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Snowy Plover reproductive success in beach and river habitats

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ABSTRACT. Poor reproductive success has contributed to the decline and low population size of the federally listed Western Snowy Plover (*Charadrius alexandrinus nivosus*), especially where it breeds on coastal beaches used by humans for recreation. From 2001–2004, we compared reproductive success of color-marked plovers breeding on ocean beaches with those on gravel bars of the lower Eel River in coastal northern California, one of six recovery units as identified by the species' recovery plan. In three of four years, more plovers (54–64%) nested in river than beach habitats, but this pattern was reversed in the last year of the study when 62% of plovers used beaches. Each year, a higher proportion of clutches hatched and more chicks fledged from river than beach habitats, producing a disproportionate number of yearlings recruited into the local population from the river. On average, river-nesting males tended significantly fewer eggs, hatched similar numbers of chicks, and fledged significantly more young compared with males breeding on beaches. Corvids were more prevalent in river habitats in two of four years, but beaches consistently had significantly greater human activity. These habitat differences in reproductive success exist despite efforts to manage predators (e.g., exclosures around nests) and humans (e.g., signs, fencing, and vehicle restrictions) on beaches and almost no management of river habitats.

SINOPSIS. **Éxito reproductico de *Charadrius alexandrinus* en habitats de playas y rios**
Un éxito reproductivo pobre ha contribuido a la merma del playero (*Charadrius alexandrinus*) particularmente cuando este anida en hábitats de playas utilizadas por humanos para la recreación. De 2001–2004, comparamos el éxito reproductivo de playeros que fueron anillados en playas y en graveros del río Eel que se encuentra en la parte norte de California. Esta es una de las seis localidades mencionadas en el Plan de Recuperación de esta especie que ha sido listada. En tres de los cuatro años, una mayor cantidad de playeros (54–65%) anidaron en el hábitat de río que en el de playa, aunque este patrón se invirtió en el ultimo año de estudio (64%). Cada año una mayor proporción de camadas eclosionaron y un número mayor de polluelos dejaron el nido en hábitats de ríos que en los de playa, produciendo una desproporción numérica de volantones de un año, reclutados en la población del río. En promedio, los machos que atendieron polluelos en ríos tuvieron que incubar menos huevos, ayudaron a eclosionar un numero similar de polluelos y produjeron más volantones que los machos que utilizaron playas. Los córvidos, que son depredadores, pasaron mas tiempo en hábitat de ríos en dos de los cuatro años, aunque las playas consistentemente tuvieron mayor actividad de humanos, significativamente. Las diferencias en el éxito reproductivo en los dos tipos de hábitats, existen a pesar del esfuerzo de manejar depredadores (e.j., sistemas que evitan que estos lleguen a los nidos), humanos (e.j., restricción al uso de vehículos y rótulos) en las playas y virtualmente ningún manejo en los ríos.

Key words: *Charadrius alexandrinus nivosus*, fledging success, habitat quality, nesting success, reproductive success, site fidelity, Snowy Plover, threatened species

For threatened and endangered species, it is essential that quantified variation in habitat quality guide management efforts to increase reproduction or survival. In 1993, the U.S. Fish and Wildlife Service (USFWS) listed the coastal population segment of the Western Snowy Plover (*Charadrius alexandrinus nivosus*) as threatened under the federal Endangered Species Act (ESA; USFWS 1993) based on a significant population decline. This population decline stemmed partly from poor reproduction associated with predation of eggs and young by corvids (*Corvus corax*, *C. brachyrhynchos*), gulls (*Larus* spp.), red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*) (USFWS 2001). In coastal central California, mammalian predator control successfully increased hatching but not fledging success of Snowy Plovers (Neuman et al. 2004). Increased human recreation in the species' breeding habitats has also been cited as a cause

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of low reproductive success (USFWS 2001). At Point Reyes National Seashore, the timing of chick mortality for beach nesting plovers occurred disproportionately on weekends, which Ruhlen et al. (2003) suggested correlated with high human disturbance of breeding plovers. European beach grass (*Ammophila arenaria*), an introduced species that colonizes and alters the open sandy habitats preferred by plovers, has also degraded breeding habitat (USFWS 2001).

