increase in nesting success conferred by exclosures, the general trend (i.e., exclosures enhancing nest survival) is, by and large, supported by previous findings, including recent studies (e.g. Isaksson *et al.* 2007, Johnson & Oring 2002) that did follow Mabee & Estelle's suggestions.

Although exclosures may increase nest survival, they do not protect nidifugous chicks. Consequently, exclosures do nothing to enhance fledging success and chick survival might actually be negatively impacted if predators learn to associate exclosures with prey (Niehaus *et al.* 2004) or if increased hatching success leads to an increase in chick predation (Isaksson *et al.* 2007, Neuman *et al.* 2004), potentially offsetting any increase in productivity. Furthermore, if exclosed nests in marginal habitats are successful (i.e. at least one egg hatches) but chicks do not survive, breeding birds may receive a false message regarding the quality of a site and continue nesting in areas where fledging success is low. Since the distribution of plovers in RU2 appears to be influenced by social attraction (Nelson 2007), immigrants entering the population could be drawn into sink habitats by aggregations of nesting birds when they might have otherwise settled in higher-quality breeding habitat elsewhere (e.g. riverine gravel bars).

Since shorebird population growth rates are often more sensitive to changes in adult survival than to changes in other demographic parameters (Larson *et al.* 2002, Sandercock *et al.* 2003, 2005), the most problematic effect of exclosure use is the potential for increased predation of incubating adults. Murphy *et al.* (2003) observed high rates of adult mortality at exclosed Piping Plover nests in the northern Great Plains. Neuman *et al.* (2004) found that Snowy Plover mortality at Monterey Bay, CA was greater than expected ($p < 0.01$) for adults incubating exclosed nests: although <50% of

Table 3. Clutch size (*C*), daily survival rate (*DSR*), Mayfield estimate ($N = DSR^{31}$), partial clutch survival (*PC*), hatchability (*H*), fledging success (*F*), and the expected number of fledglings produced from each clutch ($R_{fledge} = C \times N \times PC \times H \times F$), assuming a high rate of partial clutch loss. Results for unexclosed beach nests, exclosed beach nests, and nests in riverine gravel bar habitat (pooled data from 2001–2007) are presented.

Nests	C	DSR	N	PC	H	F	R_{fledge}
Unexclosed	3	0.876	0.016	0.976	0.95	0.316	0.014
Exclosed	3	0.985	0.617	0.948	0.924	0.265	0.430
River	3	0.966	0.346	0.972	0.883	0.624	0.556

nests were exclosed, 76% of adults that disappeared during incubation were nesting in exclosures. In pastures in western Sweden, predation of adult Redshanks *Tringa totanus* incubating exclosed nests reached such high levels that Isaksson *et al.* (2007) discontinued exclosure use at Redshank nests. Similar events prompted biologists in RU2 to cease using exclosures in 2006. The breeding population in RU2 is small and the loss of even a single adult is cause for concern, as it could have a significant impact on the persistence of the local population.

While predator exclosures usually enhance nesting success, the effects of exclosures on other aspects of reproductive biology must also be seriously considered. If predator exclosures increase the frequency of nest abandonment, cause individuals to settle or remain in low-quality habitat, and compromise adult and/or chick survival, the net impact to productivity may actually be negative. If this is the case, then exclosure use is counterproductive when not used in conjunction with an integrated approach to predator management, as it would hinder, rather than aid, recovery or conservation efforts. Managers should exercise caution when using exclosures and closely monitor adult and chick mortality, especially when dealing with small populations or threatened taxa. If exclosure use results in a marked increase in mortality or nest abandonment, alternative methods of enhancing productivity (e.g. predator removal or aversive conditioning) may be more appropriate.

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Nest exclosures were used to protect eggs of Snowy Plovers in coastal northern California. This image shows an exclosure that was constructed to keep both avian and mammalian predators away from the eggs. The yellow insulators support electrified wires meant to deter predation by gray foxes. (Photo by Sean McAllister.)