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Arrival times, laying dates, and reproductive success of Snowy Plovers in two habitats in coastal northern California

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ABSTRACT. Habitat quality, as indexed by the reproductive success of individuals, can greatly influence population growth, especially for rare species near the limits of their range. Along the Pacific coast, the Snowy Plover (*Charadrius alexandrinus nivosus*) is a threatened species that, in recent years, has been breeding on both riverine gravel bars and ocean beaches in northern California. From 2001 to 2009, we compared the habitat characteristics, breeding phenology, reproductive success, and abundance of Western Snowy Plovers occupying these two habitats. Similar percentages of yearling and adult plovers returned to gravel bars and beaches, but plovers breeding on gravel bars arrived and initiated first clutches 2–3 weeks later than those breeding on beaches. Despite this delay, however, the mean annual fledging success of plovers on gravel bars (1.4 ± 0.4 [SD]) was double that on beaches (0.7 ± 0.3). Differences in cumulative reproductive success produced a stronger pattern. By their sixth year, males on gravel bars had fledged 14.5 ± 2.1 chicks, more than four times the number of young fledged by males on beaches (3.3 ± 3.1). Over 9 years, local population size decreased by about 75%, coincident with a shift in breeding distribution away from high-quality gravel bars to ocean beaches. This unexpected population decline and shift to poorer quality beaches may have been related to occasional low survival of plovers that over-winter exclusively on beaches in our study area. Consistently low productivity of plovers breeding on ocean beaches suggests the need for intensified management to ameliorate the negative impacts of predation and human activity on the recovery of this population.

RESUMEN. **Tiempo de llegada, fecha de puesta y éxito reproductivo de *Charadrius alexandrinus nivosus* en dos hábitats costaneros del norte de California**

La calidad de hábitat es determinada por el éxito reproductivo de individuos, y esta puede influenciar el crecimiento poblacional, especialmente para especies raras cerca de los límites de su distribución. El Playero Niveo (*Charadrius alexandrinus nivosus*), a lo largo de la costa del Pacífico, es considerado una especie amenazada, que en años recientes se ha estado reproduciendo tanto en bancos de gravilla ribereños como en playas oceánicas en el norte de California. Del 2001 al 2009, comparamos las características de hábitat, fenología reproductiva y la abundancia de playeros níveos que se encontraban en los hábitats descritos. Un porcentaje similar de de individuos de primer año, como de adultos, retornaron a los bancos ribereños como a las playas. Sin embargo, aquellos que se reprodujeron en los bancos, llegaron e iniciaron su primera camada 2–3 semanas más tardes que aquellos que se reprodujeron en las playas. No empece a dicha tardanza, el promedio anual de éxito de los pichones de dejar el nido (1.4 ± 0.4 [SD]) resultó el doble en comparación con aquellos individuos que anidaron en las playas. (0.7 ± 0.3). Diferencias en el éxito reproductivo acumulativo produjeron un patrón más fuerte. Para el sexto año, los machos de bancos ribereños produjeron 14.5 ± 2.1 volantones, esto es cuatro veces más que el número de pichones producidos por machos de playas (3.3 ± 3.1). A lo largo de un periodo de nueve años, la población local se redujo en cerca de un 75%, lo que coincidió con un cambio en la distribución reproductiva, de bancos de gravilla a playas oceánicas. Este inesperado descenso poblacional y cambio a hábitats más pobres, puede estar relacionado a una baja supervivencia ocasional de playeros que pasaron el invierno, exclusivamente, en playas en nuestra área de estudios. La consistente baja productividad de playeros que anidaron en playas, sugiere la necesidad de intensificar el manejo para reducir el impacto negativo de la depredación y actividades de humanos, en el recobro de esta población.

Key words: breeding phenology, *Charadrius alexandrinus nivosus*, habitat quality, reproductive success, threatened species

Habitat loss and degradation are the greatest threat to wild bird populations (Johnson 2007). Consequently, measures of habitat quality are critical to applied ecology and they provide the foundation for management actions directed at ameliorating the effects of anthropogenic and natural factors that limit a population (Caughley 1994). This is especially true for threatened and endangered species, whose small populations often exhibit vital rates that render them vulnerable to extinction.

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For breeding birds, habitat quality is often measured indirectly using density (van Horne 1983), indices of reproductive performance (Vickery et al. 1992), or measures of productivity (e.g., hatching success, nest survival, or fledging success) of individuals (Franklin et al. 2000). However, habitat quality is best defined from the individual's perspective as the per capita rate of population increase associated with a particular habitat (Johnson 2007). This approach is especially powerful when it makes use of marked individuals studied over multiple years so that lifetime reproductive success (as a measure of fitness) can be quantified.

