WINTER DISTRIBUTION OF WESTERN SNOWY PLOVERS (*CHARADRIUS ALEXANDRINUS NIVOSUS*) IN HUMBOLDT COUNTY – 2007/08, 2008/09

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ABSTRACT

Conservation of threatened and endangered species requires managing habitat for both breeding and nonbreeding seasons. The factors that influence habitat selection by the threatened Western Snowy Plover (*Charadrius alexandrinus nivosus*) during the nonbreeding season are poorly understood. We examined the distribution of Western Snowy Plovers in coastal northern California during the nonbreeding season over two consecutive years. The plovers that wintered in northern California included residents and migrants from other areas. Individual plovers demonstrated high site faithfulness within the nonbreeding season, occupying small home ranges (1331 ± 1382.9 m). Occupied sites had more brown algae and associated invertebrates, were wider, and had less debris in the foredune than unoccupied sites. These findings suggest that during the nonbreeding season Snowy Plovers select habitats that have more food and where birds could more easily detect predators. The results from this study provide information that can be used to identify habitat for nonbreeding Snowy Plovers and to incorporate nonbreeding habitat into restoration efforts. Maintaining nonbreeding habitat in northern California is important not only to the local population, but other populations as well.

INTRODUCTION

Recent evidence indicates that many shorebird populations worldwide are in decline (Morrison et al. 2007, Delaney et al. 2009). Survival is the most critical vital rate influencing shorebird population growth (Sandercock 2003), and the nonbreeding season is the likely interval during the annual cycle when mortality is highest (Evans and Pienkowski 1984). The causes of mortality during winter are food shortages, especially at northern latitudes (Evans and Pienkowski 1984), and predation by raptors (Page and Whitacre 1975, Cresswell and Quinn 2004). Consequently, strong selective pressures shape choices of habitat by individual shorebirds during winter.

During the nonbreeding season, the spatial distribution of shorebirds is driven by the distribution and availability of food, as evidenced by positive correlations between bird densities and food abundance or availability (e.g., Bryant 1979, Colwell and Landrum 1993, Gill et al. 2001a). 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 habitats that are open with limited cover (Pomeroy 2006), and those occupying riskier habitats may suffer higher mortality rates from predation (Van den Hout 2008). In short, shorebirds aggregate in areas of high food availability and where they 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 shorebirds and anthropogenic disturbance (Pfister et al. 1992, Kirby et al. 1993). Understanding the relationship between these three factors (food, predation, and disturbance) and shorebird distribution is essential to maintaining nonbreeding habitat, especially for threatened and endangered species.

The Snowy Plover breeds and winters along the Pacific coast of North America from Washington south through Baja California, Mexico. In 1993, the U.S. Fish and Wildlife Service listed the coastal population segment as threatened under the U.S. Endangered Species Act; a recovery plan was finalized in 2007. Several factors are thought to limit the population via 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., *Ammophila arenaria*, *Carpobrotus chilensis*), restrictions on human activities that disturb plovers or compromise egg and chick survival, and predation of young by native and introduced vertebrates. Little attention, however, has been given to understanding the nonbreeding ecology of plovers, and limited management actions target this segment of the annual cycle. Accordingly, we studied a small, marked population of plovers that winter in coastal northern California with the following objectives. First, we quantified the spatial distribution of plovers along coastal beaches by estimating home range size of individually-marked birds and characterizing their movements among locations. Second, we examined second order habitat selection (or that corresponding to home range; Johnson 1980) by comparing occupied habitats with unoccupied sites using features of habitat that represented food and danger. Specifically, we predicted that plovers would select habitats of high food availability, where the risk of predation by raptors was reduced, and anthropogenic disturbance was low. Finally, we discuss management implications from our results and emphasize the importance of management actions directed at increasing food and providing diurnal roosting habitat that is attractive to over-wintering plovers.

METHODS

Study Area

We studied Snowy Plovers in Humboldt County, California (Figure 1), an area that contains the highest density of Snowy Plovers in northern California during both the breeding and nonbreeding seasons (Colwell et al. 2008). The study area included nearly all ocean-fronting beaches consisting of a sandy substrate from Centerville to Stone Lagoon. This stretch of coastline encompasses nearly all Snowy Plover beach breeding locations over the past eight years (Colwell et al. 2008), as well as other potentially suitable habitat for wintering Snowy Plovers. The study area includes approximately 90 km of continuous coastline, of which 65 km is considered suitable habitat (beaches consisting of sandy substrate). The other 25 km consists of rocky intertidal habitats that are unsuitable for plovers. The 65 km of suitable habitat was subdivided into ten beach segments that are managed by a mix of county, state, and federal agencies, as well as some private inholdings.

The beach segments in the study area can be divided into four distinct habitat components: (1) the waveslope consisting of the area below the high tide line, (2) the wrack consisting of the line of debris deposited from high tides, (3) the foredune extending from the wrack to the backdune, and (4) the backdune extending inland (east) from the vegetation line or at the crest of the western-most dunes. The composition of vegetation at the sites includes: European beachgrass (*Ammophila arenaria*), native dune grass (*Leymus mollis*), sand-verbena (*Abronia* spp.), ice plant (*Carpobrotus chilensis*), and sea rocket (*Cakile* spp.). Debris on beaches, both in the foredune and wrack, 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.

Field Methods

We surveyed the 65 km of beaches during the nonbreeding season with the aid of field assistants 16 times between October 2007 and February 2009. We defined the nonbreeding season as the period from 1 October to 28 February. Observers conducted observations between 700 and 1400 PST, completing a survey of the entire study area in approximately two weeks before repeating the process. Observers walked the beach along the wrack and used binoculars and spotting scopes to scan for plovers. Upon detection, observers recorded the location of a plover using a personal digital assistant (Dell Axim X50) with an auxiliary Global Positioning System (GPS) attachment. If a plover was in a flock (≤ 50 m from a conspecific), observers recorded a single location for the flock. Many plovers had been previously marked with unique color band combinations. In addition to the location, observers recorded the number of individuals present (flock size), the band combinations of those marked plovers, and behavior (roosting or feeding). We conducted this work under Humboldt State University IACUC # 08/09.W23-A.

We used two methods that differed in spatial scale to quantify habitat on beaches: 3 m ground plots and 500 m point counts. Observers conducted ground plots at 10 min intervals (as determined by timer) to collect data on ground cover, invertebrates, and tracks. During ground plots observers visually estimated and recorded the percent ground cover on an ordinal scale of 0-4 (0=0%, 1 = 1-10%, 2 = 11-50%, 3 = 51-90%, 4 = >90%). Ground cover included brown algae, eelgrass, small woody debris, stumps, bivalve and crustacean shells, stones, live vegetation, dead vegetation, exoskeletons of *Velella*, and garbage. Observers also classified the number of objects on a $\log_{10}$ scale (0, 1-10, 11-100, 101-1,000, > 1,000). During ground plots observers categorized and recorded invertebrates (amphipods, flies, beetles, isopods, craneflies, spiders, polychaetes, and other) on a $\log_{10}$ scale. In addition, observers recorded the number of amphipod burrows. During samples of ground plots observers recorded the number (0, 1-10, or >10) of sets of tracks of people, dogs, vehicles, horses (*Equus caballus*), and corvids (*Corvus brachyrhynchos*, *C. corax*). Observers measured the slope of the foredune during ground plot samples using a clinometer (measured from the wrackline to the base of the dune). Observers conducted point counts at 20 min intervals recording the number of people, dogs, vehicles, horses, Common Raven (*C. corax*), American Crow (*C. brachyrhynchos*), and raptors within a 500 m radius.

