The Journal of Wildlife Management 75(4):786–793; 2011; DOI: 10.1002/jwmg.106

Research Article

Habitat Selection by Western Snowy Plovers During the Nonbreeding Season

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ABSTRACT Conservation of rare populations requires managing habitat throughout the year, especially during winter when northern populations may be limited by food and predation. Consequently, we examined distribution of nonbreeding western snowy plovers (*Charadrius alexandrinus*), including individually marked birds that were year-round residents and others that were migrants, in coastal northern California. Over 2 years, banded plovers exhibited high site faithfulness, occupying small linear stretches of beach (752 ± 626 m). Sites occupied by plovers had more brown algae (e.g., *Macrocystis*, *Nereocystis*, *Postelsia*, and *Fucus*) and associated invertebrates (e.g., amphipods, and flies), were wider, and had less vegetation than unoccupied sites. Our findings suggest that wintering plovers select habitats with more food and where they could more easily detect predators. Maintaining habitat with attributes that support abundant food (i.e., brown algae) and reduce predation risk (i.e., wide beaches, limited obstructive cover) may be important to individual survival and maintaining the Pacific Coast population of snowy plovers. Protecting occupied sites from human disturbance, which adversely alters nonbreeding habitat (i.e., beach grooming) and directly causes mortality, may be essential for conserving the Pacific coast population of the snowy plover, and it may benefit other shorebirds. © 2011 The Wildlife Society.

KEY WORDS California, *Charadrius alexandrinus*, distribution, disturbance, food, habitat, Humboldt County, nonbreeding, predation, snowy plover.

Recent evidence indicates that many shorebird populations worldwide are in decline (Morrison et al. 2006, Delaney et al. 2009). Survival is the most critical vital rate influencing shorebird population growth, and the nonbreeding season is the likely interval during the annual cycle when mortality is highest (Evans and Pienkowski 1984, Hitchcock and Gratto-Trevor 1997, Sandercock 2003). The main causes of mortality for shorebird wintering at northern latitudes are food shortages and predation by raptors (Page and Whitacre 1975, Evans and Pienkowski 1984, Cresswell and Quinn 2004). Consequently, strong selective pressures shape choices of habitat by individual shorebirds during winter.

During the nonbreeding season, spatial distribution of shorebirds is correlated with the distribution and availability of food (e.g., Bryant 1979, Colwell and Landrum 1993, Gill et al. 2001*a*). Additionally, danger posed by predators, especially raptors, strongly affects the habitat choices of individuals at winter and migratory stop-over sites (Fernández and Lank 2006, Sprague et al. 2008). Shorebirds select open habitats with less obstructive cover (Pomeroy 2006); individuals occupying habitats that afford greater concealment to predators are associated with higher mortality rates (Van den Hout et al. 2008). In short, shorebirds aggregate in areas of high food availability and where birds are able to detect predators more readily. Human activity may act similar to predation by causing shorebirds to abandon habitat where disturbance is chronic and intense, as evidenced by negative correlations between shorebird abundance and anthropogenic disturbance (Pfister et al. 1992, Kirby et al. 1993).

The process through which shorebirds select habitat is unlikely the outcome of a single factor (Whitfield 2003). Yet, most studies of shorebird distribution have examined food, predation, or disturbance (Colwell and Landrum 1993, Kirby et al. 1993, Creswell and Whitfield 1994, Lafferty 2001), with few studies evaluating more than one of these factors (Gill et al. 2001*b*, Pomeroy 2006). Consequently, the influence of food, predation, and disturbance on shorebird distribution is poorly understood. Understanding this relationship may be especially important for managing threatened and endangered species.

The snowy plover (*Charadrius alexandrinus*) breeds and winters along the Pacific coast of North America from Washington south through Baja California, Mexico. Individual variation in migratory behavior make this a partial migrant population, consisting of a mix of permanent residents and migratory birds (Stenzel et al. 1994, Colwell et al. 2007). Plovers winter and breed in the same habitats, mostly sandy, ocean-fronting beaches. In 1993, the United States Fish and Wildlife Service listed the coastal population segment as threatened under the federal Endangered Species Act; a recovery plan was finalized in 2007 (U.S. Department of Interior 2007). Several factors are thought to limit the

Received: 22 January 2010; Accepted: 7 September 2010

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population through their effects on breeding productivity. Consequently, various management practices have been used to ameliorate the negative effects of the limiting factors, including restoration of coastal dune habitats to remove invasive plant species (e.g., European beachgrass [*Ammophila arenaria*], ice plant [*Carpobrotus chilensis*]) and restrictions on human activities that disturb plovers or compromise egg and chick survival. Little attention, however, has been given to understanding the nonbreeding ecology of plovers, and few management actions target this segment of the annual cycle.

We studied a small, marked population of snowy plovers in coastal northern California. We examined space use and habitat selection by plovers along coastal beaches during the nonbreeding season. We predicted that plovers would occupy small areas and select habitats of high food availability, where the risk of predation by raptors was reduced, and anthropogenic disturbance was low.