In 1993, the U.S. Fish and Wildlife Service listed the Pacific coast population of Snowy Plovers (*Charadrius alexandrinus nivosus*; hereafter "plover") as threatened under the Endangered Species Act (United States Department of the Interior 1993). The listing was prompted by a reduction in number of occupied breeding sites and declining abundance (Page et al. 1991). Virtually all plovers in the listed population segment breed on sandy, ocean-fronting beaches, saltpans, or dredge-spoil habitats from Washington south to California. Principal factors thought to limit plover productivity in these habitats are: (1) high rates of egg and chick mortality from native (e.g., Common Raven, *Corvus corax*) and introduced (e.g., red fox, *Vulpes vulpes*) predators, (2) disturbance from human recreational use and development on beaches that causes direct mortality of eggs, chicks, and adults, or degrades habitat and indirectly alters behaviors such as nest site selection or chick attendance, and (3) loss and degradation of habitat due to the spread of invasive plants, especially European beachgrass (*Ammophila arenaria*; United States Fish and Wildlife Service 2007).

In 1996, Tuttle et al. (1997) reported a small number of plovers breeding in a unique habitat: gravel bars of the lower Eel River in northern California. In 2000, a monitoring program was initiated in coastal northern California, which is one of six recovery units (United States Fish and Wildlife Service 2007). In 2005, we showed that plovers breeding on gravel bars had significantly higher reproductive success than conspecifics breeding on nearby ocean beaches (Colwell et al. 2005). At that time, most plovers bred on gravel bars. Here, we extend this earlier analysis to include five additional years of data on ∼250 individually marked adult males and females,

resident in the local breeding population for 1–8 years, and we examined return rates, breeding phenology, and a distributional shift in the population away from high quality gravel bars to beaches. We conclude with management recommendations pertaining to these two habitats.

METHODS

We studied plovers in Del Norte, Humboldt, and Mendocino counties of coastal northern California, which constitutes Recovery Unit 2 (RU2) of the species' recovery plan (U.S. Fish and Wildlife Service 2007, Colwell et al. 2009). Over the 9 years that we monitored plovers, nearly all breeding has occurred at 19 sites in Humboldt County (Colwell et al. 2009). These sites fall into two distinct habitats (Table 1): eight sandy, ocean-fronting beaches, and 11 gravel bars scattered along the lower 15 km of the Eel River near its confluence with the Pacific Ocean. On beaches, plovers breed in barren and sparsely vegetated habitats (Muir and Colwell 2010), characterized by native (e.g., *Leymus mollis*, *Abronia latifolia,* and *Cakile maritima*) and introduced (*Ammophila arenaria*) plants. Beach-breeding plovers nested and reared chicks amid a mix of driftwood of varying sizes, small stones, sun-bleached shell fragments, crustacean carapaces, decomposing wrack consisting of brown algae (e.g., *Fucus*, *Egregia*, and *Postelsia*), eelgrass (*Zostera marina*), invertebrates (e.g., *Velella*), and trash. Along the Eel River gravel bars, plovers breed amid coarser substrates ranging in size from fine sands and egg-sized stones to large rocks (Meyer 2005). Gravel bars had sparse vegetation, dominated by white sweet clover (*Melilotus alba*) and scattered willows (*Salix* spp.).

Direct measures of habitat.   From 2005 to 2009, observers collected geo-referenced data (i.e., UTM coordinates) using hand-held personal digital assistants (PDA; Dell Axim 50) equipped with a global positioning system (GPS; Holux GS-271). We collected habitat data at predetermined 20-min intervals signaled by wristwatch alarms during regular surveys for plovers. Observers occasionally skipped 20-min sampling intervals if they were busy collecting other data (e.g., sampling nest site characteristics or recording locations of individually marked plovers) using the PDA-GPS system. We

Table 1. Comparison of habitat characteristics and activity of humans and corvids at gravel bars and ocean beaches.

		Ocean				River			
		Sand	Pea-sized	Egg-sized	Cobble	Sand	Pea-sized	Egg-sized	Cobble
Substrate size[a]		98.8	1.1	0.1	0.0	14.2	10.1	46.1	29.6
			Categories				Categories		
		<10%	10–50%	51–90%	>90%	<10%	10–50%	51–90%	>90%
% Cover[a]	Total ground cover	6.8	62.4	25.8	5.0	18.3	58.4	14.5	8.8
		0	<10	11–100	>100	0	<10	11–100	>100
Number of objects[a]	Live vegetation	70.0	18.8	9.7	1.5	46.1	38.1	13.2	2.6
	Dead vegetation	57.3	32.5	7.9	2.3	77.1	18.0	4.1	0.8
	Eel grass	82.1	11.9	5.6	0.4	100.0	0.0	0.0	0.0
	Brown algae	88.7	10.5	0.8	0.0	98.6	0.8	0.3	0.3
	Large woody	92.7	7.0	0.3	0.0	98.8	1.1	0.1	0.1
	Small woody	35.0	39.0	19.6	6.4	46.6	45.0	6.8	1.6
	Shells, carapaces	45.9	44.9	8.6	0.6	99.0	1.0	0.0	0.0
	Velella	91.3	4.2	1.8	2.7	100.0	0.0	0.0	0.0
	Stones	67.3	20.7	8.7	3.3	84.7	2.9	2.3	10.1
	Garbage	86.5	13.4	0.1	0.0	93.7	6.3	0.0	0.0
Invertebrates[a]	Amphipods	86.3	8.2	4.8	0.7	99.2	0.4	0.4	0.0
	Amphipod burrows	71.7	7.6	11.5	9.2	98.1	0.2	0.7	1.0
	Isopods	99.2	0.6	0.2	0.0	100.0	0.0	0.0	0.0
	Flies	90.4	8.5	0.9	0.1	79.9	15.4	3.7	1.1
	Crane flies	100.0	0.0	0.0	0.0	98.2	1.5	0.1	0.2
	Beetles	98.4	1.6	0.0	0.0	97.7	2.3	0.0	0.0
	Spiders	99.8	0.2	0.0	0.0	98.1	1.9	0.0	0.0
		Incidence[b]		Abundance[c]		Incidence		Abundance	
Activity	Humans	28.7 ± 23.0		1.1 ± 1.3		2.5 ± 4.7		0.05 ± 0.08	
	Dogs	11.3 ± 11.7		0.2 ± 0.2		1.2 ± 3.0		0.02 ± 0.06	
	Horses	0.5 ± 1.0		0.01 ± 0.02		0.0 ± 0.0		0.0 ± 0.0	
	Vehicles	4.8 ± 5.8		0.1 ± 0.2		2.5 ± 4.5		0.03 ± 0.07	
	Corvids	36.2 ± 17.5		1.1 ± 0.8		48.8 ± 21.6		2.4 ± 2.0	

