Movements and Fledging Success of Snowy Plover (*Charadrius alexandrinus*) Chicks

CAROL A. WILSON* AND MARK A. COLWELL

Department of Wildlife, Humboldt State University, Arcata, CA, 95521, USA

*Corresponding author; E-mail: capepeirce@yahoo.com

Abstract.—Movements of adult Snowy Plovers (*Charadrius alexandrinus nivosus*) tending broods were examined in coastal northern California. Chicks moved an average of 518 ± 52 m from their nests one to three days after hatch; thereafter, movements decreased. In their first ten days, there was no difference in distances moved or home range size between chicks that eventually fledged and those that died. Plovers consistently used the same areas of the beach each year, and these areas were positively associated with nest locations and negatively correlated with human activity. A fenced refuge for breeding plovers was created in the area most used by humans. Fledging success doubled in the refuge during the five years it was protected (37% chicks survived), compared to three years when the area lacked protection (15% chicks survived). *Received 20 February 2009, accepted 28 May 2010.*

Key words.—brood, chick movements, fledging success, disturbance, human activity, management, plover, refuge, shorebirds.

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Young of precocial birds (e.g. shorebirds, waterfowl) leave the nest shortly after they hatch and are led by parents to areas that provide food, cover and protection from danger posed by predators and humans (Loegering and Fraser 1995; Lengyel 2006). Brood-rearing areas occur at varying distances from the nest (Newell *et al.* 1985; Cooper 1994; Robinson *et al.* 1997; Mainguy *et al.* 2006). The movement of chicks to these areas entails costs (Johansson and Blomqvist 1996; Kosztolanyi *et al.* 2006), especially for recently hatched chicks that are not well developed in their motor capabilities, capacity for thermoregulation and ability to evade danger (Schekkerman and Visser 2001). Furthermore, movements of young birds may be constrained by habitat (Galbraith 1988). However, little is known of age-dependent movement of precocial birds (Rupert 1997; Plissner *et al.* 2000).

Age-related movements of young Snowy Plovers (*Charadrius alexandrinus nivosus*, hereafter, plovers) were studied to evaluate the relationships between habitat and fledging success. Plover chicks fledge approximately 28 days after they hatch (Page *et al.* 1995) and are typically cared for by the male. As they age, chicks become increasingly mobile and respond to disturbance by predators and humans by moving away from threats (Colwell *et al.* 2007a). As breeding habitat is lost, knowledge of how and where chicks move will be essential to managing habitats. The Pacific Coast population segment of the Snowy Plover was listed as threatened in 1993 (U.S. Fish & Wildlife Service 1993) and its recovery plan suggests that habitat quality in breeding areas has declined. Consequently, movements of plover broods were investigated to understand how habitat, including threats from humans and predators, influenced chick distribution and likelihood of fledging. In addition, movements and fledging success were examined in an area protected from human disturbance, with the aim of increasing plover reproductive success.

METHODS

Study Area

Research was carried out from 2001-2008 at Clam Beach, a 10-km ocean-fronting beach in Humboldt County, California, that is a popular recreational site. Human activity on the beach varies seasonally, with highest use (e.g. vehicles, clammers, equestrians and dogs) occurring on the north half in most years, near where most humans accessed the beach. Driving was allowed on the waveslope (the wetted portion of the beach, in the intertidal zone). In 2004-2008, a temporary protected area was created to provide a refuge for plovers during the breeding season. The 8-ha protected area was established along a 1-km stretch of beach where high human activity co-occurred with the highest plover breeding density. The protected area was located above the high tide line and backed by dunes thickly vegetated with European Beach Grass (*Ammophila arenaria*). A symbolic rope perimeter fence was posted with signs that requested cooperation in not entering the area. Detailed descriptions of the study area are provided elsewhere (Colwell *et al.* 2005, 2007a, b).