STUDY AREA

We studied snowy plovers along 65 km of ocean-fronting beach from Centerville to Stone Lagoon in Humboldt County, California (Fig. 1), an area that contained the highest density of snowy plovers in northern California during both the breeding and nonbreeding seasons (Brindock 2009, Colwell et al. 2010). The winter climate of the study area was characterized as cool and moist; Humboldt Bay (approximate center of study area) averaged 10 °C and 97 cm of rainfall during winter, with an average tide range of 1.5 m. The study area encompassed nearly all suitable habitat (i.e., occupied and unoccupied sandy beach) in Humboldt County used by snowy plovers that bred in coastal habitats over the past 9 years (Colwell et al. 2010), as well as other potentially suitable habitat for wintering snowy plovers; we did not survey rocky intertidal habitats. Beaches were characterized by four distinct habitat types: 1) foreshore, consisting of the tidally influenced area below the high tide line, 2) wrack, made up of debris deposited from high tides, 3) backshore, extending inland from the foreshore to the foredune, and 4) foredune, extending inland from the backshore and identified by vegetation line or the crest of the dunes. Beach vegetation included European beachgrass, native dune grass (*Leymus mollis*), sand-verbena (*Abronia* spp.), ice plant, and sea rocket (*Cakile maritima*). Debris consisted primarily of brown algae (e.g., *Fucus*, *Egregia*, and *Postelsia* spp.), eelgrass (*Zostera marina*), woody debris, bivalve shells, decapod carapaces, stones, dead vegetation, and garbage.

METHODS

Field Methods

We surveyed the 65 km of beach habitat 16 times between October and February, the winter interval that spans the time of minimal movement of plovers, for 2 years (2007–2008, 2008–2009). One principal surveyor did >80% of observations; four other observers that had extensive field experience surveying plovers in the study area during the breeding season conducted the other surveys. Observers surveyed between 0700 hours and 1400 hours, walking the beach along the wrack, which provided a view of other habitats (i.e., foreshore, backshore) of the ocean-fronting beach, and scanning for plovers with binoculars and spotting scopes. The annual schedule resulted in the complete survey of the 65 km study area in approximately 2 weeks, which we repeated continuously between 1 October and 29 February. When observers detected a plover they recorded its location using a personal digital assistant (Axim X50, Dell, Inc., Round Rock, TX) with an auxiliary Global Positioning System (GPS) attachment. If a plover was in a flock (≤50 m from a conspecific), observers recorded one location

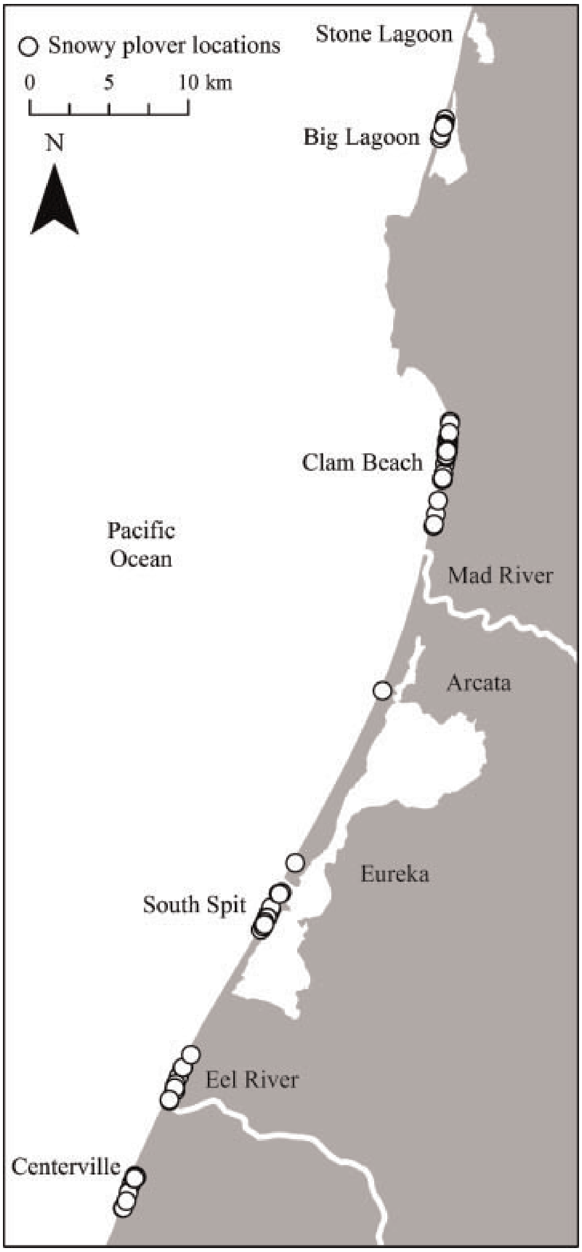

Figure 1. Study area and locations of nonbreeding snowy plovers in Humboldt County, California, October 2007–February 2009.

for the flock, as well as the number of plovers, band combinations, and behavior (roosting or feeding). Many plovers were marked with unique color band combinations as part of a long-term study (Colwell et al. 2007, 2010; Mullin et al. 2010).

We used 3-m-radius ground plots and 500-m-radius point counts to characterize habitat; these same methods are used while monitoring breeding plovers in the study area (Colwell et al. 2010). During surveys observers walked through the wrack, stopping at 10-min intervals (as determined by preset alarm) to sample ground plots, with the observer's location serving as the center point. Within each ground plot observers visually estimated: 1) percent ground cover of brown algae, eelgrass, small woody debris, stumps, bivalve and crustacean shells, stones, live vegetation, dead vegetation, and garbage on an ordinal scale ($0 = 0\%$, $1 = 1–10\%$, $2 = 11–50\%$, $3 = 51–90\%$, $4 => 90\%$); 2) the number of cover objects and invertebrates (amphipods, amphipod burrows, flies, beetles, isopods, craneflies, spiders, polychaetes, and other) on a $\log_{10}$ scale; and 3) the number (0, 1–10, or >10) of sets of tracks of people, dogs, vehicles, horses, and corvids (American crow [*Corvus brachyrhynchos*] and Common raven [*C. corax*]). We measured beach slope using a clinometer (measured from the wrack to the base of the dune). Lastly, observers conducted point counts at 20-min intervals, recording the number of people, dogs, vehicles, horses, common raven, American crow, and raptors within a 500-m radius, a spatial scale that included the foreshore, wrack, and backshore habitats.