[a] Substrate size, cover, and number of objects and invertebrates are the percent of observations recorded in each category based on 3-m ground plots.

[b] Incidence is the average (±SD) percentage of observations in which at least one individual was recorded during 500-m point counts.

[c] Abundance is the average (±SD) number of occurrences recorded during 500-m point counts.

arbitrarily set the 20-min interval as a reasonable compromise between collecting sufficient habitat data to characterize a site and maintaining some spatial independence between consecutive samples; we did not, however, assess the latter point.

Two types of habitat data were collected at different spatial scales, centered on the location of observers. On a coarse spatial scale, observers first conducted an instantaneous 500-m radius point count, recording the number of humans, vehicles, horses, dogs, corvids, and raptors. Next, we sampled a 3-m radius ground plot at the same location. Observers recorded substrate type (i.e., sand, pea-sized gravel, plover egg-sized stones, or cobble), percentage ground cover (0%, 1–10%, 11–50%, 50–90%, and >90%), and number of ($\log_{10}$ scale; i.e., 0, 1–10, 11–100, and so on) stones, shells, crustacean exoskeletons, live and dead vegetation, small and large (e.g., stumps) woody debris, eel grass, brown algae, and trash. On beaches, we also estimated the number of sets of tracks of species of mammals (e.g., foxes) and birds (e.g., corvids), as well as humans, dogs, horses, and vehicles. We could not reliably collect track data on most gravel bars because firm, coarse substrates rarely yielded imprints. Observers also estimated abundance of potential invertebrate prey (e.g., adult dipterans, beetles, spiders, and amphipods) of plovers and amphipod burrows ($\log_{10}$ scale).

Each year, seasonal patterns of precipitation in the local area varied, with potential consequences for plovers breeding on riverine gravel bars. During prolonged wet seasons or heavy precipitation events, high river flows (>2.5 m depending on the location of the gravel bar) occasionally flooded suitable breeding habitat, even as late as June. By contrast, during dry years, low flows exposed expanses of sparsely vegetated habitat in March. To evaluate annual variation in availability of gravel bars to plovers, we summarized river height based on recordings made at an automated gauge located about midway between the river's confluence with the ocean and the up-river extent of plover breeding; the gauge was within 1 km of the site occupied consistently by the largest number of breeding plovers (Colwell et al. 2009). We collated data by taking the maximum height (m) for each day averaged across month (March, April, May, and June), spanning most of the plover-breeding season. On several occasions coincident with high river levels, we examined the extent of exposed gravel bar; regular surveys for plovers occurred at river levels from 0 to 1.5 m.

Monitoring plovers. We began intensive monitoring in 2000 by banding most adults and hatchlings. Each subsequent year, we marked nearly all breeding adults with a unique combination of four color bands (including the U.S. Fish and Wildlife Service metal band wrapped with colored tape). At hatch, we banded chicks from the same brood with a metal band wrapped with brood-specific colored tape to distinguish them from others of similar age reared in a common area, which facilitated monitoring their survival (Colwell et al. 2007a) and space use (Wilson and Colwell 2010). When chicks returned to breed as adults, we recaptured them and gave them a unique color band combination.

Observers surveyed for breeding plovers during mornings (06:00–12:00) from mid-March until the last chick fledged in late July to early September. Over this 6-month period, observers working alone or, less often, in teams of two or three, visited beaches and gravel bars at a minimum interval of 7–10 days; observers commonly followed the same routes as dictated by access points. When we detected plovers at a site, we increased the frequency of visits, with occupied sites sometimes surveyed daily. During surveys, observers walked slowly through suitable breeding areas (i.e., sparsely vegetated beach, dune, or gravel bar habitats) and scanned for plovers with binoculars and spotting scopes. When we observed plovers, we recorded their color bands, behavior, flock size, and UTM coordinates using an automated data system (ArcPad, ESRI, Redlands, CA) in the PDA equipped with a GPS. Observers also searched for nests when cued by either the presence of plover tracks in the sand or the courtship behavior of adults. When broods were present, we recorded the number of chicks tended by adults for 28 days after chicks hatched (Wilson and Colwell 2010), which is the time required to fledge (Page et al. 1995).