To obtain ground cover measurements of the foredune, where plovers typically roosted, we used a different methodology on three separate surveys of the study area. We walked the entire beach along the wrack and stopped every 150 m (as measured by a GPS unit). At each point we recorded a ground plot of the wrack and estimated the distance (m) from the wrack to the base of the dune (estimated distance representing the width of the foredune at that location). We selected a random number between 1 and the estimated width of the foredune, to represent the distance in meters from the wrack to a random location where we sampled percent ground cover and the number of objects using the method for measuring ground cover. We also estimated the slope of the waveslope using a clinometer at every other location. We measured the slope of the waveslope from 30 m down slope of the most recent high tide line to the wrackline.

We defined the width of the beach as the distance between the average high tide line and the duneline (vegetation line or crest of the western-most dunes). We used ground plots of the wrackline (collected in the field during surveys) to represent the average high tide line. We conducted an additional survey of the study area using a GPS unit to trace the duneline. We collected these data between 1 January 2009 and 28 February 2009, mid-way through the second field season.

Statistical Analyses

The movement of plovers in the study area consisted of north to south movements along the beach with very limited movement east to west between the waveslope and foredune. This pattern of movement resulted in home ranges that were essentially linear. For this reason home range was estimated as a linear distance (or linear segment of beach) rather than area. We used the locations of individually-marked plovers (n = 31) to estimate home range size as a linear distance using two methods. First, we estimated the maximum distance among locations of individual plovers to determine home range size. We omitted three plovers as outliers (70.4 km, 50.2 km, and 15.9 km) from this analysis because they moved once or twice between locations that were substantially greater than 90.3% of the plovers. This method to estimate home range size is sensitive to a single, long distance movement from other locations. Moreover, this method can complicate interpretation of habitat use if individuals move among multiple locations separated by unsuitable habitat. For these reasons, we estimated home range size using a second method, fixed kernel density analysis with least squares cross validation (Seaman and Powell 1996). We estimated the 90% utilization distribution for each individual plover. Next, we fit a straight line through the 90% kernel contour that intersected it at the points along the contour that were the greatest distance apart. We used the distance of the line fit through the kernel contour to estimate the home range size for each plover. For individuals that had more than one use area (kernel) we summed the linear distances across all kernel contours. We used the average distance across the 90% kernel contour of individually-marked plovers to estimate home range size under this method.

We assumed detection probability was 100% and used the home range sizes to classify the study area into sites that were occupied or unoccupied. This was done twice using the two home range methods. We used a Geographic Information System (GIS; ArcGIS version 9.3, ESRI, Inc, Redlands, California) to estimate the average value for each variable sampled from ground plots, point counts, and measures of slope that fell in all occupied and unoccupied sites. We estimated beach width at each site as the average distance from each wrack coordinate location (collected in the field during ground plots) to the closest point along the duneline.

We analyzed the data from the occupied and unoccupied sites using logistic regression analysis. We conducted two analyses for the two methods of defining a home range. We examined a set of 20 *a priori* 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) (Burnham and Anderson 1998). We examined model fit by calculating the pseudo-R^2 for each candidate model, evaluating the correct classification rate, and examining the area under the ROC curve. To evaluate the importance of variables in the top ranked models we calculated the cumulative AIC_c weights for each variable by summing the AIC_c model weights of every model containing that variable (Burnham and Anderson 1998).

To evaluate the relationship between brown algae and invertebrates we examined correlations between brown algae and amphipods, amphipod burrows, and flies. We did not examine the relationship between brown algae and beetles, isopods, craneflies, spiders, and polychaetes due to low sample sizes ($n < 10$) of those variables. All averages are presented with standard deviations.

RESULTS

During the two nonbreeding seasons observers recorded an average of 76 ± 14 Snowy Plovers during the 16 surveys of the study area on 121 occasions. Locations were concentrated along five beaches (Figure 1, Appendices A - D). Observers detected plovers singly or in flocks of varying size, most observations (59.5%) were of flocks ≥ 5 individuals (Figure 2). Most plovers (76.1%) roosted in beach habitats whereas a few fed (23.9%). The number of plovers wintering in the study area decreased by 18% between 2007/2008 (86 ± 12) and 2008/2009 (71 ± 12) ($t = 2.38$, df =14, $P = 0.03$). Observers recorded at least 54 Snowy Plovers with color band combinations. Most (57%) were marked with unique band combinations in either Humboldt County, CA ($n = 22$), Oregon ($n = 7$), or central CA ($n = 2$). At least 23 plovers were marked as chicks with brood specific band combinations, indicating that they fledged from Oregon ($n = 18$) or Humboldt County, CA ($n = 3$). At least two plovers had a single metal USFWS band; one was from OR, the origin of the other is unknown.

Home Range

Average home range size, estimated from the maximum distance between locations of individually marked plovers, was 1331 ± 1382.9 m. Average home range size increased sharply as the number of observations for each individually marked plover increased, but quickly leveled off after five observations (Figure 3). The estimated home range size (1331 m) was reached at the tenth observation after which home range size did not increase. Average home range size, as determined using a fixed kernel density estimator, was 752 ± 626 m, or approximately half the home range size estimate from the maximum distance method.

Habitat Selection

The 16 complete surveys of the study area provided 3,479 ground plots, 971 point counts, and 1,605 measures of beach slope (Table 1). Results from the model selection using maximum distance and fixed kernel density estimator methods produced virtually identical results (Tables 2, 3, and 4). The primary difference between the two methods was sample size. Dividing the study area into beach segments of 1331 m (maximum distance) resulted in 48 sites: 15 occupied by plovers and 33 unoccupied. Using a linear distance of 752 m (fixed kernel density estimator method) resulted in 25 occupied sites and 60 unoccupied sites. Because the results are virtually identical, in the following text we present results derived from the fixed kernel density estimator. The model with the lowest AIC_c value contained the variables brown algae, beach width, and foredune ground cover (pseudo $R^2 = 0.54$) (Table 2). The second ranked model contained the variables brown algae, beach width, raptors, and dog tracks (pseudo $R^2 = 0.53$). The combined weight for the top two 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 at predicting Snowy Plover presence with the correct classification rate of the second ranked model (89.4%)

performing slightly better than the top ranked model (87.1%). The area under the ROC curve for the second rank model (0.94) was slightly higher than the top ranked model (0.93).

Results indicate that plovers wintering in Humboldt County selected wider beaches with significantly more brown algae (Tables 1, 3, and 4). The amount of brown algae on beaches was significantly correlated with invertebrate abundance, especially amphipods, their burrows, and flies (Figure 4). The data also suggest that plovers occurred on beaches with less ground cover (debris and vegetation) in the foredune (Tables 1, 2, and 3). Although Model 2 suggests Snowy Plover presence was negatively associated with both raptors and dog tracks (Table 4), the SE of those coefficients overlapped zero suggesting weak effects.

