

WINTER SHOREBIRD COMMUNITIES AND TIDAL FLAT CHARACTERISTICS AT HUMBOLDT BAY, CALIFORNIA

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Abstract. We examined winter (November–January) shorebird use at 19 sites around Humboldt Bay, California, an important site for nonbreeding shorebirds. We analyzed species richness (number of species), species densities, and incidences (presence/absence) in relation to habitat characteristics (tidal flat width, channelization, standing water, timing of tidal ebb, and sediment particle size). We included site area in analyses of incidence, and site area and substrate heterogeneity in the species richness analysis. We observed a total of 19 species, 8–16 at individual sites, and this variation correlated with substrate heterogeneity. Substrate particle size correlated positively with Sanderling (*Calidris alba*) incidence and negatively with American Avocet (*Recurvirostra americana*) incidence. Amount of standing water correlated positively with Whimbrel (*Numenius phaeopus*) and negatively with dowitcher (*Limnodromus griseus* and *L. scolopaceus*) incidence. Width of tidal flat correlated negatively with Whimbrel incidence. Sites at which tides ebbed earliest had higher incidences of Whimbrel and Sanderling and higher densities of Long-billed Curlew (*Numenius americanus*), but lower yellowlegs (*Tringa melanoleuca* and *T. flavipes*) densities. The amount of channelization correlated positively with curlew densities. These habitat relationships suggest that alteration of tidal flats at Humboldt Bay and elsewhere in coastal habitats has the potential to adversely affect patterns of shorebird distribution.

Key words: bird-habitat relationships, Charadrii, habitat characteristics, Humboldt Bay, intertidal habitats, nonbreeding distribution, shorebirds.

Comunidades Invernales de Aves Playeras y Características del Plano Mareal en Humboldt Bay, California

Resumen. Examinamos el uso invernal (noviembre–enero) de 19 sitios alrededor de Humboldt Bay, California, por parte de aves playeras. Ésta es un área importante para aves playeras no reproductivas. Analizamos la riqueza (número), densidad e incidencia (presencia/ausencia) de especies con relación a características del hábitat (ancho del plano mareal, canalización, agua estancada, momento de la disminución de la marea y tamaño de partículas del sedimento). Incluimos el área del sitio en los análisis de incidencia y el área del sitio y la heterogeneidad del sustrato en los análisis de riqueza de especies. Observamos un total de 19 especies (8–16 en sitios individuales), y esta variación se correlacionó con la heterogeneidad del sustrato. El tamaño de las partículas del sustrato se correlacionó positivamente con la incidencia de *Calidris alba* y negativamente con la de *Recurvirostra americana*. La cantidad de agua estancada se correlacionó positivamente con la incidencia de *Numenius phaeopus* y negativamente con la de *Limnodromus griseus* y *L. scolopaceus*. El ancho del plano mareal se correlacionó negativamente con la incidencia de *N. phaeopus*. Los sitios en que las mareas menguaron más temprano presentaron mayores incidencias de *N. phaeopus* y *C. alba*, y mayores densidades de *Numenius americanus*, pero menores densidades de *Tringa melanoleuca* y *T. flavipes*. El grado de canalización se correlacionó positivamente con las densidades de *N. americanus*. Estas relaciones de hábitat sugieren que la alteración de planos mareales en Humboldt Bay y en otros hábitats costeros potencialmente puede afectar adversamente los patrones de distribución de las aves playeras.

INTRODUCTION

During the nonbreeding season, many shorebirds (suborder Charadrii) concentrate at coastal sites (Senner and Howe 1984) where they forage in

intertidal habitats offering abundant invertebrate prey. Prey distribution and abundance have been shown to vary with physical characteristics of tidal flats (Yates, Goss-Custard, et al. 1993). Hence, it is not surprising that numerous studies have demonstrated shorebird preferences for particular habitats where food may be most available (see Colwell and Landrum 1993). For

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example, Quammen (1982) showed experimentally that American Avocets (*Recurvirostra americana*), dowitchers (*Limnodromus griseus* and *L. scolopaceus*), and Western Sandpipers (*Calidris mauri*) fed less in plots to which sand had been added. Wetness of substrate correlates with invertebrate activity and substrate penetrability; thus shorebirds may find more food at sites with standing water (Bradstreet et al. 1977, Evans and Dugan 1984, Kelsey and Hassall 1989). Conversely, standing water may decrease available foraging area if it is too deep for birds to use (Isola et al. 2000). The presence of tidal channels influences habitat use by some species. Avocets preferentially forage in or on the edge of channels (Evans and Harris 1994), and during inclement weather channels provide sheltered foraging areas for Black-bellied Plovers (*Pluvialis squatarola*; Townshend et al. 1984). Elevation of tidal flats affects foraging shorebirds, as earlier-exposed sites are available while most other habitats remain flooded (Ramer et al. 1991, Colwell and Mathis 2001). Lastly, the width of the tidal flat can be an important habitat feature, as it may be associated with characteristics such as prey abundance or proximity to roost sites (Congdon and Catterall 1994).