Various county, state, and federal agencies are responsible for managing plovers in our study area. In an effort to mitigate the negative effects of limiting factors, agency personnel managed habitat (i.e., restored native dune ecosystems), humans (i.e., restricted vehicle and human access), and predators. For instance, from 2001

to 2006, nest exclosures protected eggs from predators at 129 beach nests; at least 47 males and 53 females tended eggs in these exclosures on 1–12 occasions over this 6-yr interval. We did not use exclosures with gravel bar nests because the cryptic nature of coarse, heterogeneous substrates (Meyer 2005) resulted in higher nesting success (Hardy and Colwell 2008) and chick survival (Colwell et al. 2007a). Exclosures increased survival of beach nests (Hardy and Colwell 2008) and this undoubtedly altered habitat-specific patterns of reproductive success (i.e., beach-breeding plovers hatched equivalent numbers of eggs, on average, than those breeding on gravel bars; Colwell et al. 2005), although nidifugous chicks reared on beaches perished at higher rates once they left exclosures (Colwell et al. 2007a). Despite the confounding effects of this predator management, we analyzed reproductive success without incorporating the effects of exclosures or other management practices.

Definitions. Analyses are based on individual reproductive histories of 96 males and 119 females monitored over nine years. We defined philopatry and breeding site fidelity as the return of yearlings or adults, respectively, to breed in the habitat where they hatched or bred in a previous year. Arrival date was the first observation of a marked individual in the study area each breeding season. Some plovers were permanent residents in the study area whereas others were migrants (Colwell et al. 2007b). Consequently, we defined the start of the breeding season as 1 March and recorded a resident's arrival as occurring on this date despite being present year-round.

Clutch initiation date was the date on which a female laid her first egg each year; we determined values for males based on social pairings with females. On ocean beaches, plover tracks were often apparent in the sand, which facilitated finding courtship scrapes and nests; as a result, we found many beach nests during the egg-laying stage. By contrast, we were rarely able to find nests using tracks in the coarse substrates of gravel bars. Most gravel-bar nests were found by watching females return to incubate a clutch. For completed clutches, we determined the date of clutch initiation by either back-dating 33 days (65% of clutches require 5–6 days to lay eggs plus 28 days incubation, slightly longer than reported by Page et al. 1995) from the date of hatch or using egg flotation to estimate initi-

ation date (Westerkov 1950). Each individual contributed a single observation (i.e., the average date for the years they bred locally) to analyses of dates of arrival and laying.

To summarize annual reproductive success of marked plovers in the two habitats, we used social pairings between males and females to assign nests, eggs, chicks, and fledglings to individuals. We assumed that extra-pair copulations and nest parasitism were rare in the population, although extra-pair copulations have been reported at low rates in populations breeding at higher density than the one we studied (Küpper et al. 2004). We determined reproductive success based on the total number of young fledged (i.e., reached 28 days of age; Page et al. 1995) by individuals each year and over the years they bred locally. We determined a bird's cumulative reproductive success by summing annual records across years. In a few cases, individuals skipped years; we omitted these birds from analyses comparing reproductive success in gravel bar and beach habitats.

Data summary and analyses. We summarized habitat data based on ~10,750 plots (i.e., 500-m point counts and 3-m ground plots) sampled on gravel bars (28% of observations) and beaches (72%) over 5 years. For the two habitats, we summarized data as the percentage of total observations in various categories of cover and abundance. We summarized human and corvid (Common Raven and American Crow, *C. brachyrhynchos*) activity based on the incidence (percentage of total point counts with at least one occurrence) and abundance (average number of encounters during a point count) of humans, vehicles, dogs and horses separately, and combined observations of ravens and crows.

We analyzed philopatry and site fidelity based on the return of individuals to the habitat (gravel bar vs. beach) where they either fledged or bred in a prior year. Many yearlings first bred within a few kilometers of their natal sites (Colwell et al. 2007b). In analyzing philopatry, we tallied the return of individuals once (nearly always as yearlings) for comparisons using chi-square analysis. For adult returns, however, we included each individual's "return" for as many years as they bred locally, yielding a chi-square analysis based on "bird years." In other words, we used individual records across multiple years to describe return rates of plovers occupying the two habitats. We did not account for the

effects of reproductive success in these analyses because there was no clear difference in dispersal for known-age plovers that were successful and unsuccessful in hatching chicks (Colwell et al. 2007b). Likewise, we used records of arrival and nest initiation for comparisons of breeding phenology between habitats. We summarized data for each year as the average Julian date, and compared habitats using a paired *t*-test to control for annual variation in weather and its effects on the timing of breeding.