Field Methods

Adult plovers were banded with a combination of four color bands; siblings in a brood were marked with a single metal band (U.S. Fish & Wildlife Service), wrapped with brood-specific colored tape to distinguish broods of similar age. Surveys for plovers were conducted every 1-4 d from mid-March through the end of the breeding season by walking and scanning with binoculars and spotting scope for plovers, and searching for nests. During surveys, locations of nests, adults and broods were recorded with a handheld global positioning system -personal digital assistant (GPS-PDA) (GPS; 2001-2004, Garmin 76, Garmin Corporation, Olathe, Kansas, accuracy 15 m; 2005-2008, Axim X50 PDA, Dell Corporation, Round Rock, Texas with Ultra chip, Holux Corporation, Hsinchu City, Taiwan, accuracy 3 m). These locations were used to calculate movements of chicks. On rare occasions (4/653 observations) when observers could not see chicks, brood tracks or the behavior (alarm calls, distraction displays) of the male indicated that young were present (Page *et al.* 1983). In these instances, the location where a male had brooded chicks, as indicated by clustered tracks in sandy substrates, was recorded.

In 2005 and 2006, data indexing human activity, predation threat and habitat were collected at two spatial scales (500 m and 3 m) using the PDA-GPS system. Sampling occurred at predetermined intervals (20-min) prompted by a wristwatch alarm. A 500-m radius, instantaneous point count method was used to tally the number of Common Ravens (*Corvus corax*), American Crows (*C. brachyrhynchos*), raptors, humans, dogs, horses and vehicles. Next, a 3-m radius plot was sampled on the ground, tallying the number (0, 1-10, >10) of sets of animal (corvids, dogs, horses, feral cats) and human (pedestrian, vehicle) tracks less than 24 h old. Tracks were used as an index of predators (Engeman and Allen 2000; Kruse *et al.* 2001). Finally, percent and type of ground cover were estimated for live and dead vegetation, tide cast marine algae and invertebrates, woody debris and stones (see Wilson 2007 for details).

Data and Analysis

Brood locations were projected onto an ortho-rectified aerial photograph of the study area with a scale of 0.17 m/pixel (13 November 1999, U.S. Fish & Wildlife Service, Arcata, California) in a Geographic Information Systems (GIS; ArcGIS version 9.1, ESRI, Inc., Redlands, California). Two measures of daily movements of adults tending broods were estimated using Hawth's Analysis Tools extension (Beyer 2004), the straight-line distance between a daily location and: 1) the previous day's location, and 2) the nest where chicks hatched. A third measure, brood home range, was estimated on a north-south axis, due to the long and narrow extent of suitable breeding habitat at Clam Beach, which constrained east-west movements of adults rearing broods to less than 100 m. The brood home range was determined from the distance between the most southerly and northerly locations used by a brood (Novoa *et al.* 2006); cumulative home range was calculated each day.

ANOVA was used to test for annual differences in each of the three measures of brood movements. There were no differences among years in distances that males with broods moved between consecutive days ($F_{5,49} = 2.4$, $P = 0.93$) or from the nest site ($F_{5,51} = 0.95$, $P = 0.46$). Likewise, the size of brood home range did not differ among years ($F_{5,52} = 0.47$, $P = 0.80$). Consequently, data were pooled across years. Linear regressions were used to assess the relationship between chick age and each of the three measures of brood movements.

Fledging success was determined as the percentage of chicks and broods that survived 28 d. The three measures of movement were compared between broods that fledged at least one chick and those that failed. Analyses were restricted to a brood's first 10 d because the majority (83%) of broods failed by this time (Colwell *et al.* 2007a). Comparing older broods would have biased the sample toward the movements of fledged chicks. A Mann-Whitney *U*-test was used for comparisons because data were not normally distributed.

The spatial distribution of broods was characterized by partitioning the study area into 18 500-m sections from north to south and calculating the annual proportion of total locations in each section (hereafter, brood use). Kendall's coefficient of concordance (*W*; Siegel 1956) was used to evaluate the consistency of brood distribution among the beach sections across years. For each year, the 18 sections were ranked in order of brood use. The null hypothesis was that the sections ranked differently (e.g. were randomly used by broods) each year. The alternative hypothesis was that the sections ranked (by brood use) in the same order during at least two years. The value of *W* assesses the degree to which the years exhibited a concordant ranking of the beach sections, with 0 being no agreement among years and 1 being complete agreement among all years (Legendre 2005).