Along the Pacific coast, Snowy Plovers breed in sparsely vegetated habitats of salt pans and levees, dredge spoil islands, river gravel bars, and ocean beaches from central Washington south to Baja California, Mexico; within the U.S., most individuals breed in California (USFWS 2001). In northern California, plovers winter and breed along ocean beaches (Page and Stenzel 1981) and river bars of the lower Eel River (Tuttle et al. 1997), which led the USFWS (2001) to designate coastal northern California as a discrete management unit (Recovery Unit 2). Within this area, the number of breeding plovers has probably never been high. In 1977, Page and Stenzel (1981) reported 80 plovers (26 nests) at 10 locations and estimated that this represented 6% of the population in coastal California. In the early 1990s, this area supported 22–50 breeding plovers annually (USFWS 2001). Until recently, these plovers were not known to nest in habitats other than coastal beaches. In 1996, however, Tuttle et al. (1997) first observed breeding plovers in a unique habitat, river bars of the lower Eel River; it remains unknown how long plovers have bred in this habitat. Currently, the population size (for coastal northern California) represents < 5% of the estimate for the listed population and 40% of the recovery objective for the recovery unit (USFWS 2001).

From 2001–2004, we intensively monitored a marked population of plovers in Recovery Unit 2. Here, we compare annual reproductive success of plovers breeding in river and beach habitats, and provide evidence that corvids and humans compromise the quality of breeding habitat for beach-breeding plovers.

STUDY AREA

We monitored plovers at three principal sites in Humboldt County, California (Fig. 1) and several secondary sites in Humboldt and Mendocino counties (Colwell et al. 2004). Two sites (Clam Beach and South Spit/Eel River Wildlife Area) are ocean-fronting beaches with vegetation dominated by European beach grass. At these beaches, most plovers nested on relatively homogeneous sandy substrates, often amidst shells, driftwood, and other debris. Plovers (and especially their tracks) were conspicuous in these fine substrates, making nests and broods easy to find and vulnerable to predation (Colwell et al. 2004). After hatch, adults moved chicks to the upper reaches of ocean-fronting beach, where debris offered food and cover. At both beach sites, but especially Clam Beach, humans used plover breeding habitats for recreation such as clamming, jogging, horseback riding, dog walking and driving vehicles.

Plovers bred at gravel bars along the lower Eel River, from its confluence with the Pacific Ocean upriver approximately 14 km (Colwell et al. 2004). River-breeding plovers nested in coarse, heterogeneous substrates varying in size from sand to pea-sized gravel and large stones, which were sparsely vegetated by willow (*Salix* spp.) and white sweet clover (*Melilotus alba*). Compared to beaches, plovers are more difficult to observe along the river, nests are more cryptic, and plover tracks are rarely seen in these coarse substrates. Adults tended broods in the same areas where they nested. Humans frequented the river much less than beach sites.

METHODS

Field observations. Intensive monitoring of color-marked plovers began in 2001. Each year, we captured plovers at nests using noose mats and circular nest traps, and banded nearly all breeding plovers. Each individual received a unique combination of colored leg bands. From mid March to early September, observers surveyed breeding plovers almost daily within each habitat. During surveys, we recorded the identity of banded plovers, found nests, and monitored broods. Upon finding a nest, we recorded the number of eggs and estimated hatch date (for complete clutches) using egg flotation methods (Alberico 1995) or by the timing of clutch completion for nests found with an incomplete clutch. On beaches, we erected predator exclosures at most (61%) nests; we never exclosed river nests.