We obtained measures of ground cover of the backshore using a different method on three separate occasions. Walking along the wrack and stopping at 150-m intervals we recorded a ground plot of the wrack. At the 150-m interval we recorded a ground plot of the backshore sampled at a random distance between the wrack and the duneline (using a random number generator to identify the distance [m] from the wrack). We also estimated the slope (°) of the foreshore at 300-m intervals using a clinometer from 30 m down slope of the most recent high tide line to the wrack.

We defined beach width as the distance between average high tide line and duneline (identified as the vegetation line or crest of the western-most dunes). We used coordinate locations of ground plots taken along the wrack to represent the average high tide line. We traced the duneline with a GPS between 1 January 2009 and 28 February 2009.

Statistical Analyses

We estimated space use of plovers along beaches as a linear distance (or segment of beach) because the habitat of ocean-fronting beaches limited plovers to linear (north–south) movements (Wilson and Colwell 2010). We used the locations of 31 individually marked plovers to estimate the 90% utilization distribution using fixed kernel density analysis with least squares cross validation (Seaman and Powell 1996). Next, we fit a straight line through the 90% kernel intersecting the contour at the greatest distance apart. We used this distance to estimate the space use (linear segment of beach) for each uniquely marked plover. For individuals with multiple 90% kernels (use areas), we summed the linear distances across all kernel contours. Finally, we estimated the average (±SD) linear distance (linear stretch of beach) of individually marked plovers. Additionally, we estimated area from the fixed kernel density analysis; these results provide a comparison to the home range of other nonbreeding shorebirds.

We divided the study are into linear segments of beach with lengths equal to the mean linear distance estimated from the 90% kernel density analysis. We divided the study area into sequential segments using a random location (generated using ArcGIS version 9.3, ESRI, Inc., Redlands, CA) as a starting point. We considered sites to be occupied if we observed a plover during ≥ 1 of the 16 surveys. We used ArcGIS to spatially analyze the data characterizing habitat. We buffered data collected during ground plots by 3 m (radius) at each location. We buffered point count data by 500 m (radius) at each location; where buffers overlapped we assigned the average value to that location. We then estimated the average value for each habitat variable sampled from multiple locations within each occupied and unoccupied stretch of beach.

We compared habitat characteristics of occupied and unoccupied sites with logistic regression analysis using an information theoretic approach (Burnham and Anderson 1998). We developed a set of 20 a priori candidate models based on literature review of habitat associations of nonbreeding shorebirds (Colwell 2010). From these candidate models and the null model (intercept only), we selected the most parsimonious models using Akaike's Information Criterion with a small sample bias correction (AIC_c). We evaluated model fit by calculating the pseudo-coefficient of determination for each candidate model and the area under the receiver operating characteristics (ROC), which plots sensitivity against $1 -$ specificity to provide a measure of model performance. We also examined the correct classification rate, setting cutpoint at 0.5 and using the ROC curve and commission and omission errors to set the cutpoint (Zweig and Campbell 1993); these results were nearly identical, therefore we present results from the 0.5 cutpoint. To evaluate the importance of variables in the top ranked models, we calculated the relative importance for each variable by summing the AIC_c model weights of every model containing that variable (Burnham and Anderson 1998).

To assess the degree of spatial autocorrelation in the response variable we calculated the Moran's index (I). We then incorporated an autocovariate term into the candidate models to account for spatial effects of neighboring locations of the response variable. We calculated the autocovariate term as:

$$A_i = \frac{\sum\limits_{j \in k_i} w_{ij} y_j}{\sum\limits_{j \in k_i} w_{ij} y_j}$$

where y_j is the response value of y at site j among the set of k_i neighbors of site i, and w_{ij} is the weight of the influence of j over site i (Augustin et al. 1996). The weight function is related to the geographical distance between locations (Augustin et al. 1996), which in our case is associated with the estimate of space use (linear stretch of beach).

To evaluate the relationship between brown algae and invertebrates, we examined correlations between brown algae and amphipods, amphipod burrows, and flies across all sites (occupied and unoccupied) in the study area. We did not examine relationships between brown algae and other invertebrates because we detected these potential food items rarely ($n < 10$). We present averages (±SD).

RESULTS

During two consecutive winters we recorded an average of 76 ± 14 snowy plovers per survey ($n = 16$) concentrated at five beaches (Fig. 1). The number of plovers in the study area decreased by 18% between the first (86 ± 12) and second (71 ± 12) winter ($t_{14} = 2.38$, $P = 0.03$). There were 54 marked plovers in the study area (Brindock 2009); most (57%) of these individuals had unique band combinations and either bred locally ($n = 22$) or were immigrants from Oregon ($n = 7$) or central California ($n = 2$). Twenty-three plovers had band combinations indicating that they fledged from Oregon ($n = 18$) or Humboldt County, California ($n = 3$). An additional two plovers had one metal (uncolored) band; one fledged from Oregon, the origin of the other is unknown.

Plover abundance varied in a similar manner across the 2 years. Fewer plovers were present during October (2007–2008: 84 ± 10; 2008–2009: 50 ± 14) than the rest of the winter, when numbers remained consistent from November through January (2007–2008: 92 ± 2; 2008–2009: 75 ± 2); numbers decreased slightly in February (2007–2008: 75 ± 12; 2008–2009: 71 ± 9). Plovers occurred singly, but they most often (60% of 121 occasions) occurred in flocks ≥5 (Fig. 2). More plovers roosted (76%) than fed (24%). When feeding, we observed plovers in the same sites in which they roosted. Plovers roosted in backshore (69%), wrack (26%), or foreshore (5%) habitats. Feeding plovers occurred mostly in wrack (75%) and less often on the foreshore (23%) or backshore (2%).