Here, we examine shorebird-habitat relationships at Humboldt Bay, California, an ideal study site owing to the diverse and abundant shorebird community (Colwell 1994) and varied intertidal habitats (Gerstenberg 1979, Barnhart et al. 1992, Danufsky 2000). Specifically, we analyzed shorebird species richness (number of species) and species use (densities or presence/absence) at 19 tidal flats that varied in physical characteristics. Based on a rich literature detailing a positive relationship between habitat diversity and bird species diversity (Wiens 1989), we predicted that site use by shorebird species would correlate positively with habitat heterogeneity.

METHODS

STUDY AREA

Humboldt Bay (40°45'N, 124°13'W), the largest estuary between San Francisco Bay, California, and Coos Bay, Oregon, is an important site for shorebirds on the Pacific flyway (Senner and Howe 1984, Page et al. 1999). It consists of two shallow tidal basins, Arcata Bay and South Bay, connected by a deeper, narrow shipping channel

(Fig. 1). The bay is characterized by mixed, mainly semidiurnal tides, which expose variable amounts of intertidal habitat. Tidal flats vary greatly in sediment composition, from fine clays and silts in upper reaches to coarse sandy substrates adjacent to large channels (Barnhart et al. 1992). These differences are correlated with water content, standing water, channelization, and timing and velocity of tides. During this study the tidal range (lowest low to highest high) was from -0.68 to 2.74 m (NOAA/NOS 1999). Approximately 61 km² of intertidal flats are exposed at mean lower low water (MLLW; Barnhart et al. 1992).

We selected 19 sites for shorebird surveys based on accessibility, ability to delineate distinct boundaries, and distribution throughout the bay (Fig. 1). We delineated boundaries of sites using channels, navigation markers, saltmarsh edges, and islands. The boundary farthest from the shore at each study site was the edge of the tideline after approximately 2 hr of tidal ebb. At most sites a large channel delineated this edge. We mapped site boundaries on high-resolution (0.3-m pixels) digital aerial photographs (TerraMar, San Mateo, California) taken on 10 December 1997 during an ebbing tide, one year prior to fieldwork.

SURVEY METHODS

Six observers surveyed shorebirds from 13 November 1998–18 January 1999, a period of minimal migratory movement by most species at Humboldt Bay (Colwell 1994, Harris 1996). We surveyed during ebb tides when exposure of tidal flats at a site went from 0–100%; among the 19 sites this range was 0.1 to 1.3 m above MLLW (Appendix). We arrived at sites prior to exposure of tidal flats during an ebbing tide and began surveys when tidal flats began to be exposed. We scan-sampled (Altmann 1974) sites and tallied all nonroosting (mostly foraging) birds during half-hour intervals (Colwell and Cooper 1993) until the site was 100% exposed. In all cases, it was possible to count all birds within the half-hour interval. Hereafter, we refer to each half-hour tally as a count, and each series of counts at a site on a given day as a survey. We surveyed each site on four different days, at approximately 2-week intervals. Surveys consisted of four counts with the exception of one five-count survey and one six-count survey (during exceptionally slow-moving tides).