At hatching, we marked chicks with a brood-

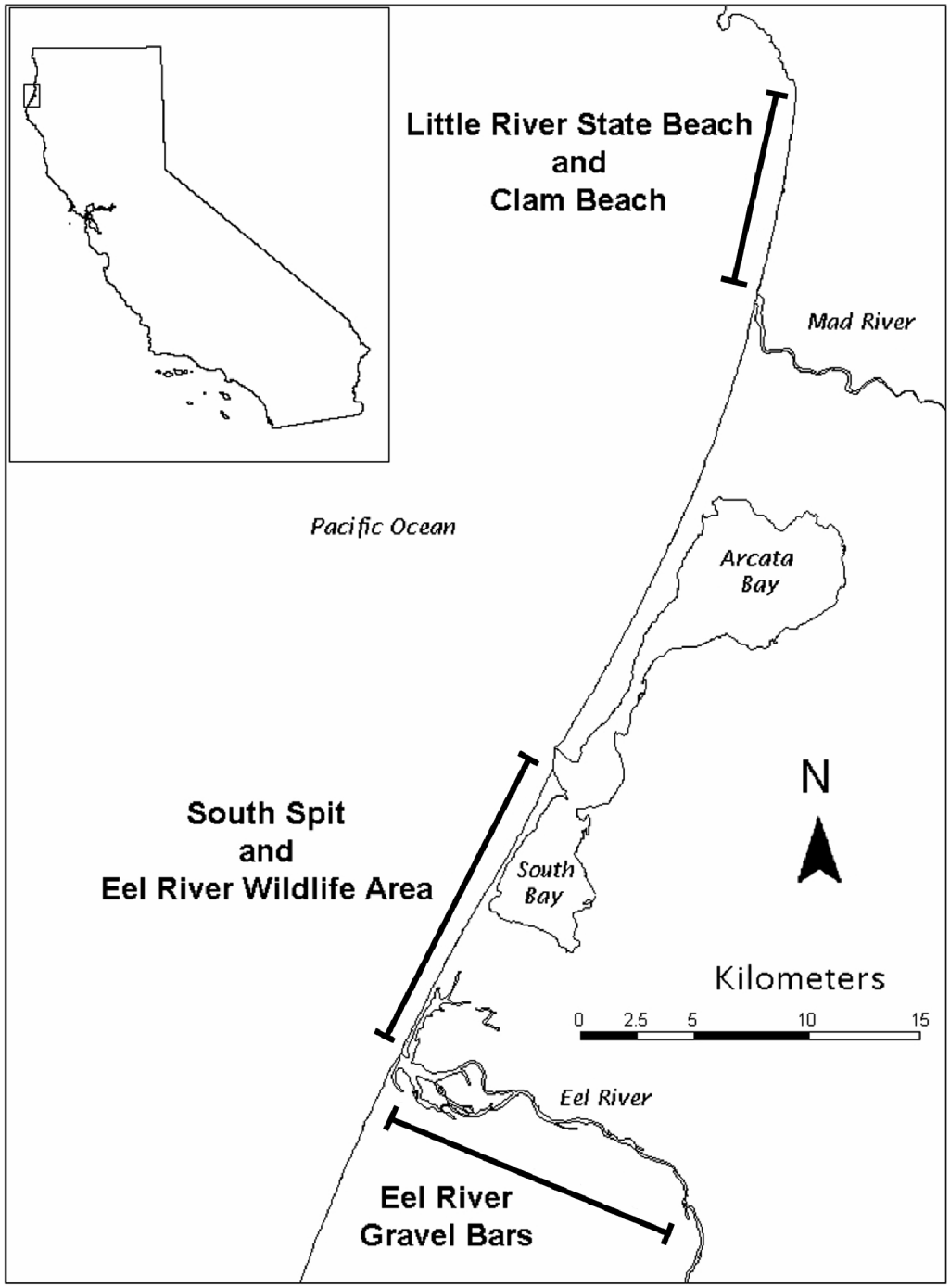

Fig. 1. Location of beach (Clam Beach; South Spit and Eel River Wildlife Area) and river (Eel River gravel bars) habitats where Snowy Plovers bred in Humboldt County, California, 2001–2004.

specific color band to distinguish young of similar age at a site. Observers monitored chicks at 1–4 d intervals until they fledged (28 d; Page et al. 1995) or died, recording brood location with a global positioning system, identity of the tending adults, and the number of young in a brood; these observations were conducted opportunistically during regular surveys. In 2001 and 2002, observers conducted 30-min observations (Altmann 1974) of broods, tallying the number of potential predators (corvids) and human activity (humans, dogs, and vehicles) within 100 m of the initial brood location. In an attempt to better quantify differences in predator and human activity among sites, we altered our method of sampling in 2003 and 2004. In these years, we used instantaneous point counts to tally the number of predators and humans within 500 m of the observer. We conducted point counts at 20-min intervals during regular surveys of beach and river habitats.