An information theoretic approach incorporating multiple linear regression was used to evaluate the influences of human activity, habitat and predator activity on the spatial distribution of broods (Burnham and Anderson 2002). Two sets of candidate models were developed for the two years (2005 and 2006) in which detailed data on human activity, habitat and predator activity were collected. The response variable was the proportion of brood use each year that occurred within various 500-m sections of beach; this analysis only used broods that survived at least 10 d. The spatial distribution of broods aged from 1-10 d was highly correlated with that of broods that fledged in 2005 ($R^2 = 0.91$, $P < 0.0001$) and 2006 ($R^2 = 0.98$, $P < 0.0001$), suggesting that this sample of broods was representative of habitat characteristics that may influence fledging success.

Selection of predictor variables was based on previous research (Colwell *et al.* 2005, 2007a, b), field observations, and factors contributing to the population's decline (U.S. Fish and Wildlife Service 2007). Some variables were highly correlated; consequently, one was chosen as an index (Driscoll *et al.* 2005). Human tracks were positively correlated with several other variables (e.g. number of humans, number of dogs and dog tracks), and all categories of ground cover (including wrack, a source of invertebrates) were positively correlated and collapsed into "cover". Proximity to the intertidal zone (beach width) and areas of persistently wet sand were included to examine brood use of habitats that may provide sources of invertebrate prey. To evaluate the influence of nest proximity on brooding areas, the annual proportion of nests in each section of beach was included in one set of models. Nests were excluded in the second analysis to assess variables that may have influenced the selection of brood rearing areas, but were masked because they also influenced nest site selection (e.g. if nest sites and brood rearing areas co-occurred). Otherwise, all predictor variables were the same for both years: vehicle tracks, human tracks, cover, wet sand, beach width, corvid tracks and the frequency with which corvids were recorded during point counts.

Akaike's Information Criterion adjusted for small sample size (AIC_c, Burnham and Anderson 2002) was used to assess relative support for the different models. The AIC_c weights (w_i) (representing the weight of evidence in favor of model *i* being the best model) were used to evaluate the best-fitting models. When there was no best fit (i.e. when a number of models had similar weights, or the weight of the highest-ranked model was low), inference was based on more than a single model (Anderson *et al.* 2001; Greaves *et al.* 2006), and model averaging [w_+ (*j*)] was used to evaluate the relative importance of single predictor variables (*j*).

To examine the effect of the protected area on fledging success, a chi-square goodness-of-fit test was used (Neu *et al.* 1974). In cases where an expected cell frequency was less than 5 (due to small sample size), the *P*-value for Fisher's Exact Test was reported. To determine if there was a difference in fledging success before (2001-2003) and after (2004-2008) creation of the protected area, a Before-After-Control-Impact analysis was used (Stewart-Oaten *et al.* 1986). The percentage of chicks and broods that fledged before and after establishment of the protected area were compared on three areas of the beach: 1) the protected sections within the fence, 2) unprotected sections on the north half of the beach, and 3) unprotected sections on the south half of the beach. These areas were selected because they were the most similar to (and thus the most likely to be influenced by the same factors as) the protected area (Eberhardt and Thomas 1991). However, neither unfenced site was a perfect match to the fenced area in all characteristics. The unfenced north half of the beach, adjacent to both ends of the protected area, had similar traffic and human-use levels, but lower brood use. The unfenced south half of the beach had the most similar levels of brood use to the protected area, but it was approximately one km away from the protected area and experienced lower traffic and human-use levels. Though chicks within a brood are not considered independent samples in some studies (Winterstein 1992; Flint *et al.* 1995), the authors of this study make the case that as chicks age, they behave and move independently of one another and, therefore, can be considered independent, a finding supported by our data (Colwell *et al.* 2007a).