DISCUSSION

There were two main findings of this study. First, individual Snowy Plovers were predictably encountered in flocks of varying size at the same few sites, and most plovers demonstrated high site faithfulness and had comparably small home ranges within the nonbreeding season. Second, the habitat where Snowy Plovers wintered differed from unoccupied sites with plovers occurring in habitats with high food abundance and low risk of predation. Plovers selected sites that had significantly more brown algae and associated invertebrates, were wider, and had less cover in the foredune than unoccupied sites.

Individual plovers occupied small home ranges with limited movement observed during the course of the study. The home range size of Snowy Plovers (1331 m - maximum distance between observed locations and 752 m – fixed kernel density estimator) was fairly small for a nonbreeding shorebird. While most studies examining home range size of shorebirds use area, in this study a linear distance (linear segment of beach) was used because this approach best characterized the movement of plovers. However, area was also estimated from the fixed kernel density estimator used to estimate home range size. These results (0.36 km^2) provide a relative comparison to the home range size of other nonbreeding shorebirds in coastal habitats. The home range size for nonbreeding Bristle-thighed Curlews (*Numenius tahitiensis*) was estimated between 12 and 30 ha (Marks and Redmond 1996). Western Sandpipers (*Calidris mauri*) wintering in central California had a mean home range size of 22 km^2 and mean core use area of 9.5 km^2 (Warnock and Takekawa 1996). Nonbreeding Piping Plovers (*Charadrius melodus*) had an average home range size of 12.6 km^2 and average mean linear distance of 3.3 km (Drake at al. 2001). While there is no previous estimate of home range size for nonbreeding Snowy Plovers, data collected on plovers in the study area during the breeding season suggests home range size is larger in the breeding than nonbreeding season (M. A. Colwell, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, unpublished data).

In this study we estimated home range size from diurnal observations of plovers. Most of those observations were of roosting plovers, with few observations of plovers feeding. The amount and type of nocturnal activity of Snowy Plovers in the study area is unknown. Activity such as nocturnal foraging could yield different results and potentially a larger home range size. The results from this study are derived from, and thus limited to, diurnal activity of plovers.

Nonbreeding Snowy Plovers occupied wide beaches that had more brown algae and associated invertebrates and had less cover in the foredune. These findings suggest that Snowy Plovers select habitats that provide more food and have lower risk of predation. Past studies have found evidence supporting the importance of either food (Colwell and Landrum 1993), predation (Rosa et al. 2006), or disturbance (Kirby et al. 1993) on shorebird distribution. This study suggests that more than one of these factors may act collectively to influence an individual's selection of wintering habitat.

Amphipods and flies are considered major food items for Snowy Plovers in coastal habitats (Page et al. 1995), and plovers have been observed consuming them in the study area (M. A. Colwell and K. M. Brindock, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, unpublished data). In all models containing amphipods or flies those variables were either significant ($P < 0.05$) or approached significance ($P < 0.10$) and adding either of those variables to any candidate model (including the top ranked models) improved model fit. However, due to the correlation between brown algae and invertebrates these variables were not included in the same model. Although invertebrates were not in the top two models for predicting snowy plover presence, amphipods and flies were positively associated with brown algae. The importance of brown algae and the direct measures of food in predicting Snowy Plover presence emphasizes the importance of food on the distribution of Snowy Plovers during the nonbreeding season. The relationship between brown algae and nonbreeding shorebirds has been reported elsewhere. Snowy Plover and Black-bellied Plover abundance correlated positively with the amount of brown algae on beaches in southern California (Dugan et al. 2003). A study examining the relationship between kelp beds and shorebirds found the abundance of shorebirds increased on beaches after the recovery of kelp beds in that area (Bradley and Bradley 1993). Brown algae may serve as an important habitat component of the food chain on beaches for plovers and other shorebirds by providing a food source for invertebrates.

Snowy Plovers also occurred on beaches that had the physical features that reduce the risk of predation and that tended to have fewer raptors. The presence of plovers was positively associated with beach width and negatively associated with the amount of debris cover in the foredune, suggesting a preference for habitats that are more open. Studies of foraging Western Sandpipers found similar results, with sandpipers occurring in habitats that are more open at both migratory stop-over sites and wintering sites (Fernández and Lank 2006, Pomeroy 2006). Beach width was also found to be a significant variable in predicting the nonbreeding distribution of Piping Plovers along the Gulf Coast where individuals occurred more frequently at wide sites (Nicholls and Baldassarre 1990).

In addition to the physical attributes in a habitat, flocking can reduce the risk of predation to nonbreeding shorebirds (Page and Whitacre 1975, Myers 1984). As flock size increases the probability of predation for an individual decreases (Page and Whitacre 1975, Kus 1980). Snowy Plovers were most frequently observed in flocks, with few observations of single plovers and most observations of intermediate to large size flocks (≥ 5 individuals). In other coastal areas Snowy Plovers are most often observed in flocks while roosting or feeding during the nonbreeding season (Page et al. 1995). The flocking behavior of plovers may be a behavioral response by individuals to reduce the risk of predation.

Equally important to the physical attributes and behavioral responses that influence the threat of predation is the abundance of raptors at sites. The abundance of raptors, particularly falcons, in the nonbreeding season is likely influenced by the distribution of their prey (shorebirds), potentially resulting in a positive correlation between shorebirds and raptors (Conklin et al. 2008). During the nonbreeding season some raptors may rely on shorebirds as their primary food (Page and Whitacre 1975), and thus may select habitats with high concentrations of shorebirds. In northern California, overall shorebird density along beaches was positively correlated with proximity to Humboldt Bay (Colwell and Sundeen 2000). Snowy Plovers occupied few sites that are in close proximity to Humboldt Bay and occurred most often where overall shorebird densities are low (M. A. Colwell and K. M. Brindock, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, unpublished data). Colwell and Sundeen (2000) suggested that shorebird distribution on ocean beaches in northern California was influenced by the distance that birds must travel to feeding sites in Humboldt Bay. Unlike most wintering shorebirds in northern California, however, Snowy Plovers are not dependent on estuarine tidal flats for feeding. This may allow plovers to select habitats away from high densities of shorebirds that have fewer predators.

Similar to predation, disturbance can have negative impacts on shorebirds during the nonbreeding season (Burger and Gochfeld 1991, Kirby et al. 1993, West et al. 2002). Previous studies have shown a negative relationship between disturbance and shorebird presence (Burger 1981, Kirby et al. 1993). We did not find a negative relationship possibly because the levels of disturbance occurring on beaches in my study area were relatively low. In other coastal areas the influence of disturbance on habitat selection by Snowy Plovers may vary as the level of disturbance varies. In southern California, Snowy Plovers abandoned both breeding and wintering sites in response to an increase in disturbance (Lafferty 2001).

This study suggests that food and predation influence habitat selection by Snowy Plovers during the nonbreeding season, emphasizing the importance of food and danger on the nonbreeding distribution of shorebirds. The habitats shorebirds utilize during the nonbreeding season are important to maintaining viable shorebird populations (Baker and Baker 1973, Clark et al. 1993). Considering that roughly fifty percent of shorebird (suborder Charadrii) populations in North America are declining (Brown et al. 2001) and habitat loss is the leading cause of endangerment to bird species in the United States (Johnson 2007), understanding habitat selection is essential to managing and maintaining shorebird populations. Examining the variables that contribute to the abundance of food and the level of danger in habitats may provide insight to further understanding the processes through which shorebirds select habitat.