Most plovers bred in just one habitat (Colwell et al. 2007b), and they often did so for multiple years. We examined reproductive success between habitats in two ways. First, we compared annual reproductive success of males breeding in the two habitats using a paired *t*-test; the 9 years constituted the paired observations. Second, we tested for habitat differences in cumulative reproductive success using a *t*-test of the slopes of the lines for gravel bar and beach habitats. We used regressions with number of years breeding (i.e., one, two, three, and so on) and habitat (gravel bar vs. beach) as predictors of cumulative reproductive success. We conducted separate analyses for males and females because of differences in parental care (Page et al. 1995) and survival (Mullin et al., in press). Each bird contributed a single observation to analyses, corresponding to the cumulative number of young it had fledged in its final year in the local population. We report means ±1 SD.

Fig. 1. Mean (±SD) (A) seasonal (*N* = 9 years) and (B) annual (*N* = 5 months) variation in height of the Eel River, Humboldt County, California over 9 years. Dashed line indicates the height of the river at which gravel bars were inundated.

RESULTS

Habitat characteristics. The habitat features of gravel bars and beaches differed (Table 1). Open, sparse vegetation predominated in both habitats, but the types of ground cover differed. Gravel bars were covered by a heterogeneous mix of sand and coarse substrates, whereas beaches were typified by uniform fine sands. Marine debris (brown algae, eel grass, shells, and carapaces) was more abundant on beaches and nearly absent from gravel bars. Woody debris was present in both habitats to a similar extent. Potential invertebrate prey for plovers differed between habitats. Amphipods (*Megalorchestia* spp.) were especially numerous on beaches and absent from gravel bars where terrestrial arthropods were more abundant. Finally, human activity was nearly 10 times higher
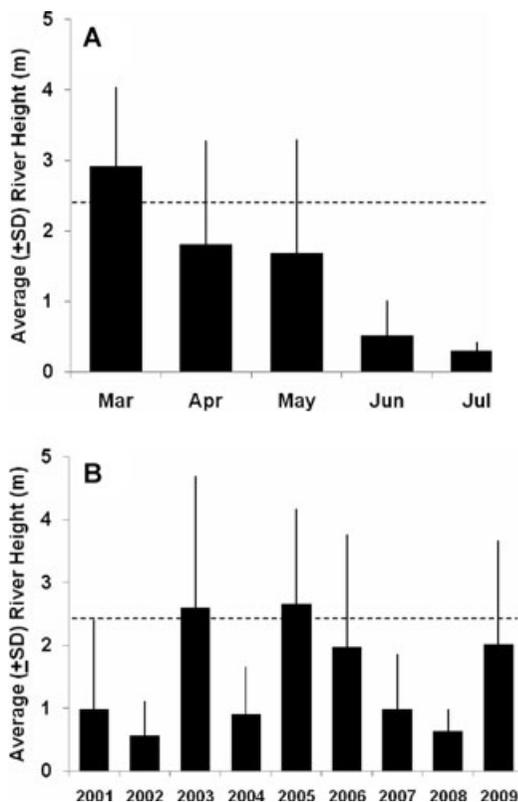
on beaches than gravel bars. Corvid activity, although variable, was similar between habitats.

High river levels commonly flooded gravel bars, especially early in the breeding season (Fig. 1A). During the 9 years we monitored plovers, there was substantial annual variation in availability of breeding habitat (Fig. 1B). Four years were especially wet, with high water during March, April, May, and even June. In other years, low river levels exposed extensive gravel bars beginning in March. On beaches, spring tides and high surf occasionally over-washed nests. However, this cause of nest failure was rare and constituted a small percentage of breeding attempts annually (Colwell et al. 2009).

Philopatry and fidelity to habitats. From 2001 to 2008, 369 chicks fledged, including 200 from gravel bars and 169 from beaches (Table 2). Fifty-eight (16%) fledglings

Table 2. Return rates of female and male Snowy Plovers to their natal habitats in coastal northern California. Data are percentage (*N*) of individuals reared in river or ocean habitats that returned locally to breed.

Breeding habitat	Natal habitat			
	River		Ocean	
	Female	Male	Female	Male
River	77 (10)	73 (11)	36 (5)	19 (3)
Ocean	23 (3)	27 (4)	64 (9)	81 (13)
Total fledglings	200		169	
Total returning	13	15	14	16

Fig. 2. Mean (±SD) date of arrival and initiation of the first nest of the year was significantly earlier for beach-breeding male and female Snowy Plovers compared to those on gravel bars of the Eel River, Humboldt County, CA.

returned to breed locally, including 31 males and 27 females; all but four of these plovers first bred locally as yearlings. Nearly equal numbers of returning young came from gravel bars ($N = 28$) and beaches ($N = 30$). Overall, philopatry did not differ between habitats ($\chi_1^2 = 1.0$, $P = 0.40$), with 14% and 18% of hatchlings returning to gravel bars and beaches, respectively. Similarly, we found no gender difference in philopatry ($\chi_1^2 = 0.1$, $P = 0.76$), with 77% of males and 70% females returning to breed in the habitat type where they fledged. Overall, fledglings from gravel bars (75%) and beaches (73%) returned to their natal habitats at similar rates ($\chi_1^2 = 0.0$, $P = 1.0$).