RESULTS

Over six years (2001-2006), 26 males and one female cared for 58 broods (154 chicks) that survived at least one day (Wilson 2007). Of these broods, 29 fledged at least one chick and 29 failed. Individuals reared one to eight broods over the six years. Six males produced two consecutive broods in a year, but only one fledged both broods. Most (22) males bred on Clam Beach for one or two years; five males were present for three to six years.

Movements

Chicks varied in the distances moved in the first three days after hatch, ranging from 0 to 2723 m and averaging 518 ± 52 m from their nest. There was no strong relationship between chick age and distance moved on a daily basis, from the nest, or as a home range (Fig. 1). However, as chicks matured, the distances they moved tended to decrease. Broods that fledged at least one chick did not differ from unsuccessful broods in the distances they moved, either between consecutive days, from their nests, or in home range size (Table 1).

Habitat Relationships

The distribution of brood locations in the study area was consistent among most years (2001-2006; $W = 0.44$, $P < 0.001$; Fig. 2). Brood use was high in the protected area across all years and grew substantially higher on a 1 km stretch of beach in the south part of the study area during the latter four of six years. No single habitat model ranked high in predicting brood distributions (Table 2) in 2005 (all AIC weights < 0.28) or 2006 (all AIC weights < 0.19). In both years, the distribution of nest locations was the most important variable predicting brood use: areas of high nest density tended to have high brood use. In 2006, brood use was also positively associated with areas of wet sand. With nest removed from analyses, no single model clearly outperformed any other (Table 2). "Human tracks" was the strongest predictor, negatively associated with brood use in both years.

Effectiveness of the Protected Area

The protected area was established in a location favored by plovers between two

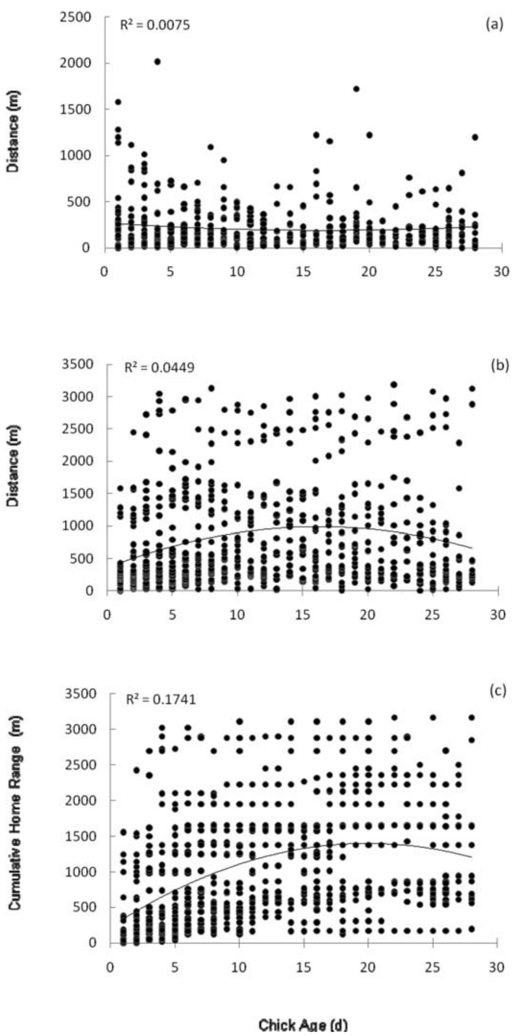

Figure 1. Age-related variation in distance of adult Snowy Plovers and broods a) between consecutive days, b) from nest, and c) between the most northerly and southerly locations (i.e. cumulative home range) on Clam Beach, Humboldt County, California, 2001-2006. Note scale change in b and c.

principal access points for recreationists. Prior to establishment of the protected area, males rearing broods in this area moved shorter distances (Table 3) from their nests compared with males elsewhere on the north end of Clam Beach; however, distances between successive daily locations were similar. Once the fence was in place, broods in the protected area moved shorter distances on a daily basis and from their nest compared with those reared elsewhere on the beach; both these differences were significant (Table 3).