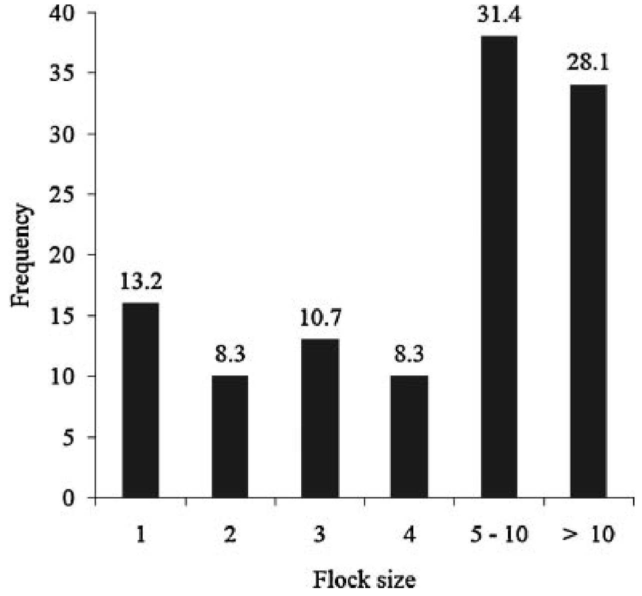

Figure 2. Frequency and percent (above bars) of observations of snowy plovers observed singly and in flocks (roosting and feeding) of different size in Humboldt County, California, October 2007–February 2009.

Marked plovers ($n = 31$; 12 ± 3 observations) occupied linear stretches of beach that averaged 752 ± 626 m; area was 0.36 km^2. The linear distance of beach occupied by plovers increased with number of observations, but quickly leveled off after the fifth observation and remained stable after the tenth observation, which suggests that this estimate was representative of winter movements. Linear distance of movement (estimate of space use) was not correlated with average flock size ($t_{29} = 1.16$, $r^2 = 0.06$, $P = 0.26$). Using the linear estimate (752 m), we divided the study area into 25 occupied and 60 unoccupied sites. We observed plovers in occupied sites during varying tidal heights (0.3–2.4 m) and time of day (0730 hours through 1337 hours). Plover abundance was not correlated with tide height ($t_{120} = -0.02$, $r^2 = < 0.01$, $P = 0.98$) or time of day ($t_{120} = -1.08$, $r^2 = 0.07$, $P = 0.25$).

The 16 surveys of the study area provided 3,479 ground plots, 971 point counts, and 1,605 measures of beach slope. The method of sampling habitat data using timed intervals resulted in 526 ± 126 m between successive ground plots and 1,057 ± 240 m between successive point counts. Average number of samples in occupied sites (ground plots: 43 ± 4; point counts: 13 ± 3; measures of beach slope: 20 ± 4) was slightly more than unoccupied sites (ground plots: 40 ± 4; point counts 11 ± 3; measure of slope of beach: 18 ± 3).

The top ranked model for predicting snowy plover presence included brown algae, beach width, and vegetation (pseudo $R^2 = 0.54$; Table 1). The second ranked model contained brown algae, beach width, raptors, and dog tracks (pseudo $R^2 = 0.53$). The combined weight for the top 2 models was 0.99, indicating that there was a high probability that one of these models was the best model of the 20 considered. Both models performed well, predicting plover presence with similar correct classification rates for the top (89.7%) and second ranked (87.1%) models. Area under the ROC curve for the top and second ranked model was the same (0.94). Spatial distribution of plovers was not autocorrelated (Moran's $I = 0.029$, $P = 0.251$). Consequently, adding an autocovariate term to the top 2 ranked models had little effect, producing nearly identical results as models without the autocovariate term.

Wintering plovers selected sites that were 84% wider ($P < 0.001$) and contained over 100% more brown algae ($P < 0.001$) than unoccupied sites (Tables 1–3). Amount of brown algae on beaches was significantly positively correlated with invertebrate abundance, especially amphipods, their burrows, and flies (Fig. 3). Plovers also occurred in sites with 35% less vegetation than unoccupied sites (Tables 1–3). Although model 2 suggests snowy plover presence was negatively associated with both raptors and dog tracks (Table 2), those variables had low relative importance and

Table 1. Top 2 models plus the null model for predicting snowy plover presence at occupied ($n = 25$) and unoccupied ($n = 60$) sites in Humboldt County, California, October 2007–February 2009.

Model	K[a]	AIC_c [b]	$\Delta\mathrm{AIC}_c$ [c]	w_i [d]
Brown algae + width + vegetation	4	52.72	0	0.94
Brown algae + width + raptors + dog tracks	5	58.71	5.99	0.05
Null model	1	105.03	52.31	0

[a] No. of parameters in the model.
[b] Akaike's Information Criterion with small sample bias adjustment.
[c] $\Delta\mathrm{AIC}_c$ is equal to the AIC_c value of model i minus the min. AIC_c model value.
[d] AIC_c weight (w_i) is the percentage of total weight that can be attributed to an individual model.

Table 2. Parameter estimates, standard errors, P values, and relative importance of variables in the top 2 models for predicting snowy plover presence at occupied ($n = 25$) and unoccupied ($n = 60$) sites in Humboldt County, California, October 2007–February 2009.

Model	Estimate	SE	P	Relative importance
Model 1				
Brown algae	13.840	3.452	<0.001	0.99
Beach width	0.058	0.020	0.004	0.99
Vegetation	−14.312	7.997	0.074	0.94
Model 2				
Brown algae	12.554	3.427	<0.001	0.99
Beach width	0.061	0.020	0.003	0.99
Raptors	−8.344	7.657	0.276	0.05
Dog tracks	−0.590	1.337	0.659	0.05

coefficient estimates with high standard errors, suggesting weak effects.