Over 9 years, 215 individually marked adult plovers (119 females and 96 males) bred in gravel bar and beach habitats. Site fidelity to gravel bars and beaches differed between the sexes, with females (54%) returning to gravel bars at a lower rate than males (72%; $\chi_1^2 = 6.0$, $P = 0.01$). However, we found no sex bias in site fidelity on beaches (48% for females and 57% for males; $\chi_1^2 = 1.6$, $P = 0.21$). Males were more likely to return to gravel bars than beaches ($\chi_1^2 = 4.8$, $P = 0.03$), whereas females returned to gravel bars and beaches at similar rates ($\chi_1^2 = 0.4$, $P = 0.52$).

Arrival and clutch initiation dates. Breeding schedules of plovers in the two habitats differed, especially when high water delayed the return of birds to gravel bars (Fig. 2). Plovers arrived earlier at beaches (males: 17 days, $t = 3.0$, $P = 0.03$; females: 33 days, $t = 5.5$, $P = 0.003$) than gravel bars. As a result, beach-breeding females laid their first eggs an average of 18 days earlier than those on gravel bars ($t = 4.0$, $P = 0.004$).

Reproductive success. Mean annual fledging success of males on gravel bars (1.4 ± 0.4) was double that of males on beaches (0.7 ± 0.3; $t = 4.0$, $P = 0.004$; Table 3). These consistent annual differences resulted in a significant gain in cumulative reproductive success for river-breeding males based on a significant difference in slopes ($t = 4.3$, $P = 0.0001$; Fig. 3A). In their first year, gravel bar-breeding males produced approximately 1.4 fledglings, and added an average of 2.8 ± 1.5 offspring with each successive year so that, after 6 years, individuals had produced an average of approximately 14 fledglings. By contrast, males breeding for the first time on beaches reared 0.6 chicks, and added an average of 0.5 ± 1.1 young each successive year; by a comparable age, they had fledged an average of approximately four young. The pattern for females was marginally significant ($t = 2.0$, $P = 0.05$; Fig. 3B). Females in the population were present for shorter intervals and, consequently, their cumulative reproductive success was half that of males. Still, females breeding in their first year on gravel bars produced an average of 1.6 ± 1.5 fledglings, whereas beach-breeding females produced less than half that number of fledglings (0.7 ± 1.0). With each successive year, females on gravel bars (1.2) and beaches (1.5) added similar numbers of fledglings.

Population size. The number of plovers breeding in our study area declined by 75% over the 9 years of our study, and the remaining plovers shifted from breeding on high-quality

Table 3. Annual variation in the distribution and per capita reproductive success of Snowy Plovers breeding in riverine gravel bar and ocean beach habitats in coastal northern California.

	Year								
	2001	2002	2003	2004	2005	2006	2007	2008	2009
Breeding adults									
River	48	41	31	31	18	18	5	4	4
Beach	21	29	28	40	42	39	24	32	15
Percent population									
River	65.6	54.0	50.8	39.0	27.3	28.8	25.0	13.5	21.0
Beach	34.4	46.0	49.2	61.0	72.7	71.2	75.0	86.5	79.0
Fledging success									
River	1.3 ± 1.6	0.7 ± 1.0	1.6 ± 1.5	1.3 ± 1.1	1.1 ± 1.2	1.1 ± 1.3	1.7 ± 0.6	2.0 ± 1.4	1.5 ± 2.1
Beach	1.3 ± 1.0	0.4 ± 1.1	0.8 ± 1.3	0.9 ± 1.1	0.7 ± 1.0	0.5 ± 0.7	0.5 ± 0.9	0.3 ± 0.8	0.8 ± 1.4

gravel bars to beaches (Table 3). From 2001 to 2006, there were 57–71 breeding adults. In 2007, the population began to decline and, by 2009, was down to 19 breeding adults. Coincident with this decline, the total number ($r_s = -0.95$, $P = 0.001$) and percentage ($r_s = -0.97$, $P = 0.001$) of plovers breeding on gravel bars declined. Although the number of plovers breeding on beaches remained steady ($r_s = -0.11$, $P = 0.76$), a greater percentage bred on beaches with each successive year ($r_s = 0.97$, $P = 0.0001$).

DISCUSSION

Habitat quality. Reproductive success, both annual and cumulative, differed markedly between habitats. Gravel bar-breeding males produced twice the number of fledglings annually and nearly four times the number of young over their local tenure compared with males breeding on beaches and, for females, the pattern held, but was less pronounced. These differences occurred despite average arrival and clutch initiation dates that were 2–3 weeks earlier on beaches than gravel bars. In particularly wet years (2003 and 2005), breeding on gravel bars was delayed nearly 2 months of the 4-month nesting season. Thus, earlier arrival did not confer a reproductive advantage to beach-breeding Snowy Plovers in our study. In contrast, for sequentially polyandrous Spotted Sandpipers (*Actitis macularius*), experienced adults (those that bred locally in a previous year) arrived 7–10 days earlier than newcomers (Oring and Lank 1982), giving older birds a significant reproductive advantage (Oring and Lank 1986).