Over eight years (including three years when the fence was not in place), all 15 broods that hatched in the protected area remained there. Broods hatched elsewhere on the north end of the beach often moved into the protected area both before (80%, n = 5) and after (50%, n = 8) the fence was in place. Some broods moved 1-3 km shortly after hatch to reach this area of the beach. Most (96%) of these broods came from the north end of Clam Beach.

The protected area was used disproportionately by broods ($\chi^2 = 523_1$, $P < 0.001$). Over eight years, 34% (N = 20) of broods were reared in this area, which represented 11% of the length of the study area. The protected area increased plover reproductive success (Table 4). Within the protected area, fledging success doubled compared to the same area when the fence was not in place; by contrast, fledging success decreased in unfenced areas on the north half of the beach. A similar pattern of increased fledging success occurred on the south end of the beach which was not protected by a fence.

DISCUSSION

There was no clear age-related pattern to the movements and distribution of Snowy Plovers. Adults sometimes reared broods within 500 m of where chicks hatched, but broods were capable of moving long distances (i.e. >2 km) early in life to reach high quality areas. As chicks aged, they settled into their eventual home ranges, moving highly variable distances with each successive day; brood home range may have stabilized after about 17 days. Other species of nidifugous birds exhibit age-related patterns of movement. Mountain Plover (*Charadrius montanus*) chicks undertook their longest daily movements in the first few days after hatching (Knopf 1996). Similarly, young Pectoral Sandpipers (*Calidris melanotos*; Holmes and Pitelka 1998), Least Sandpipers (*Calidris minutilla*; Cooper 1994) and American Avocets (*Recurvirostra americana*; Robinson *et al.*

Table 1. Average (±SE) daily distance moved and brood home range size of Snowy Plovers tending broods that fledged or failed in their first ten days on Clam Beach, Humboldt County, California 2001-2006.

			Distance (m)	Mann-Whitney U	
Measure	Broods	n	Mean ± SE	Z	P
From previous day's location	Fledged	26	236 ± 37	0.41	0.69
	Failed	10	231 ± 45		
From nest	Fledged	29	751 ± 152	0.45	0.98
	Failed	11	644 ± 150		
Brood Home Range size	Fledged	29	1027 ± 172	-0.10	0.92
	Failed	12	855 ± 154		

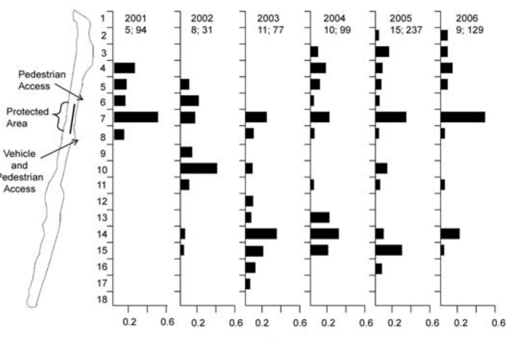

Figure 2. Annual variation in distribution of adult Snowy Plovers with broods on Clam Beach, Humboldt County, California, expressed as a proportion of total observations, in 18 500-m sections of beach. Dimensions of the protected area are approximate. Numbers at top of individual graphs represent year, followed by number of broods; number of locations.