DISCUSSION

Wintering plovers occupied short segments (<1 km) of beach and areas (<1 km^2), which is a small estimate of home range for a nonbreeding shorebird. By comparison, western sandpipers (*Calidris mauri*) wintering in San Francisco Bay had a mean home range size of 22 km^2 and mean core use area of 9.5 km^2 (Warnock and Takekawa 1996). Average home range size of nonbreeding piping plovers (*Charadrius melodus*) in Texas (12.6 km^2; Drake et al. 2001) and North Carolina (2.2 km^2; Cohen et al. 2008) were larger than those we observed for snowy plovers. Although there is no previous estimate of home range size for nonbreeding snowy plovers, breeding season data from the study area (M.A. Colwell,

Table 3. Means, standard deviations, test statistics, and P values of variables sampled at snowy plover occupied ($n = 25$) and unoccupied ($n = 60$) sites in Humboldt County, California, October 2007–February 2009.

	Occupied		Unoccupied			
Variable	$\bar{x}$	SD	$\bar{x}$	SD	t	P
Ground plot						
Amphipods	0.19	0.13	0.13	0.13	1.94	0.06
Amphipod burrows	0.53	0.27	0.33	0.24	3.28	<0.01
Brown algae	0.42	0.18	0.18	0.09	6.49	<0.001
Corvid tracks	0.06	0.07	0.05	0.05	0.94	0.35
Dog tracks	0.42	0.32	0.48	0.34	−0.84	0.40
Eelgrass	0.38	0.49	0.58	0.52	−1.65	0.11
Flies	0.19	0.13	0.08	0.06	4.49	<0.001
Ground cover-backshore	1.21	0.30	1.43	0.21	−2.45	0.02
Ground cover-wrack	1.76	0.33	1.75	0.24	0.25	0.81
Human tracks	0.55	0.39	0.47	0.35	0.88	0.39
Vegetation	0.08	0.05	0.12	0.09	−2.52	0.01
Vehicle tracks	0.36	0.23	0.26	0.29	1.57	0.12
Woody debris	0.91	0.45	0.96	0.42	−0.47	0.64
Point counts						
Corvids	1.52	1.26	0.86	0.95	2.34	0.09
Dogs	0.24	0.36	0.30	0.42	−0.65	0.52
People	0.63	0.67	0.50	0.60	0.81	0.42
Raptors	0.04	0.04	0.08	0.06	−1.43	0.16
Vehicles	0.09	0.11	0.06	0.24	0.74	0.46
Slope						
Backshore	4.83	0.92	4.55	0.96	1.30	0.20
Foreshore	5.80	2.36	5.45	2.24	0.63	0.53
Beach width	46.81	16.59	25.47	15.94	5.46	<0.001

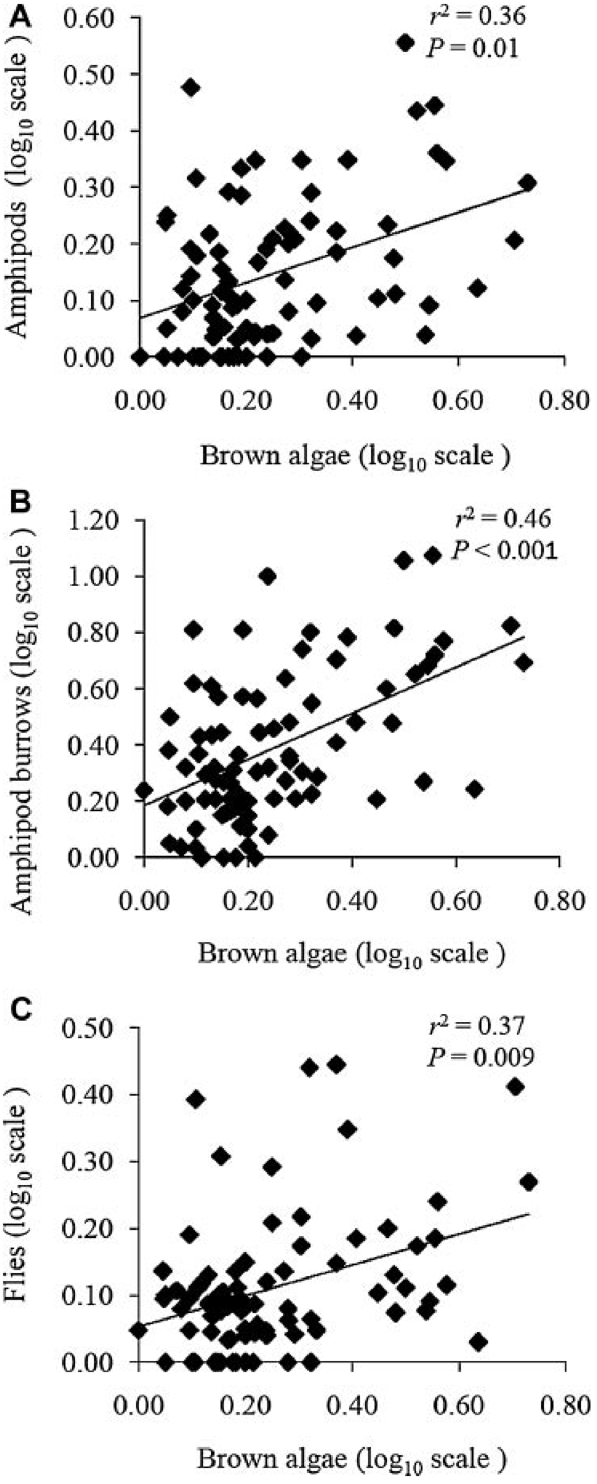

Figure 3. The relationship between brown algae and abundance of invertebrates (A: amphipods, B: amphipod burrows, C: flies) at all sites ($n = 85$) designated as a 752-m linear stretch of beach in Humboldt County, California, October 2007–February 2009.