Data summary and analyses. For beach and river habitats separately, we compared the number of breeding plovers in each habitat and measures of reproductive success (e.g., nest success was the percentage of clutches that hatched at least one chick; fledging success was the percentage of broods that fledged at least one juvenile). Using individual reproductive histories, we summarized habitat patterns in the total number of nesting plovers of each sex and the average (± SD) eggs tended, chicks hatched, and juveniles fledged per male. We present data for males for comparison with information published in the species' population viability analysis (USFWS 2001). Moreover, each year there were only minor sex differences in reproductive success (Colwell et al. 2004), mostly attributable to higher variance in (local) female reproductive success owing to their tendency for greater within-year breeding dispersal compared to males (Stenzel et al. 1994).

We compared overall performance (e.g., nesting and fledging success) of plovers using beach and river habitats with chi-square tests. We used a two-factor ANOVA (proc GLM; SAS 1991) to compare untransformed measures of male reproductive success, using habitat and year as class variables. In the ANOVA, the unit of measure was an individual male's annual reproductive success (number of eggs, chicks hatched, or fledglings), such that each male contributed as many observations as years present in one or the other habitat. Individuals often bred for multiple years in the study area and seldom switched habitats. As an additional habitat comparison of reproductive success, we examined the cumulative number of chicks fledged by beach- and river-breeding males over their first, second, third, and fourth year in the study population. We omitted from analyses the few ($N = 4$) individuals that switched habitats within or between years.

To evaluate the danger to eggs and young plovers in beach and river habitats, we compared prevalence (percentage of total observations with one or more instance) of corvids and human activity (humans, vehicles, and dogs) using brood-centered focal observations (2001 and 2002) or point counts (2003 and 2004).

RESULTS

Population size. Annually, the total number of plovers breeding at beach and river sites combined ranged from 56–74, with nearly equal proportions of males and females (Table 1). During the first three years of study, most (54–67% annually) plovers nested on the river, but this pattern was reversed in 2004 when 59% of plovers bred on beaches. Over four years, we monitored 62 marked adult males (29 beach, 33 river), 29 of which bred in the study area in multiple years.

Nesting and fledging success. Each year, plovers initiated 57–75 clutches (Table 1) over a 4 mo period (Fig. 2). Overall, plovers initiated slightly more nests on beaches (147) than along the river (129). Nesting phenology (based on dates of clutch initiation) differed in beach and river habitats (Kolmogorov-Smirnov test, $D = 0.16$, $P < 0.05$), with more early nests on beaches. Despite our attempts to protect nests using exclosures, plovers on beaches had significantly lower ($\chi^2_1 = 4.93$, $P = 0.03$) nesting success (40%) than those on the river (53%). In total, 276 clutches hatched 314 chicks, 54% of which were on the river. A greater proportion (60%) of chicks occupying river habitats successfully fledged ($\chi^2_1 = 30.97$, $P < 0.0001$), compared with beaches (29%). As a result, river habitats produced 71% of the 144 juveniles produced over the 4 yr period.

Individual reproductive success. Males breeding in beach and river habitats differed significantly in two of three measures of repro-

Table 1. Annual variation in numbers and reproductive measures of Snowy Plovers breeding in river and beach habitats of coastal northern California, 2001–2004.

		2001		2002		2003		2004	
		River	Beach	River	Beach	River	Beach	River	Beach
Number of adults	males	21	10	19	14	17	11	15	22
	females	19	10	15	15	14	14	15	22
Number of nests		38	19	30	45	36	38	25	45
Number chicks hatched		61	36	41	35	37	28	30	46
Number fledged juveniles		36	14	20	4	28	4	18	20
Nest success (%)[a]		66	74	57	31	42	34	48	40
Chick success (%)[b]		59	39	48	11	76	14	60	44

[a] Percentage of nests that hatched at least one chick.
[b] Percentage of chicks that survived 28 d.

ductive success (Fig. 3); experience (number of years breeding locally) did not explain differences in reproductive success ($P > 0.25$). Beach-nesting males cared for significantly more eggs (6.1 ± 3.5) than males on the river (4.6 ± 2.5) ($F_{7,104} = 6.65$, $P = 0.01$). There was no difference, however, in the average number of chicks hatched ($F_{7,104} = 1.21$, $P = 0.30$) by males residing on beaches (2.7 ± 1.9) vs. the river (2.5 ± 1.7). Lastly, males were nearly twice as productive in fledging chicks from river (1.5 ± 1.4) than beach (0.8 ± 1.0) habitats ($F_{7,105} = 9.32$, $P = 0.003$). There was significant annual variation in average number of eggs ($F = 2.63$, $P = 0.05$), chicks ($F = 2.67$, $P = 0.05$), and young ($F = 3.36$, $P = 0.02$), with higher values in 2001 compared with 2002, especially for the number of young fledged. There was no interaction between habitat and year for any measure of reproductive success ($P > 0.19$).