Management Implications

Although the extent to which the nonbreeding season limits the population is not clear, the recovery plan for the Snowy Plover identifies the importance of nonbreeding habitat for the recovery of the species (U.S. Department of Interior 2007). Maintaining habitat with the attributes that support an abundance of invertebrates (i.e. brown algae) and reduce the risk of predation (i.e. wide beaches, limited cover in the foredune) may be important to maintaining the Pacific Coast population of Snowy Plovers. Along the Pacific coast there are, and have been, several projects aimed at restoring habitat for Snowy Plovers (U.S. Department of Interior 2007). The focus of those projects has targeted breeding habitat, primarily removing vegetation. The results from this study suggest that restoration efforts that decrease vegetative cover and increase openness may also benefit plovers during the nonbreeding season. Land managers should also consider the potential effects of beach grooming on food availability to Snowy Plovers. Invertebrate diversity and abundance has previously been demonstrated to be negatively correlated with beach grooming (Dugan et al. 2003). Additionally, beach grooming can adversely affect breeding habitat by making sites unsuitable for nesting (Page et al. 1995).

While the relationship between breeding and nonbreeding habitats is poorly understood, in one case protecting wintering sites resulted in the establishment of a breeding population (Lafferty 2006). The plovers that wintered in northern California included local breeders, migrants from other coastal areas, and unmarked plovers (likely from other coastal beaches and inland breeding sites). The sites where plovers occurred were predictably occupied both within and between nonbreeding seasons. Thus, these nonbreeding sites should be identified and protected. Maintaining nonbreeding habitat in northern California is important not only to the local population, but other coastal populations and inland populations as well.

Although disturbance was not a significant variable in predicting snowy plover presence, we observed plovers responding to disturbance from people, dogs, vehicles, and horses. The observed impact from disturbance ranged from short flights to direct mortality (one Snowy Plover was run over by a vehicle on Centerville Beach, 19 February 2009). Given the faithfulness to sites exhibited by Snowy Plovers in the study area, plovers would benefit from managing for these types of disturbance at nonbreeding sites.

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LITERATURE CITED

Baker, M. C., and A. E. Baker. 1973. Niche relationship among six species of shorebirds on their wintering and breeding ranges. Ecological Mongraphs 43:193-212.

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

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.

Brown, S., C. Hickey, B. Harrington, and R. Gill. 2001. The U.S. Shorebird Conservation Plan. 2nd edition. Manomet Center for Conservation Sciences, Manomet, MA, USA.

Burger, J. 1981. The effect of human activity on birds at a coastal bay. Biological Conservation 21:231-241.

Burger, J., and M. Gochfeld. 1991. Human activity influence and diurnal and nocturnal foraging of sanderlings (*Calidris alba*). Condor 93:259-265.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer, 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.

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., K. M. Brindock N. S. Burrell, M. A. Hardy, J. J. Muir, S. A. Peterson, S. E. McAllister, K. G. Ross, and L. L. LeValley. 2008. Final Report: 2007 Snowy Plover Breeding in Coastal Northern California, Recorery Unit 2. Submitted to MRB Research, Inc.

Conklin, J. R., M. A. Colwell, and N. W. Fox-Fernandez. 2008. High variation in roost use by Dunlin wintering in California: Implications for habitat limitation. Bird Conservation International 18:275-291.

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

Delaney, S., D. Scott, T. Dodman, and D. Stroud [eds.]. 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. Pp. 83-123 *In* Burger, J. and B. L. Olla [eds.] Shorebirds: Breeding behavior and populations. Plenum Press, New York, NY.

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. Depletion models can predict shorebird distribution at different spatial scales. Proceedings Royal Society London B 268:369-376.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, M. D. 2007. Measuring habitat quality: A review. Condor 109:489-504.

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.

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.

Marks, J. S., and R. L. Redmond. 1996. Demography of bristle-thighed curlews *Numenius tahitiensis* wintering on Laysan Island. Ibis 138:438-447.

Morrison, R. I. G., B. J. McCaffery, R. E. Gill, Jr., S. K. Skagen, S. L. Jones, G. W. Page, C. L. Gratto-Trevor, and B. A. Andres. 2007. Population estimates of North American shorebirds, 2006. Wader Study Group Bulletin 111:66-84.

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

Nicholls, J. L., and G. A. Baldassare. 1990. Habitat associations of piping plovers wintering in the United States. Wilson Bulletin 102:581-590.

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.

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.

Rosa, S., A. L. Encarnacao, J. P. Granadeiro, and J. M. Palmeirim. 2006. High water roost site selection by waders: maximizing feeding opportunities or avoiding predation? Ibis 148:88-97.

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.

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.

West, A. D., J. D. Goss-Custard, R. A. Stillman, R. W. G. Caldow, S. E. A. le V. dit Durell, and S. McGrorty. 2002. Predicting the impacts of disturbance on shorebird mortality using a behavior-based model. Biological Conservation 106:319-328.

Table 1. Average (± SD) of variables sampled at Snowy Plover occupied (*n* = 25) and unoccupied (*n* = 60) sites in Humboldt County, CA, October 2007 – February 2009.

Variable	Occupied	Unoccupied
Ground plot		
Amphipods	0.19 ± 0.13	0.13 ± 0.13
Amphipod burrows	0.53 ± 0.27	0.33 ± 0.24
Brown algae	0.42 ± 0.18	0.18 ± 0.09
Corvid tracks	0.06 ± 0.07	0.05 ± 0.05
Dog tracks	0.42 ± 0.32	0.48 ± 0.34
Eelgrass	0.38 ± 0.49	0.58 ± 0.52
Flies	0.19 ± 0.13	0.08 ± 0.06
Ground cover-foredune	1.12 ± 0.30	1.43 ± 0.21
Ground cover-wrack	1.76 ± 0.33	1.75 ± 0.24
Human tracks	0.47 ± 0.35	0.55 ± 0.39
Vegetation	0.08 ± 0.05	0.12 ± 0.09
Vehicle tracks	0.36 ± 0.23	0.26 ± 0.29
Woody debris	0.91 ± 0.45	0.96 ± 0.42
Point counts		
Corvids	1.52 ± 1.26	0.86 ± 0.95
Dogs	0.30 ± 0.42	0.24 ± 0.36
People	0.63 ± 0.67	0.50 ± 0.60
Raptors	0.04 ± 0.04	0.08 ± 0.06
Vehicles	0.09 ± 0.11	0.06 ± 0.24
Slope		
Foredune	4.83 ± 0.92	4.55 ± 0.96
Waveslope	5.80 ± 2.36	5.45 ± 2.24
Beach width	46.81 ± 16.59	25.47 ± 15.94

Table 2. Top five models plus the null model for predicting Snowy Plover presence in Humboldt County, CA, October 2007 – February 2009.