Humboldt State University, unpublished data) suggest that home range size is larger in the breeding season, when individuals may sometimes disperse long distances and often move among multiple breeding locations (Stenzel et al. 1994, Colwell et al. 2007).

Our estimates of space use of wintering plovers were based solely on diurnal observations, which may bias interpretations of habitat use (Gillings et al. 2005). Most observations were of roosting snowy plovers, suggesting that nocturnal feeding may be an important facet of plover foraging ecology, as it is among wintering Kentish plovers (*C. alexandrinus*) in Japan (Kuwae 2007) and Wilson's plovers (*C. wilsonia*) in Venezuela (Thibault and McNeil 1994). A primary prey item of plovers resident on ocean-fronting beaches is burrowing amphipods, which are more active at night (Page et al. 1995, Kennedy et al. 2000). Activity such as nocturnal foraging could yield different results. However, the concentration of food, including amphipods, at occupied sites suggests that plovers restrict movements for feeding within the observed linear stretches of beach where food densities are highest. Relationships between foraging and roosting sites and diurnal and nocturnal habitat use are poorly understood for this species. Our results are derived from, and thus limited to, diurnal activity of plovers.

Snowy plovers occupied wide beaches that had more brown algae and associated invertebrates and less vegetation compared with unoccupied sites, suggesting that plovers selected habitats that provide more food and have lower risk of predation. Amphipods and flies, both considered major food items for snowy plovers (Page et al. 1995), were significantly positively correlated with brown algae, which was a significant variable in predicting snowy plover presence. Additionally, all models containing the variable amphipods or flies had coefficients that were either significant ($P < 0.05$) or marginally so ($P < 0.10$); adding either variable to any candidate model (including the top ranked models) improved model fit. Similar results were reported in southern California where snowy plover abundance correlated positively with the amount of brown algae on beaches (Dugan et al. 2003). Elsewhere along the Pacific coast, brown algae is an important habitat component of the food chain for plovers and other shorebirds because it provides a food source for invertebrates (Bradley and Bradley 1993, Dugan et al. 2003, Hubbard and Dugan 2003).

Snowy plovers occurred on wide beaches that had low amounts of vegetation; occupied sites also had fewer raptors than unoccupied sites, although this latter relationship was weak. Collectively, the habitat features suggest that plovers select diurnal habitats that reduce the risk of predation. During the nonbreeding season, raptors, especially falcons, which often hunt by approaching prey low to the ground (Whitfield 2003), are the most frequent predator of shorebirds (Page and Whitacre 1975, Creswell and Whitfield 1994). Selecting habitats that are open (or wide) and have less vegetative cover can facilitate early detection of raptors, reducing predation risk, as evidenced in previous studies demonstrating a positive correlation between raptor predation rates on shorebirds and openness and vegetative cover (Dekker and Ydenberg 2004, Van den Hout et al. 2008). Additionally, negative correlations between shorebirds and vegetation suggest that individuals select habitats with attributes (i.e., vegetation, width) that reduce predation risk (Fernández and Lank 2006, Pomeroy 2006).

In addition to the physical attributes in a habitat, flocking can reduce the risk of predation to shorebirds (Myers 1984).

Individuals in small flocks are at greater risk of predation than those in large flocks (Page and Whitacre 1975, Cresswell and Quinn 2004). Snowy plovers occurred most frequently in flocks, with few observations of single plovers, consistent with observations from other coastal areas (Page et al. 1995, Lafferty 2001). Flocking behavior of plovers is likely a behavioral response by individuals to reduce the risk of predation.

Despite appreciable variation in human activity across the study area, we found limited evidence that this activity correlated with plover distributions, which contradicts some (Pfister et al. 1992, Kirby et al. 1993) but not all (Colwell and Sundeen 2000, Gill et al. 2001*b*) studies. The relationship between shorebirds and disturbance is likely influenced by the type, frequency, and intensity of disturbance, which is comparatively low in northern California. In southern California, where levels of disturbance are higher, management of human disturbance led to an increase in plover abundance during the nonbreeding season and the reestablishment of breeding plovers after a 30-year absence (Lafferty et al. 2006).

The effect of heterogeneous detection probability on bird surveys has received considerable attention in recent years (Thompson 2002). In particular, we considered the possibility that our finding that plovers were negatively associated with cover could have been an artifact of lower detectability in areas with high cover. We doubt this was the case in our study because detectability increases with sample intensity, and sampling intensity in our study was very high (16 visits/site). Furthermore, as we pointed out above, the finding that shorebirds are negatively associated with cover is supported by the observations of other researchers (Fernández and Lank 2006, Pomeroy 2006, Van den Hout et al. 2008).

Habitats plovers selected had high food availability and low predation risk, emphasizing the importance of food and danger on the winter distribution of shorebirds and for maintaining viable populations (Clark et al. 1993). These habitat components (food and danger) may be especially important for shorebird conservation considering that roughly 50% of shorebirds (suborder Charadrii) in North America are declining and habitat loss is the leading cause of endangerment to bird species in the United States (Brown et al. 2001, Johnson 2007). Examining variables that influence food availability and predation risk may provide further insight to the processes through which shorebirds select habitat and thus may aid conservation efforts for shorebirds.