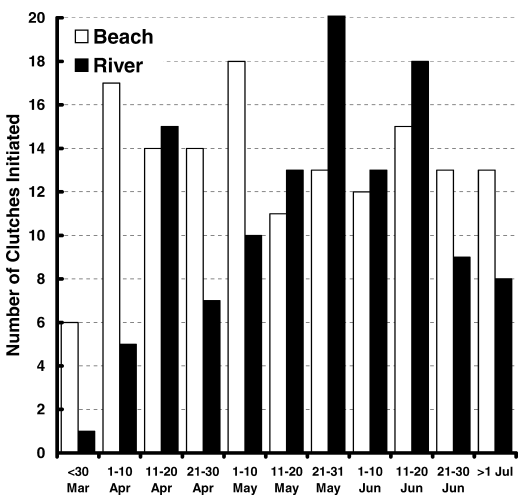

Fig. 2. Cumulative (2001–2004) seasonal distribution of 129 river and 147 beach clutches initiated over 10-d intervals in coastal northern California.

For males, cumulative reproductive success (average total chicks fledged by males present 1, 2, 3, or 4 yr) differed markedly between habitats (Fig. 4). In river habitats, the cumulative number of chicks fledged increased steadily (by increments of 2.0–2.8 fledglings) with each additional yr of breeding experience. The few males that bred for 4 yr produced an average of more than eight juveniles. By contrast, cumulative reproductive success of beach-breeding males increased more slowly (by increments of 0–1.6 fledglings) such that males present 4 yr produced an average total of three juveniles.

Indices of predation and human activity. There were consistent differences between beach and river habitats in the danger posed by corvids and humans, regardless of whether indices were derived from focal observations of broods (Fig. 5a) or point counts (Fig. 5b). Corvids were more prevalent in river habitats, although the difference was significant in only two yr (2001, $\chi^2 = 9.05$, $P = 0.003$; 2004, $\chi^2 = 16.18$, $P < 0.0001$). Corvid abundance on the river averaged 2–3 times that of beaches, but there was appreciable variation within habitats. Conversely, humans, dogs, and vehicles were more prevalent and 5–10 times more abundant on beaches than the river.

DISCUSSION

Snowy Plovers breeding on beaches of coastal northern California have higher reproductive