Model	K[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]
Maximum distance				
Brown algae+width+foredune cover	4	38.48	0	0.79
Brown algae+width+raptors+dog tracks	5	42.49	4.01	0.11
Brown algae+foredune cover+raptors	4	42.85	4.37	0.08
Flies+vehicles+foredune slope	4	45.54	7.06	0.02
Eelgrass+invertebrates+humans	3	53.07	14.59	0
Null model	1	61.70	23.23	0
Fixed kernel density estimator				
Brown algae+width+foredune cover	4	56.13	0	0.78
Brown algae+width+raptors+dog tracks	5	58.71	2.59	0.21
Brown algae+foredune cover+raptors	4	66.78	10.66	0
Width+foredune slope+corvid tracks	4	78.81	22.69	0
Width+burrows	3	81.77	25.65	0
Null model	1	105.03	48.91	0

[a] Number of parameters in the model.
[b] Akaike's Information Criterion with small sample bias adjustment.
[c] ΔAIC_c is equal to the AIC_c value of model *i* minus the minimum 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 3. The cummulative AIC_c weight of covariates in the top two models for predicting Snowy Plover presence in Humboldt County, CA, October 2007 – February 2009.

Covariate	Maximum distance Cumulative AIC_c *w*	Fixed kernel density estimator Cumulative AIC_c *w*
Brown algae	0.98	0.99
Beach width	0.90	0.99
Foredune cover	0.87	0.78
Raptors	0.19	0.21
Dog tracks	0.11	0.21

Table 4. Parameter estimates, standard errors, and *P* values of variables in the top two models for predicting Snowy Plover presence in Humboldt County, CA, October 2007 – February 2009.

	Maximum distance			Fixed kernel density estimator		
Model	Estimate	SE	*P*	Estimate	SE	*P*
Model 1						
Brown algae	15.737	5.712	0.006	13.291	3.384	<0.001
Beach width	0.062	0.031	0.041	0.056	0.018	0.003
Foredune cover	-2.931	2.247	0.192	-1.952	1.507	0.195
Model 2						
Brown algae	14.940	5.767	0.009	12.554	3.427	<0.001
Beach width	0.051	0.026	0.045	0.061	0.020	0.003
Raptors	-4.257	9.681	0.660	-8.344	7.657	0.276
Dog tracks	-0.792	1.737	0.648	-0.590	1.337	0.659

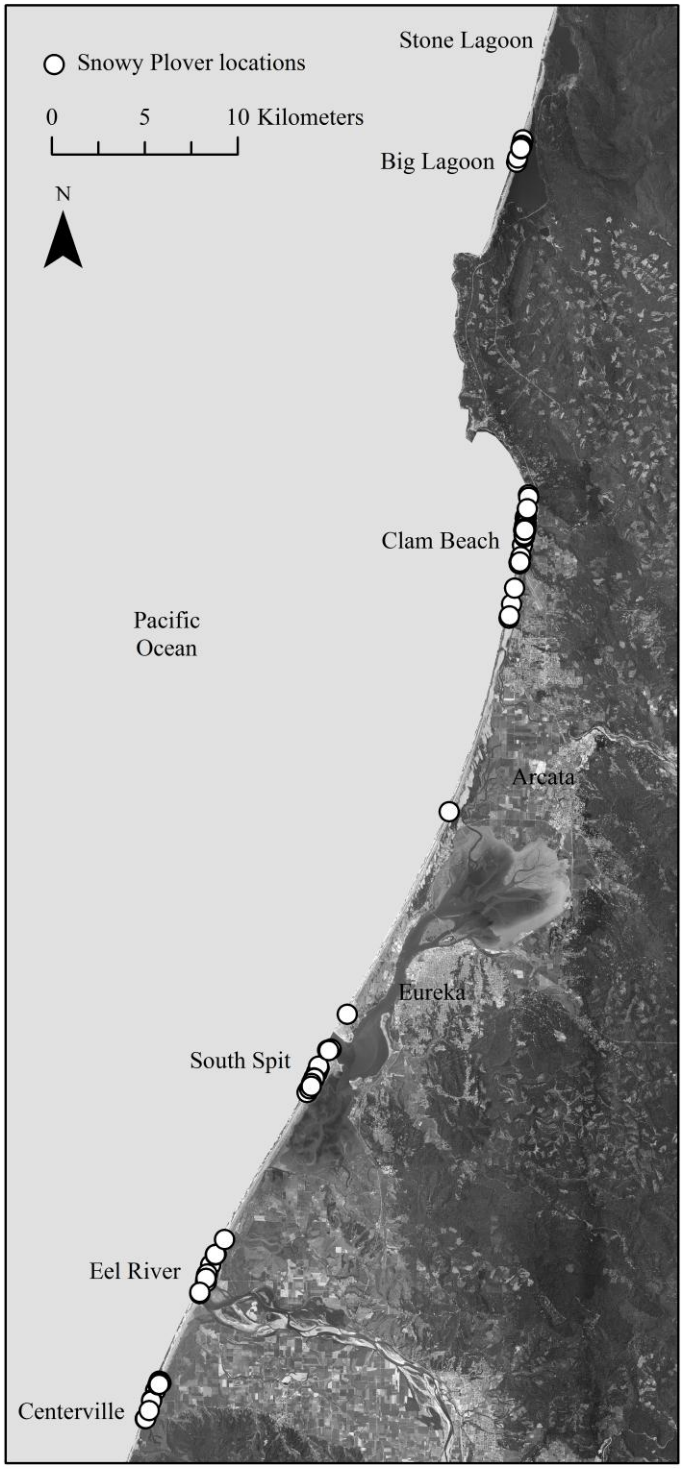


Figure 1. Locations of nonbreeding Snowy Plovers observed in Humboldt County, CA, October – February 2007 – 2009.