Snowy Plovers also have a sequentially polygamous mating system (Page et al. 1995). Females pair with males and share in incubation of a three-egg clutch; after hatching, males perform most parental care of chicks, and females search for additional mates. As a result, females may breed successfully up to three times a year along the Pacific coast, whereas males may breed successfully only twice. Therefore, advantages of early arrival and clutch initiation should result in higher reproductive success, especially for beach-breeding plovers.

Habitat, however, was not comparable between gravel bars and beaches, as indexed by direct measures of habitat and reproductive success. Human activity was much higher on beaches and, although corvid activity was similar, the heterogeneous substrates resulted in greater crypsis of eggs and chicks, resulting in higher survival of nests (Hardy and Colwell 2008) and broods (Colwell et al. 2007a) on gravel bars. The principal causes of nest failure in our study were predation by corvids and, to a lesser extent, direct mortality and disturbance caused by humans (Colwell et al. 2009). Recently, we used video cameras to show conclusively that corvids, principally Common Ravens, predated >90% of clutches at one beach location that consistently has a large proportion of the local population (Colwell et al. 2009). Cameras and other indirect evidence show that humans also cause nest failure in both habitats (Colwell et al. 2009).

Assessment of habitat quality based on cumulative reproductive success of females was less clear than for males, which may be related to several facets of their mating system. Although
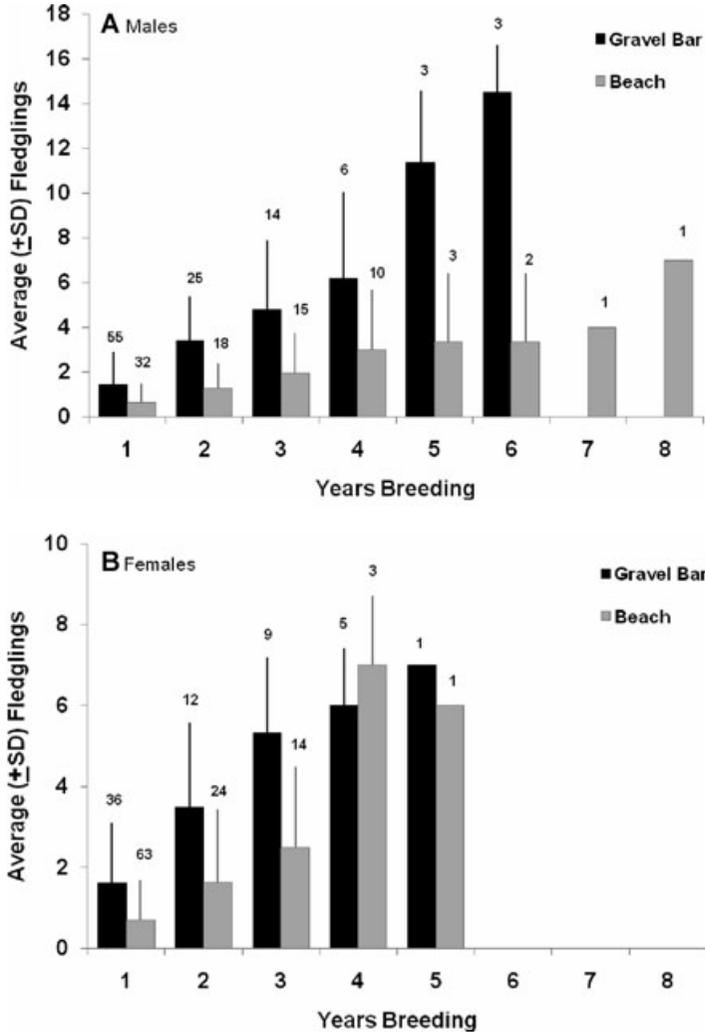
Fig. 3. Mean (±SD) cumulative reproductive success of (A) male and (B) female Snowy Plovers breeding on gravel bars was significantly greater than for those on ocean-fronting beaches in Humboldt County, CA. Samples sizes are shown above columns.

males and females have similar detection probabilities (Mullin et al., in press), females have lower apparent survival (Stenzel et al. 2007, Mullin et al., in press), possibly because females tend to wander more widely during the breeding season in search of mates. Support for this comes from differences in short- and long-term tenure in the local population. Females were present for a maximum of 5 years; by contrast, males bred locally for up to 8 years. In many, but not all, species of shorebird, females experience lower survival and sometimes lower detectability than males (Colwell 2010).

In our study area, apparent survival of females was lower than for males, but there was no sex difference in detection probabilities (Mullin et al., in press). These differences indicate that habitat quality is best assessed with measures of reproductive success collected for the sex that exhibits stronger site fidelity and that limits population productivity, in this case male Snowy Plovers.