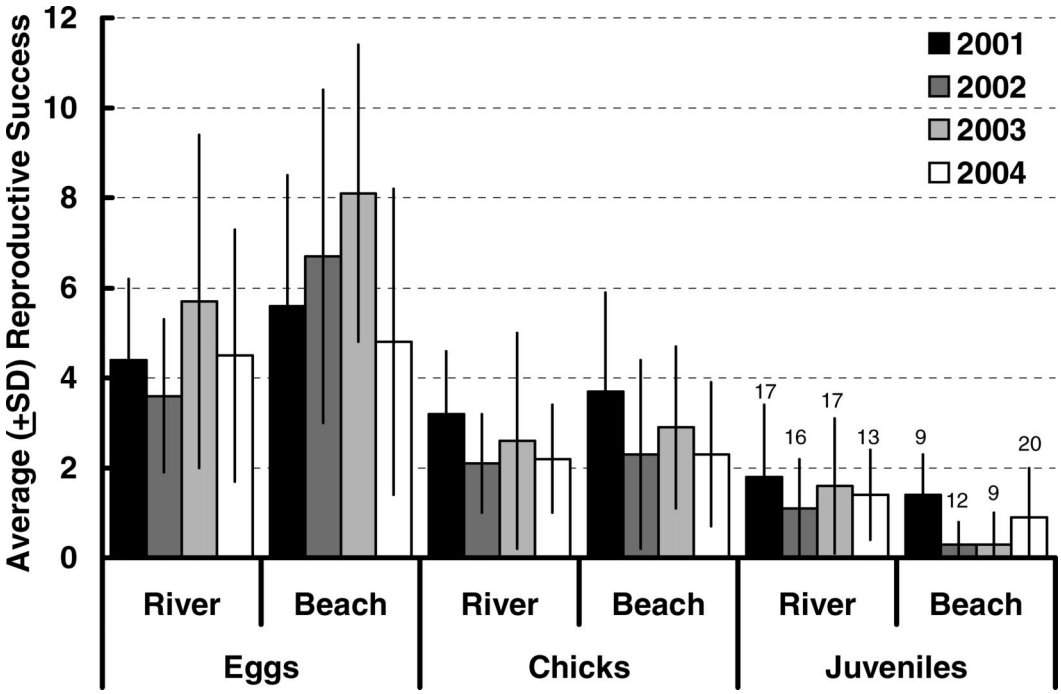

Fig. 3. Annual differences in average (±SD) eggs tended, chicks hatched, and young fledged per male Snowy Plover breeding in beach and river habitats in coastal northern California, 2001–2004. Sample size (number of plovers) is shown above the histograms for juveniles.

effort (number of eggs tended by males but not laid by females), yet lower reproductive success (fledged chicks) than those breeding along gravel bars of the lower Eel River. These habitat differences are magnified over multiple years as individuals gain breeding experience: river-breeding plovers substantially increased their cumulative reproductive success with each year of breeding whereas beach-breeding plovers did not. Overall, plovers in Recovery Unit 2 are roughly equally distributed between beach and river habitats, although a few individuals move between habitats both within and between years (M. A. Colwell, unpubl. data). As a result of individual and population patterns, river habitats have produced a disproportionately greater number of fledged young and yearlings recruited into the local population as breeders (Colwell et al. 2004). Collectively, these demographic data (based on intensive monitoring of marked individuals) combined with information on the distribution and productivity of plovers argue strongly that river gravel bars are of higher quality than ocean beaches.

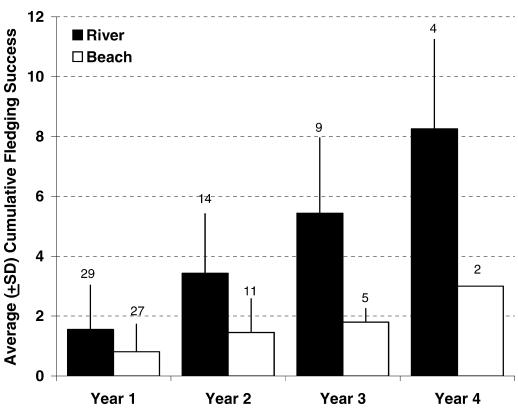

Fig. 4. Cumulative changes in reproductive success of male Snowy Plovers breeding in beach and river habitats during their first, second, third, and fourth years in the study population. The number of individual plovers is shown above each histogram.

Quality of breeding habitat (as measured by reproductive success) may be influenced by a combination of factors, including predation of eggs and chicks, food availability, natural dis-

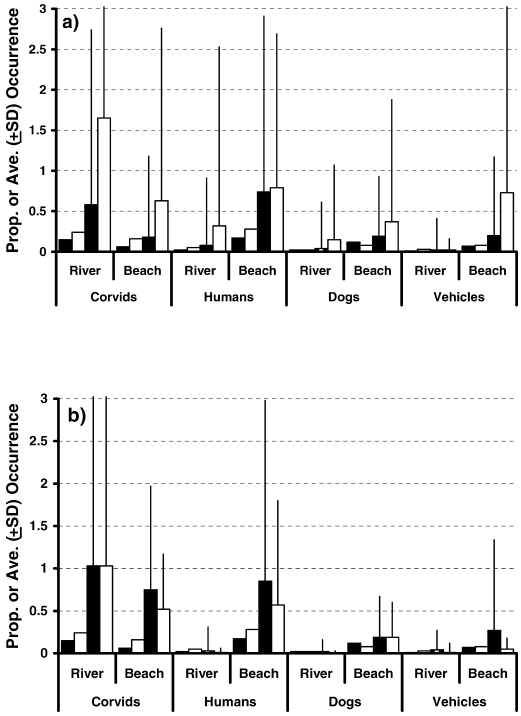

Fig. 5. Proportion (left two histograms) and average (±SD; right two histograms) occurrence of corvids, humans, dogs, and vehicles in river and beaches in coastal northern California based on a) focal observations of Snowy Plover broods in 2001 (■) and 2002 (□) and b) point counts in 2003 (■) and 2004 (□).