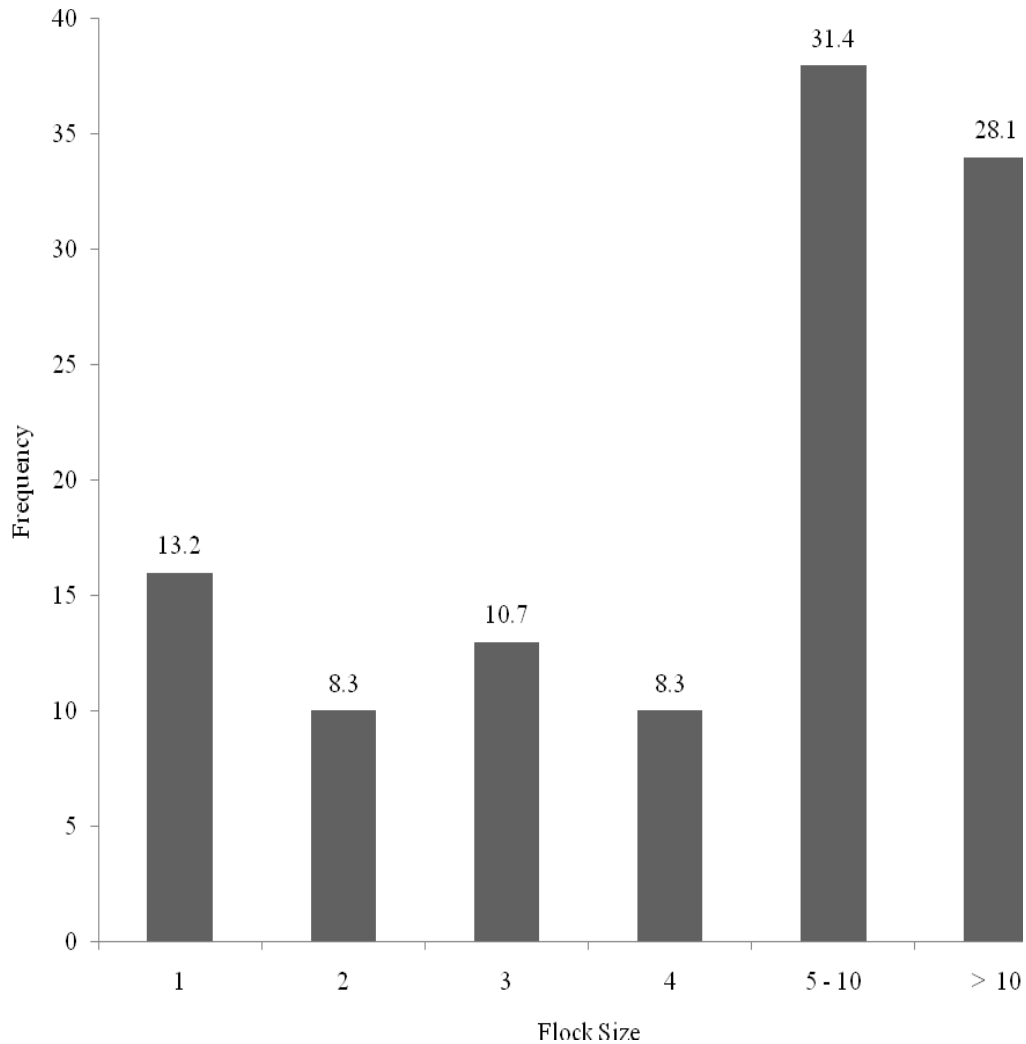


Figure 2. Frequency and percent (above bars) of observations of Snowy Plovers observed singly and in flocks (≤ 50 m from a conspecific) of different size in Humboldt County, CA, October 2007 – February 2009.

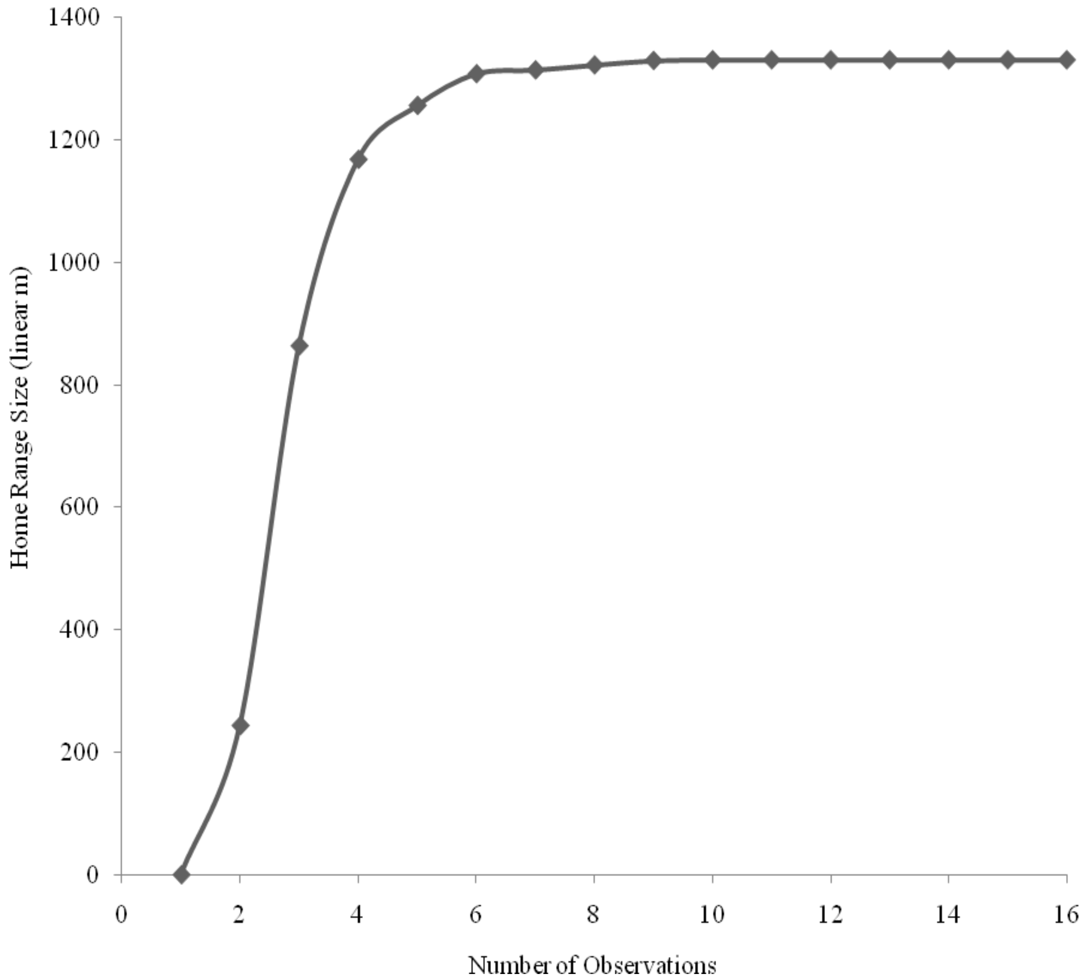


Figure 3. Average home range size (m) plotted against the total number of observations for individually marked plovers in Humboldt County, CA, October 2007 – February 2009.