1997) moved farthest soon after they hatched. Overall, distances moved on a daily basis fall within a broad range observed for a wide variety of other precocial species, including Semipalmated Sandpiper (*Calidris pusilla;* Gratto-Trevor 1992), Piping Plover (*Charadrius melodus*; Haig 1992), American Avocet (Demers *et al.* 2008) and Black Turnstone (*Arenaria melanocephala*; Handel and Gill 2001). However, other species, moved longer distances to brood-rearing areas, often several kilometers away from the nest. Average distance moved by young Northern Lapwing (*Vanellus vanellus*; Blomqvist and Johansson 1995), Pied Avocet (*Recurvirostra avosetta*; Lengyel 2006), Greater Snow Goose (*Chen caerulescens*; Mainguy 2006), Wood Duck (*Aix sponsa*; Granfors and Flake 1999) and Mallard (*Anas platyrhynchos*; Yerkes 2001) greatly exceed the average daily distance moved (216 ± 12m) by Snowy Plovers on Clam Beach. We hypothesize that this interspecific variation stems from landscape features (i.e. the linear nature of a beach versus a broad expanse of tundra or prairie) and habitat requirements, including the absence of disturbance by humans, for nesting versus rearing of broods (Galbraith 1988; Yasué and Dearden 2006). However, understanding the causes of variation in movements requires much more detailed information on the moment-to-moment changes in habitat associated with transient danger posed by predators and humans.

Our data indicate that creation of a protected area influenced plover movements and may have increased reproductive success. Family groups tended to avoid areas of high human activity, and they preferentially settled in a protected area that was created to minimize threats posed by humans. Chicks hatched outside the protected area traveled greater distances, probably in response to higher levels of human disturbance, than those hatched within it. This was evidenced by a 22% reduction in daily distance moved by broods inside the protected area compared with a 38% increase in the average daily movements of broods outside the refuge. We conclude that broods within the protected area did not move as far because they were less disturbed, due to the absence of human traffic.

Although chicks reared in the fenced area experienced similar fledging success compared to chicks reared in all other stretches

Table 2. Highest ranking multiple linear regression models and single variables predicting Snowy Plover brood presence on Clam Beach, Humboldt County, California, 2005 and 2006. There was no best-fit model; thus model averaging [w+ (j)] was used to evaluate the relative importance of single predictor variables (j) across all models.

	Highest-ranking model							Single variable weights averaged across all models				
Nest inclusion in candidate models	model	K	Adj R^2	AIC_c	ΔAIC_c	Likelihood	AIC_c Weight	variable	w+ (*j*)	R^2	P-value	Relation to brood use
NEST												
2005 models	nest	1	0.33	-84.70	0.00	1.0000	0.28	nests	1.00	0.37	0.01	positive
2006 models	nest	1	0.22	-74.52	0.00	1.0000	0.19	nests	0.85	0.27	0.04	positive
								wet sand	0.29	0.56	0.001	positive
NO NEST												
2005 models	human tracks	1	0.33	-84.70	0.00	1.0000	0.23	human tracks	0.98	0.37	0.01	negative
2006 models	human tracks	1	0.22	-74.52	0.00	1.0000	0.20	human tracks	0.88	0.27	0.04	negative

Table 3. Average (± SE) distances moved between consecutive days and daily from nest by male Snowy Plovers with broods hatched within vs. outside an area protected from human traffic on the north half of Clam Beach, Humboldt County, California 2001-2006.

				Mann-Whitney U			Mann-Whitney U	
Period	Broods hatched	n	Daily Distance (m)	Z	P	Daily Distance from Nest (m)	Z	P
During protection (2004-2007)	Inside Fence	10	171 ± 19	2.4	0.02	438 ± 42	5.2	<0.0001
	Outside Fence	9	241 ± 34			732 ± 65		
Before protection (2001-2003)	Inside Fence	5	220 ± 46	0.77	0.44	780 ± 90	-3.1	0.002
	Outside Fence	5	175 ± 27			1353 ± 90		

Table 4. Fledging success of Snowy Plover chicks and broods before (2001-03) and after (2004-08) creation of a protected area on Clam Beach, Humboldt County, California.