turbance associated with weather, and anthropogenic effects. As ground-nesters, shorebirds naturally experience high rates of clutch loss owing to predation (Pienkowski and Evans 1984). Snowy Plover nesting success varies greatly depending on location and year (Page et al. 1983, 1985, 1995). Along the Pacific coast, chronically low reproductive success was identified as a main cause of the population's decline, and control of mammalian predators successfully increased hatching, but not fledging, success (Neuman et al. 2004). Throughout the range of the listed distinct population, corvids are widely recognized as important predators of eggs and chicks (USFWS 2001). In coastal northern California, corvids are probably the principal predator of eggs and chicks, since red foxes have not been recorded in the area; the contribution of gray foxes (*Urocyon cinereoargenteus*) to reproductive failure is unknown. As predators, birds search for prey visually (Blanco and Bertellotti 2002; Underwood and Sealy 2002). Thus, to protect eggs and chicks, managers erect exclosures around nests, and haze, translocate, and kill predators (USFWS 2001).

River-breeding plovers experienced comparatively high nesting (51% overall, 40–66% nests hatch annually) and fledging success (60% overall, 50–77% chicks fledge annually). Consequently, we never used exclosures to protect river nests. By contrast, reproductive success in beach habitats was poor (nesting success: 41% overall, 31–74% annually; fledging success: 28% overall, 9–43% annually) despite the use of exclosures at most nests. On beaches, many failed nests were depredated during the laying stage before we could protect them with exclosures. In 2003, for example, we found 76% (N = 37) of beach clutches with a single egg (i.e., early in the laying period), but predators consumed five of these clutches before we could erect exclosures. Drifting sand driven by strong winds and tidal overwash occasionally caused clutch failure (Colwell et al. 2004).

Greater prevalence of corvids in river than beach habitats suggests that differences in reproductive success derive from habitat features that influence detectability (or crypsis) of eggs and chicks in these two habitats. Specifically, on sandy beaches, observers find nests and occasionally track broods by following plover tracks that are easily followed early in the morning before wind-driven sand covers tracks; this tracking method is not possible in the coarse substrates of the river gravel bars. On several occasions, we observed corvids (*Corvus brachyrhynchos* and *C. corax*) and gulls (*Larus delawarensis*) depredate eggs or chicks, and we often found corvid tracks at depredated clutches in beach habitats (Colwell et al. 2004). We suspect that eggs and chicks are more cryptic in the heterogeneous river substrates (varying in substrate size and color) compared to homogeneous substrates of beaches. Experimental evidence using artificial eggs shows that plover clutches on the river are significantly more cryptic to a naïve human observer than on beaches, and this correlates positively with size and heterogeneity of substrates (M. A. Colwell, unpubl. data). We are currently exploring this hypothesis.

Food availability also may differ between habitats and influence reproductive success. High mortality of Piping Plover (*C. melodus*)

chicks on Atlantic Ocean beaches was caused by starvation, as evidenced by low mass (Loegering and Fraser 1995). Beach-reared Piping Plover chicks starved because they could not reach the wrack line to forage owing to high human use. If food differs between habitats to limit Snowy Plover reproductive success, then beach-breeding plovers may breed later or for shorter periods, lay fewer or smaller eggs, have longer inter-clutch intervals (between failed nests and the first egg of a replacement clutch), incubate and brood longer, and fledge fewer or smaller juveniles. Limited evidence suggests that if food influences reproductive success, it is not consistent with the predictions above. First, breeding chronology differed between habitats, with more early-season nests on beaches than along the river (Fig. 2). Second, the number of eggs laid by females was similar in the two habitats (M. A. Colwell, unpubl. data). Third, there was no difference in egg size between river and beach-breeding plovers (M. A. Colwell, unpubl. data). Collectively, this information suggests that food availability does not strongly influence patterns of reproductive success in beach and river habitats. Unfortunately, we lack additional data to assess these predictions based on food limitation.

Humans may influence habitat quality, in the form of direct mortality to eggs or chicks, chronic disturbance limiting the amount of time that adults incubate eggs or brood chicks, or indirect effects such as attracting predators that scavenge garbage left by humans. Elsewhere in North America, evidence indicates that human activity reduces plover productivity on ocean beaches. In Nova Scotia, Piping Plover reproductive success correlated negatively with human activity (Flemming et al. 1988). In California, mortality of Snowy Plover chicks raised on ocean beaches occurred disproportionately on weekends as opposed to weekdays (Ruhlen et al. 2003), presumably coincident with greater human activity.