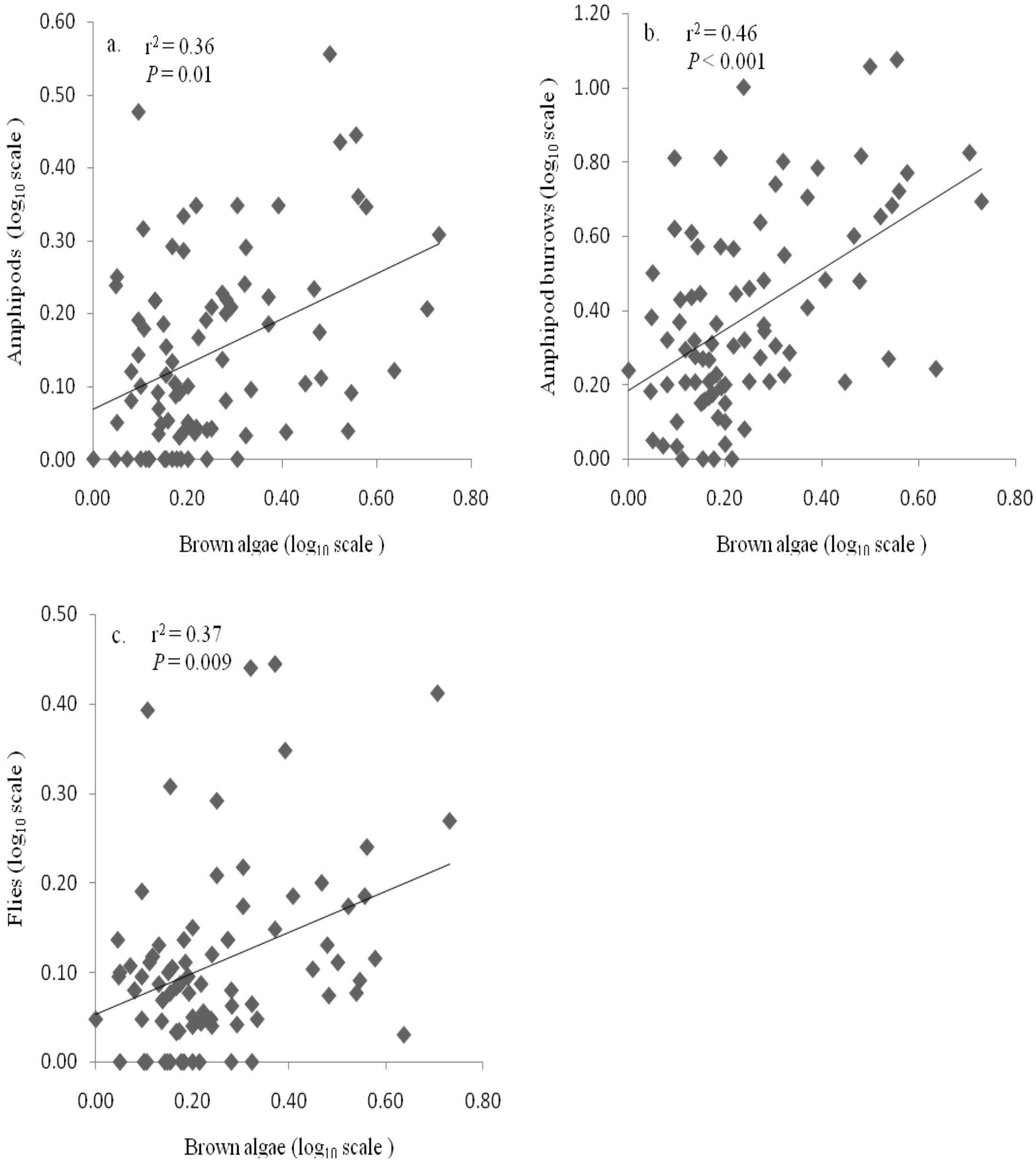
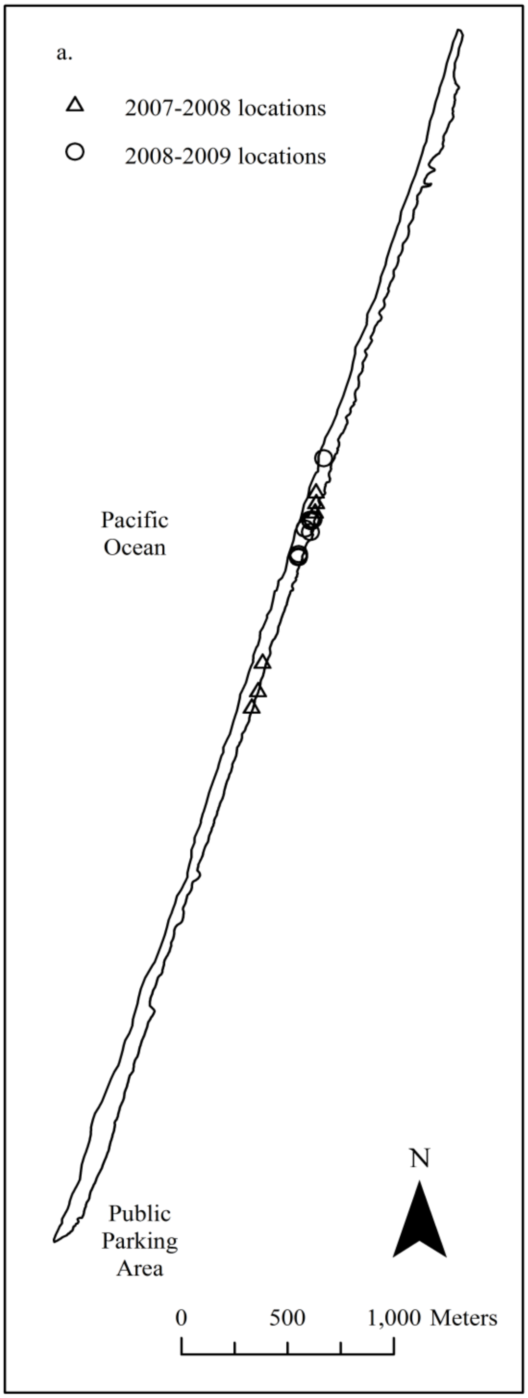
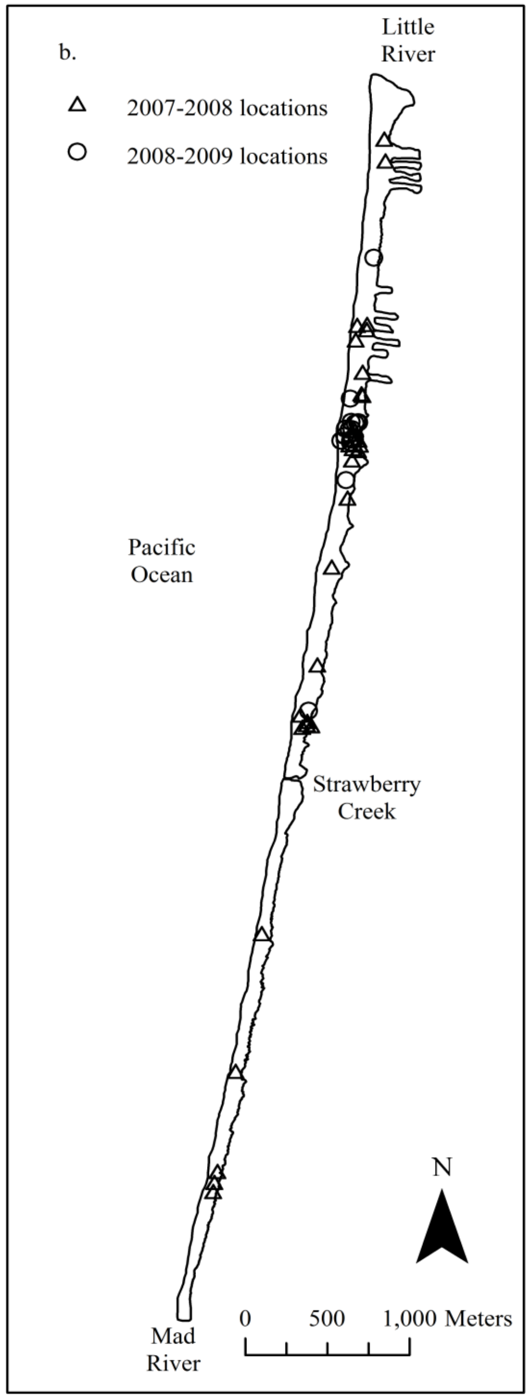