MANAGEMENT IMPLICATIONS

The recovery plan for the Pacific Coast population of the snowy plover requires long-term management and protection of wintering sites, including prevention of disturbance by humans and their pets, restricting off-road vehicles, and creating and enhancing existing winter habitat (U.S. Department of Interior 2007). Managing habitat to increase food availability and reduce predation risk may be important to maintaining the Pacific Coast population of snowy plovers. Introduced European beachgrass is the dominant vegetation on beaches in the study area (Barbour et al. 1976); restoration efforts, including current projects aimed at restoring breeding habitat through removal of non-native vegetation, that increase openness of habitat would benefit wintering plovers by reducing predation risk. Activities, such as beach grooming, that decrease invertebrate abundance may adversely affect nonbreeding habitat by reducing food availability. Although human activity was not a significant variable predicting snowy plover distributions, we recorded the death of a plover from a vehicle strike, which suggests that chronic levels of disturbance (as indexed here) may not adequately represent the threat to individuals and populations as represented by single events.

ACKNOWLEDGMENTS

We thank M. D. Johnson and T. L. George for valuable comments and feedback throughout this study. We extend our gratitude to field assists N. S. Burrell, M. A. Hardy, J. J. Muir, and S. A. Peterson. We thank R. R. LeValley, S. E. McAllister, K. G. Ross, and A. N. Transou for their support and assistance. We are grateful to J. H. Watkins for supporting this project. We thank the California Department of Fish and Game, California Department of Parks and Recreation, Humboldt County Parks, and the United States Bureau of Land Management for allowing access to sites and for their cooperation with this project. This work was funded by the California North Coast Chapter of The Wildlife Society, Rotary Club of Eureka, The Garden Club of America, United States Fish and Wildlife Service, and the Western Section of The Wildlife Society.

LITERATURE CITED

Augustin, N. H., M. A. Mugglestone, and S. T. Buckland. 1996. An autologistic model for the spatial distribution of wildlife. Journal of Applied Ecology 33:339–347.

Barbour, M. G., T. M. DeJong, and A. F. Johnson. 1976. Synecology of beach vegetation along the Pacific coast of the United States of America: a first approximation. Journal of Biogeography 3:55–69.

Bradley, R. A., and D. W. Bradley. 1993. Wintering shorebirds increase after kelp (*Macrocystis*) recovery. Condor 95:372–376.

Brindock, K. M. 2009. Habitat selection by western snowy plovers (*Charadrius alexandrinus nivosus*) during the nonbreeding season. M.Sc. thesis, Humboldt State University, Arcata, California, USA.

Brown, S., C. Hickey, B. Harrington, and R. Gill. 2001. The U.S. shorebird conservation plan. Second edition. Manomet Center for Conservation Sciences, Manomet, Massachusetts, USA.

Bryant, D. M. 1979. Effects of prey density and site characters on estuary usage by over-wintering waders (Charadrii). Estuarine and Coastal Marine Science 9:369–384.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Clark, K. E., L. J. Niles, and J. Burger. 1993. Abundance and distribution of migrant shorebirds in Delaware Bay. Condor 95:694–705.

Cohen, J. B., S. M. Karpanty, D. H. Catlin, J. D. Fraser, and R. A. Fischer. 2008. Winter ecology of piping plovers at Oregon Inlet, North Carolina. Waterbirds 31:472–479.

Colwell, M. A. 2010. Shorebird ecology, conservation and management. University of California Press, Berkeley, USA.

Colwell, M. A., and S. L. Landrum. 1993. Nonrandom shorebird distribution and fine-scale variation in prey abundance. Condor 95:94–103.

Colwell, M. A., and K. D. Sundeen. 2000. Shorebird distribution on ocean beaches of northern California. Journal of Field Ornithology 71:1–15.

Colwell, M. A., S. E. McAllister, C. B. Millet, A. N. Transou, S. M. Mullin, Z. J. Nelson, C. A. Wilson, and R. R. LeValley. 2007. Philopatry and natal dispersal of the western snowy plover. Wilson Journal of Ornithology 119:378–385.

Colwell, M. A., N. S. Burrell, M. A. Hardy, K. Kayano, J. J. Muir, W. J. Pearson, S. A. Peterson, and K. A. Sesser. 2010. Arrival times, laying dates, and reproductive success of snowy plovers in two habitats in coastal northern California. Journal of Field Ornithology 81:349–360.

Cresswell, W., and J. L. Quinn. 2004. Faced with a choice, sparrowhawks more often attack the more vulnerable prey group. Oikos 104:71–76.

Creswell, W., and D. P. Whitfield. 1994. The effects of raptor predation on wintering wader populations at the Tyningharne estuary, southeast Scotland. Ibis 136:223–232.

Dekker, D., and R. Ydenberg. 2004. Raptor predation on wintering dunlin in relation to the tidal cycle. Condor 106:415–419.

Delaney S., D. Scott , T. Dodman D Stroud. editors. 2009. An atlas of wader populations in Africa and western Eurasia. Wetlands International, Wageningen, The Netherlands.

Drake, K. R., J. E. Thompson, and K. L. Drake. 2001. Movements, habitat use, and survival of nonbreeding piping plovers. Condor 103:259–267.

Dugan, J. E., D. M. Hubbard, M. D. McCrary, and M. O. Pierson. 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuarine, Coastal and Shelf Science 58:133–148.

Evans, P. R., and M. W. Pienkowski. 1984. Population dynamics of shorebirds. Pages 83–123 *in* J. Burger and B. L. Olla, editors. Shorebirds: breeding behavior and populations. Plenum Press, New York, New York, USA.

Fernández, G., and D. B. Lank. 2006. Sex, age, and body size distributions of western sandpiper during the nonbreeding season with respect to local habitat. Condor 108:547–557.