Population decline. Despite high reproductive success of a large number ($N = 48$) of plovers breeding on gravel bars, our study population (RU2) declined by 75%; this decline

was especially precipitous over the last 5 years beginning in 2005. With each year, fewer plovers bred on gravel bars and a smaller number (albeit a greater proportion of the population) bred at several beaches, where productivity was especially low (Colwell et al. 2009). This distributional shift coincided with a series of years (2003–2006) when river levels delayed arrival and clutch initiation, and occasionally washed away nests (Colwell et al. 2009). Although the population decline may have stemmed from high river levels prompting plover movement away from gravel bars to beaches, several observations suggest otherwise and point to a region-wide decline in the Snowy Plover population. First, there was no significant difference in philopatry and adult female site fidelity between habitats; in fact, males exhibited higher fidelity to gravel bars than beaches, a pattern consistent with a positive relationship between breeding success and site fidelity (Oring and Lank 1984). Second, few birds moved between gravel bars and beaches either within or between years, and these individuals moved in both directions (Colwell et al. 2007b). Third, during the last 5 years of monitoring, the abundance and site fidelity of beach-breeding plovers declined parallel to those on gravel bars. Finally, the abundance of wintering plovers in our study area correlated positively (0.42) with numbers of breeding plovers over the 9 years we studied the population (Colwell, unpubl. data). Collectively, these observations suggest that the decline in the local breeding population, and specifically the subset of plovers that bred on gravel bars, was driven more by regional scale annual variation in population vital rates rather than the effects of high river flows on productivity and dispersal. Mullin et al. (in press) reported a significant drop in adult survival for this population in 2007, and Stenzel et al. (2007) demonstrated appreciable annual variation in survival (0.28–0.58) of juvenile Snowy Plovers in a population in coastal central California that is connected to the RU2 population by dispersal (Stenzel et al. 1994, Colwell et al. 2007b).

Our findings offer a perplexing contradiction between individual-based measures of habitat quality (i.e., reproductive success) and population-level responses (i.e., local density) for a small population. On the one hand, reproductive success was much higher on gravel bars, but numbers there declined despite comparable

or higher levels of site fidelity by young and adults. By contrast, poorer quality beach habitats continue to be occupied, albeit by fewer plovers that constitute an increasing proportion of the local breeding population. Increasing evidence indicates that shorebird population growth is most sensitive to annual variation in adult survivorship rather than productivity (Sandercock 2003). Currently, we lack sufficient data to analyze habitat-specific patterns of survival for plovers in our study area. However, the overwintering habits of marked birds suggest that analyzing habitat-specific survival will be complex. All plovers that breed on gravel bars leave these habitats at the end of the breeding season to overwinter on beaches, often only a few kilometers away. This is probably because food availability is higher on beaches than gravel bars during the winter, and attachment to specific locations provides benefits from social interactions with conspecifics (Brindock and Colwell in press). By contrast, beach-breeding plovers commonly over-wintered in the same habitats and near where they bred (Colwell et al. 2007b). We suspect that the dynamics of social interactions of wintering plovers, especially yearlings searching for a mate or breeding site, may shed additional light on why numbers of gravel bar-breeding plovers have declined. Specifically, if young birds pair for the first time with an experienced breeder while resident in a late winter flock, they may be more likely to follow their mate to another breeding site rather than being philopatric. However, yearlings that remain unpaired later in spring (i.e., after winter flocks have broken up) may be more likely to return to their natal site as first-time breeders.

Management recommendations. Annual estimates of reproductive success bracket the per capita value (1.0 fledgling per male) necessary to maintain the listed population segment (Nur et al. 1999). The higher fledging success on gravel bars indicates that this may be a source habitat, whereas beaches are sinks (Pulliam 1988, Mullin et al., in press). These habitat contrasts are surprising given that management of limiting factors (United States Fish and Wildlife Service 2007) in our study area has occurred to varying extents at many beaches and was almost nonexistent on gravel bars. For instance, on beaches: (1) nest exclosures were successfully used to reduce egg predation and boost hatching success for 6 years (Hardy and

Colwell 2008), (2) fences and signage have been used to reduce disturbance to breeding plovers and increase fledging success at one site (Wilson and Colwell 2010), and (3) restoration has increased the amount and quality of native dune habitat, thus making it more attractive to nesting plovers (Muir and Colwell 2010). Still, the productivity of beach-breeding plovers declined steadily over 9 years (Colwell et al. 2009), and it was consistently lower than on gravel bars. Clearly, management has been ineffective in addressing factors limiting population recovery in our study area. Therefore, we urge renewed efforts to manage productivity in beach habitats. In particular, given the strong evidence that predators, especially corvids, are the main cause of lowered productivity (Colwell et al. 2009), we argue for more intensive management, including consideration of lethal methods of predator control at some locations. In addition, we stress the need for continued efforts to protect from human disturbance the few plovers that breed in high quality habitat along the Eel River. Finally, recovery of the population may hinge on increasing over-winter survival. If so, then managing the causes of over-winter mortality to adults and juveniles will be especially challenging, especially if raptors are the main predators of wintering plovers.

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