In coastal northern California, human activity was far greater on beaches than on the river, regardless of whether the index was derived from focal observations within 100 m of broods or point counts covering broader areas. Each year, we observed instances of humans directly causing clutch (e.g., vandalism of exclosures and removal of eggs, humans stepping on nests, vehicles driving over nests) or brood failure (e.g., humans lingering near a nest and keeping adults from brooding chicks in cold weather). We suspect that the actual rate of reproductive failure owing to humans is higher.

Our monitoring and management efforts may have contributed to some differences in reproductive success between habitats. For example, compared to river habitats, we found nests sooner on beaches owing to the ease of following plover tracks in the sand. Although our footprints near newly found nests may have led predators to clutches, we erected predator exclosures quickly (in 2004, 2.5 ± 3.2 days; range 0–13 d; 70% of nests protected within 2 d), which likely increased hatching success above natural levels. However, once precocial chicks hatched, they left exclosures and were subject to predation and effects of human activity in a less managed setting. Our monitoring also differed somewhat between habitats. Compared to beaches, we visited river habitats less often (Colwell et al. 2004) and checked nests from a closer distance, but we monitored broods similarly in the two habitats. Thus, higher fledging success of river-breeding plovers exists despite greater management on beaches.

Relationship to population status. Snowy Plovers breeding in coastal northern California represent a relatively small, geographically isolated group near the northern limit of the species' range (Page et al. 1995). The 54–74 breeding adults recorded annually during 2001–2004 (Colwell et al. 2004) is similar to the total number (64) counted at seven locations 25 yr ago (Page and Stenzel 1981). However, the estimate provided by Page and Stenzel (1981) is probably low, given their short visit to the area and that nesting along the Eel River was unknown until 1996 (Tuttle et al. 1997)

The average number of young produced annually by river-nesting males (1.5) exceeds that identified in population viability analysis (1.2; USFWS 2001) as necessary for the population to grow moderately for the next 25 yr. High reproductive success of river-breeding plovers is noteworthy given that little management occurs along the river. High reproductive success of river-breeding plovers indicates the need to maintain this high-quality habitat by minimizing future threats such as increased vehicle access and gravel mining, which is restricted dur-

ing the breeding season (mid-March to mid-September).

In contrast to river habitats, reproductive success (0.8) of beach-nesting males is below that required to recover populations (USFWS 2001). Given efforts to manage humans and predators on beaches, it is surprising that productivity is consistently lower than river sites, and it suggests that this habitat may be a demographic sink for the local breeding population. Loegering and Fraser (1995) reached similar conclusions for Piping Plovers breeding on Atlantic Ocean beaches compared to salt marsh and bay beach habitats.

Poor reproductive success of beach-nesting Snowy Plovers suggests that current management practices should be altered to improve fledging success. Although exclosures have increased hatching success, positive covariation between hatching and fledging success for ground-nesting shorebirds (Oring et al. 1991) suggests that predators adept at finding eggs are similarly effective at depredating chicks. Data from coastal central California corroborate this notion. In a comparison of Snowy Plover reproductive success before (7 yr) and after (9 yr) removal of non-native mammalian predators, Neuman et al. (2004) demonstrated an increase in hatching but not fledging success. They suggested that this resulted from other (avian) predators eating chicks.

Low reproductive success of beach-breeding plovers suggests that additional approaches (e.g., hazing, trash clean-up, predator removal) to current predator control measures (e.g., exclosing nests, fencing breeding areas) may be warranted. By contrast, high reproductive success in river habitats does not warrant predator control measures. Humans may have numerous potentially negative impacts on plovers (USFWS 2001) including destruction of nests and chicks by vehicles, pedestrians, and dogs, increased disturbance leading to reduced incubation or brooding constancy, and decreased foraging opportunities by adults and chicks. In 2004, we used symbolic fencing to protect nesting and brooding habitats in an area heavily used by humans. This resulted in an increase in number of fledged chicks over the previous two years (Colwell et al. 2004); however, this same area had high fledging success in 2001 when no fence existed. We endorse this method of improving habitat quality for beach-nesting plovers where plovers breed in close proximity to areas of high human activity.

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