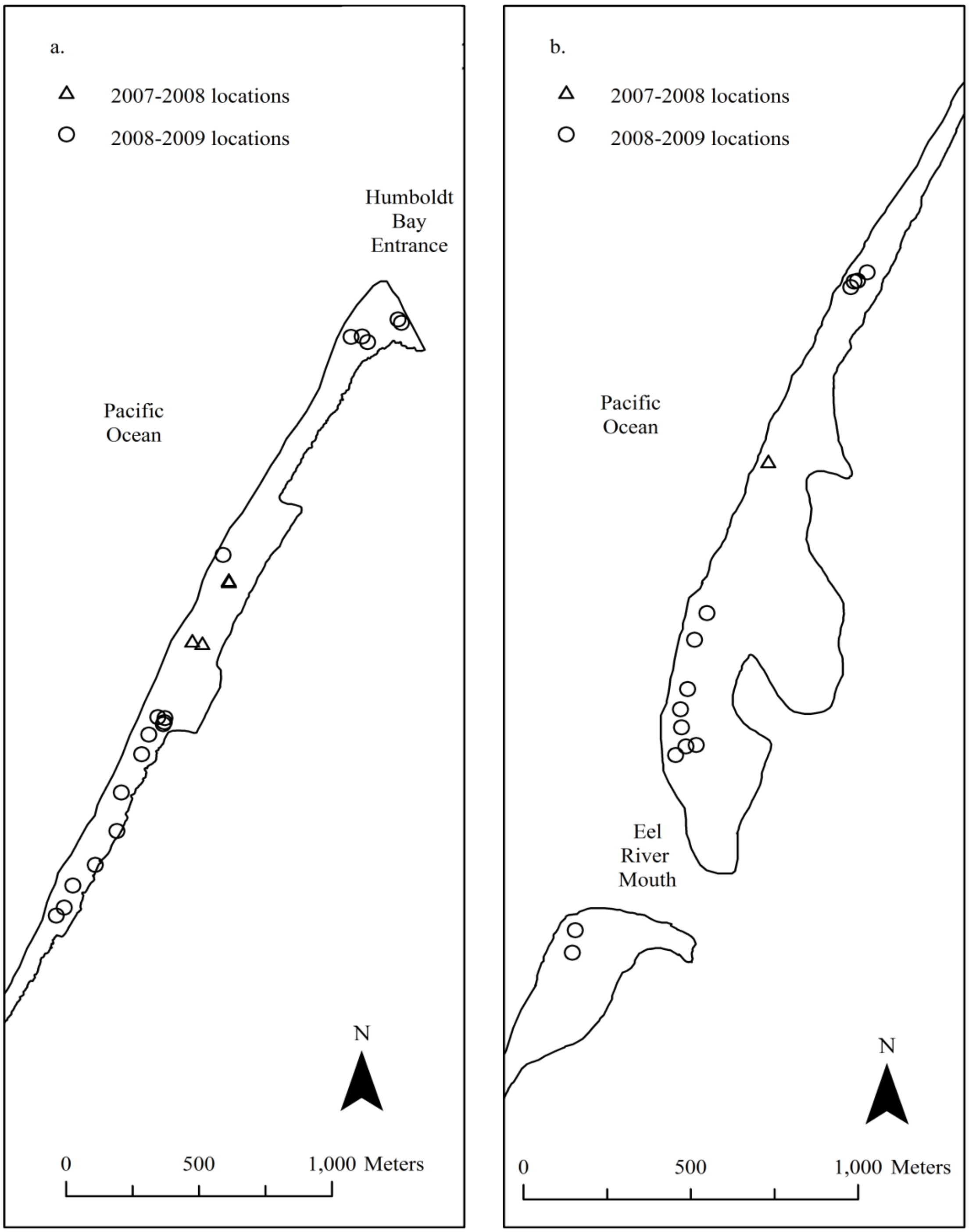
Figure 4. The relationship between brown algae and the abundance of invertebrates (a: amphipods, b: amphipod burrows, c: flies) at all sites (n = 85) designated as a 752 m linear stretch of beach.

Appendix A. Locations of Snowy Plovers observed on Big Lagoon (a) and Clam Beach (b), October 2007 – February 2009.

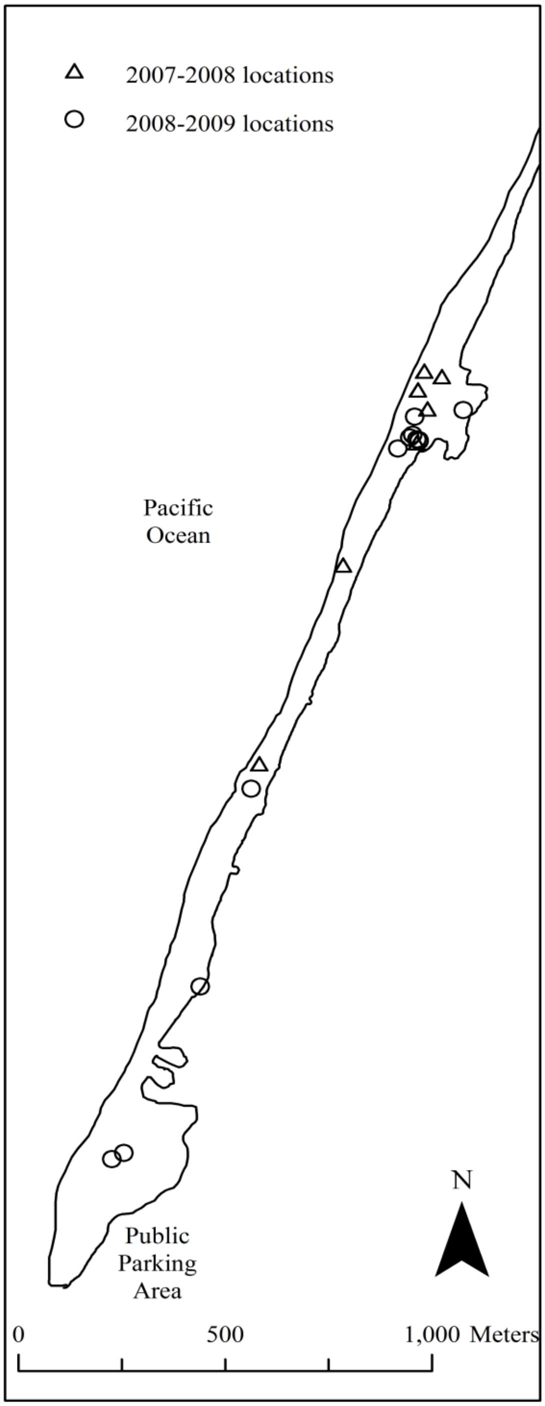




Appendix B. Locations of Snowy Plovers observed on South Spit (a) and at the mouth of the Eel River (b), October 2007 – February 2009.



Appendix C. Locations of Snowy Plovers observed on the south half of Centerville Beach, October 2007 – February 2009.



Appendix D. Number of nonbreeding Snowy Plovers observed on five beaches in Humboldt County, CA, 2007 – 2009.

Beach	Range of UTMs	$\bar{x} \pm SD$	Minimum	Maximum
Big Lagoon	406777E, 4563335N 404902E, 4557496N	4.0 ± 1.9	0	7
Clam Beach	406582E, 4542477N 405171E, 4534751N	32.9 ± 4.4	28	45
South Spit	395759E, 4512511N 392102E, 4505941N	7.2 ± 3.7	0	12
Eel River Wildlife Area	392102E, 4505941N 389127E, 4499526N	3.3 ± 3.3	0	9
Centerville	388840E, 4499388N 395640E, 4492222N	25.4 ± 11.0	2	40