	CHICKS				BROODS			
	% Fledged (N)				% Fledged (N)			
	Before	After	χ^2	P	Before	After	χ^2	P
PROTECTED AREA	15% (33)	37% (41)	4.26_1	0.04	31% (13)	60% (15)	2.34_1	0.12
UNPROTECTED AREAS								
North (Sections 2-5 and 9[a]); adjacent to protected area; heavy human traffic	80% (5)	35% (20)	3.29_1	0.10[b]	100% (2)	57% (7)	2.14_1	0.42[b]
South (Sections 10-17); distant from protected area; light human traffic	13% (23)	39% (38)	4.81_1	0.03	22% (9)	56% (16)	2.70_1	0.10[b]

[a]To describe the spatial distribution of broods, Clam Beach was partitioned into 18 500-m sections from north to south. Sections 1 and 18 were excluded from analysis, because broods were never observed in these areas

[b]Fisher's Exact Test (one-tail) Probability Level is reported for those instances where any expected cell frequency is less than 5.

of beach, success doubled in the refuge after it was created. During the same period, fledging success dropped by more than half in beach stretches adjoining the refuge. These findings suggest that fencing and educational materials (e.g. signs posted on perimeter fence posts) can be used to enhance reproductive success of threatened species in habitats of high human recreational activity. In southern California, Snowy Plover fledging success increased when management actions were undertaken to protect them from human disturbance (Lafferty *et al.* 2006). Similar results have been reported for other species of shorebird that breed in coastal and agricultural habitats with high human activity, including Malaysian Plover (*C. peronii*; Yasué and Dearden 2006), European Golden-plover (*Pluvialis apricaria*; Finney *et al.* 2005) and African Black Oystercatcher (*Haematopus moquini*; Leseberg *et al.* 2000).

The protected area was selected based on the location of the coincidence of plover breeding density and human activity. Plovers already favored this area for brood-rearing before the initiation of the refuge. Chick survival, however, was low in this area, probably owing to high levels of human activity, compounded by predation by corvids, which has been related to human activity (Marzluff and Neatherlin 2006). Fledging success, though doubled, was not significantly higher for broods (though it was for chicks) in the area during the five years it was protected from human disturbance for breeding plovers. The protected area had low human activity (as indexed by ground plots and tracks, Nelson 2007), even though it was situated between the two main beach access points for humans.

Coincident with the increased fledging success inside the protected area, there was a reduction by more than half in fledging success in unprotected areas adjoining the refuge, where human activity was high. However, it must be cautioned that the sample size was small for the "before" period. Furthermore, on an unprotected and similar-sized area of beach 1 km to the south of the protected area, there was also a doubling of fledging rate. But this area was similar to the protected area, in that it experienced lower foot traffic, due to more difficult access. Additionally, vehicle use was prohibited (though still occasionally occurred). Though this makes it difficult to conclude unequivocally the success of the protected area, it appears that low human activity benefited fledging success, and that this can be best achieved by protecting areas from disturbance.

Management Recommendations

The establishment of a fenced area to protect breeding plovers was based on three years' data, which showed that areas of high nest and brood density co-occurred with high human activity. As such, there was potential for negative effects on productivity (i.e. reproductive success) and recovery of the local population. We conclude that the fence was successful in altering plover behavior and increasing productivity, and should be useful in other areas with similar circumstances of coincident activity of plovers and humans, a conclusion supported by others (e.g. Lafferty *et al.* 2006, etc.). However, there are two important caveats to this statement. First, shorebird population growth is most strongly influenced by adult survivorship (Sandercock 2003), rather than annual variation in productivity. Therefore, we urge that managers of beach habitats occupied by wintering plovers consider using fencing to protect plovers in areas of high human recreational activity, especially vehicles (Brindock and Colwell 2010). Second, and equally important, predation of eggs and chicks by corvids is a significant factor limiting the local population of plovers, and this problem has grown over the short time we have monitored the population (Colwell *et al.* 2009). With each successive year, plover productivity has declined in the study area such that only a small number of chicks hatch and few fledge; no chicks fledged on Clam Beach in 2008 and 2009. Corvids are the most important cause of reproductive failure in the population we studied (Colwell *et al.* 2009) and elsewhere in the plover's range (U.S. Fish and Wildlife Service 2007). Unless stronger measures of predator control are implemented, use of protected areas to increase reproductive success will be futile and only serve to exacerbate negative reactions from sectors of the public that view the fencing as an unsightly management tool that unnecessarily restricts access to beaches.

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