Gill, J. A., W. J. Sutherland, and K. Norris. 2001*a*. Depletion models can predict shorebird distribution at different spatial scales. Proceedings Royal Society London B 268:369–376.

Gill, J. A., K. Norris, and W. J. Sutherland. 2001*b*. The effects of disturbance on habitat use by black-tailed godwits *Limosa limosa*. Journal of Applied Ecology 38:846–856.

Gillings, S., R. J. Fuller, and W. J. Sutherland. 2005. Diurnal studies do not predict nocturnal habitat choice and site selection of European golden-plovers (*Pluvialis apricaria*) and northern lapwings (*Vanellus vanellus*). Auk 122:1249–1260.

Hitchcock, C. L., and C. Gratto-Trevor. 1997. Diagnosing a shorebird local population decline with a stage-structured population model. Ecology 78:522–534.

Hubbard, D. M., and J. E. Dugan. 2003. Shorebird use of an exposed sandy beach in southern California. Estuarine, Coastal and Shelf Science 58: 41–54.

Johnson, M. D. 2007. Measuring habitat quality: a review. Condor 109:489–504.

Kennedy, F., E. Naylor, and E. Jaramillo. 2000. Ontogenetic differences in the circadian locomotor activity rhythm of the talitrid amphipod crustacean *Orchestoidea tuberculata*. Marine Biology 137:511–517.

Kirby, J. S., C. Clee, and V. Seager. 1993. Impact and extent of recreational disturbance to roosts on the Dee estuary: some preliminary results. Wader Study Group Bulletin 68:53–58.

Kuwae, T. 2007. Diurnal and nocturnal feeding rate in Kentish plovers *Charadrius alexandrinus* on an intertidal flat as recorded by telescopic video systems. Marine Biology 151:663–673.

Lafferty, K. D. 2001. Disturbance of wintering western snowy plovers. Biological Conservation 101:315–325.

Lafferty, K. D., D. Goodman, and C. P. Sandoval. 2006. Restoration of breeding by snowy plovers following protection from disturbance. Biodiversity and Conservation 15:2217–2230.

Morrison, R. I. G., B. J. McCaffery, R. E. Gill, S. K. Skagen, S. L. Jones, G. W. Page, C. L. Gratto-Trevor, and B. A. Andres. 2006. Population estimates of North American shorebirds, 2006. Wader Study Group Bulletin 111:67–85.

Mullin, S. M., M. A. Colwell, S. E. McAllister, and S. J. Dinsmore. 2010. Apparent survival and population growth of snowy plovers in coastal northern California. Journal of Wildlife Management 74:1792–1798.

Myers, J. P. 1984. Spacing behavior of nonbreeding shorebirds. Pages 271–321. *in* J. Burger, B. L. Olla, editors. Behavior of marine animals. Vol. 6. Plenum Press, New York, New York, USA.

Page, G. W., and D. F. Whitacre. 1975. Raptor predation on wintering shorebirds. Condor 77:73–83.

Page, G. W., J. S. Warriner, J. C. Warriner, and P. W. C. Paton. 1995. Snowy plover (*Charadrius alexandrinus*). Pages 1–24. *in* A. Poole, and F. Gill, editors. The birds of North America, No 154. The Academy of Natural Sciences, Philadelphia, Pennsylvania and The American Ornithologists' Union, Washington, D.C., USA.

Pfister, C., B. A. Harrington, and M. Lavine. 1992. The impact of human disturbance on shorebirds at a migration staging area. Biological Conservation 60:115–126.

Pomeroy, A. C. 2006. Tradeoffs between food abundance and predation danger in spatial usage of a stopover site by western sandpipers, *Calidris mauri*. Oikos 112:629–637.

Sandercock, B. K. 2003. Estimation of survival rates for wader populations: a review of mark-recapture methods. Wader Study Group Bulletin 100:163–174.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Sprague, A. J., D. J. Hamilton, and A. W. Diamond. 2008. Site safety and food affect movements of semipalmated sandpipers (*Calidris pusilla*) migrating through the upper Bay of Fundy. Avian Conservation and Ecology 3 (2):4. <http://www.ace-eco.org/vol3/iss2/art4>. Accessed 12 Aug 2009.

Stenzel, L. E., J. C. Warriner, J. S. Warriner, K. S. Wilson, F. C. Bidstrup, and G. W. Page. 1994. Long-distance breeding dispersal of snowy plovers in western North America. Journal of Animal Ecology 63:887–902.

Thibault, M., and R. McNeil. 1994. Day/night variation in habitat use by Wilson's plovers in northeastern Venezuela. Wilson Bulletin 106:299–310.

Thompson, W. L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. Auk 119:18–25.

U.S. Department of Interior. 2007. Western snowy plover (*Charadrius alexandrinus nivosus*). Pacific coast population recovery plan, Portland, Oregon, USA.

Van den Hout, P. J., B. Spaans, and T. Piersma. 2008. Differential mortality of wintering shorebirds on the Banc d'Arguin, Mauritania, due to predation by large falcons. Ibis 150:219–230.

Warnock, S. E., and J. Y. Takekawa. 1996. Wintering site fidelity and movement patterns of western sandpipers *Calidris mauri* in the San Francisco Bay estuary. Ibis 138:160–167.

Whitfield, D. P. 2003. Raptor predation on nonbreeding shorebirds: some thoughts for the future. Wader Study Group Bulletin 100:134–137.

Wilson, C. A., and M. A. Colwell. 2010. Movements and fledging success of snowy plover (*Charadrius alexandrinus*) chicks. Waterbirds 33:331–340.

Zweig, M. H., and G. Campbell. 1993. Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. Clinical Chemistry 39:561–577.

Associate Editor: David King.