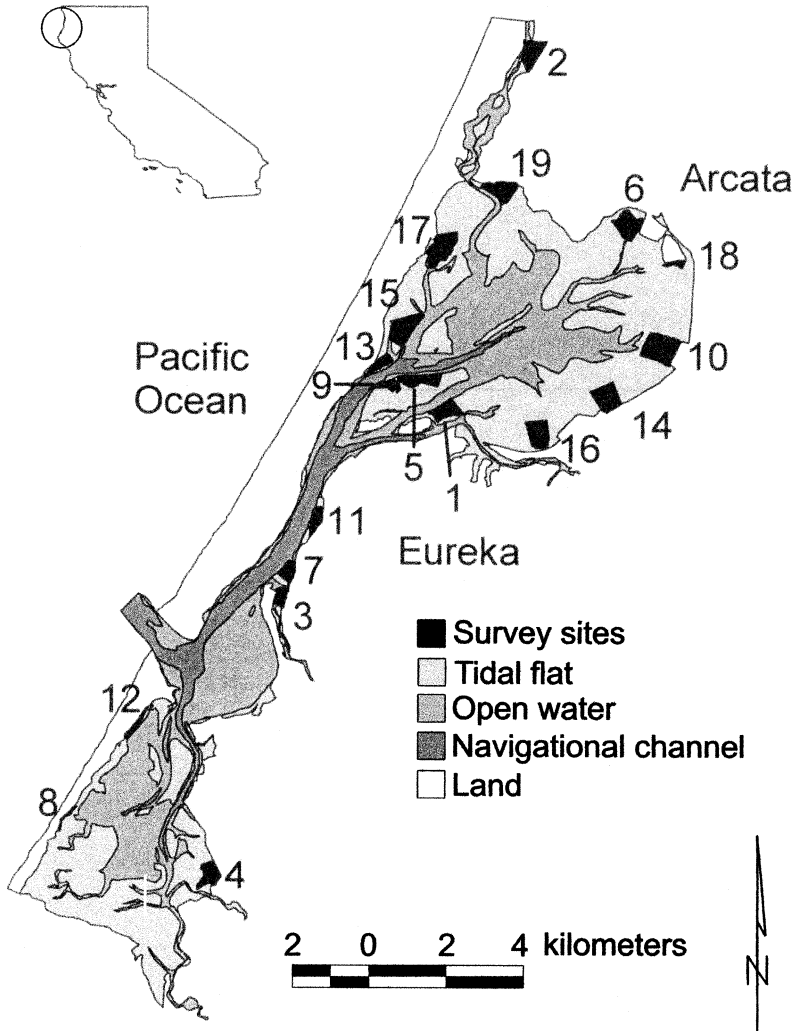


FIGURE 1. Locations of shorebird study sites and extent of tidal flats on Humboldt Bay, California, at mean lower low water. Site numbers correspond to those given in the Appendix.

Observers identified birds to species except for two groups that were difficult to distinguish in the field, especially at great distances and in poor visibility. Observers grouped Greater and Lesser Yellowlegs (see Table 1 for scientific names) as “yellowlegs”, and Short-billed and Long-billed Dowitchers as “dowitchers”. We treated these groups as species in all analyses. When small *Calidris* were indistinguishable (5% of all observations of these species), we assigned unidentified birds to species in proportion to other counts at that site (Page et al. 1999).

HABITAT CHARACTERISTICS

Based on literature review, we identified (*a priori*) seven variables as physical descriptors of tidal flats with the potential to influence types and availability of shorebird prey, and shorebird distributions. We measured the following variables (Appendix) using ArcView 3.1 and ArcInfo 7.2.1 geographic information system (GIS) software (ESRI 1996, 1998).

Site area (length of tideline). A well-known relationship exists between area and number of species (Connor and McCoy 1979). However,

since most shorebirds forage along the tideline (Recher 1966), a better measure of sampling area is length of the tideline. Since tideline changes as the tide ebbs, we estimated mean tidelines by calculating the mean of the lengths (m) of the shoreline (interface between tidal flat and marsh or dike) and the tidal flat edge (waterline of the receding tide when the site is completely exposed).

Tidal flat width. We calculated mean width of the tidal flat by delineating the shoreline and the tidal flat edge, as defined above. We converted the shoreline to a series of points spaced 1 m apart, then calculated the shortest distance (m) between each of the points and the tidal flat edge. We calculated the mean of these distances as the mean width of the tidal flat.

Channelization. On the digital aerial photographs we measured the lengths of all channels 1–3 m wide with the image displayed at a scale of 1:5000. Channels narrower than 1 m were not readily discernible at that scale, and channels wider than 3 m were flooded during surveys. We calculated channelization as the ratio of the sum of channel lengths to site area (m ha^{-1}).

Standing water. Pools are distinct features of the tidal flat surface and are visible even when there is shallow water covering the flats. At the range of tide heights when the aerial photographs were taken (0.12–0.49 m) 15 of 19 sites averaged over 90% tidal flat exposure and the remaining 4 averaged over 70% exposure. At each site, we measured the area of standing water at low tide by tracing outlines of pools on digital aerial photos. We divided total area of pools by site area and multiplied this ratio by 100 for percent area covered by standing water.

Timing of tidal ebb. We recorded the actual tide height (m above MLLW) at the North Spit buoy station (NOAA/NOS 1999) for each survey start time, (excluding surveys where the observer estimated that more than 10% of the site was exposed at the start of the survey) and calculated the mean tide height (m) at which each site began to become exposed. The timing of tidal movements at a site depends on both the elevation of the tidal flat and its distance from the mouth of the bay. Thus, although recorded in meters, this variable measures the timing of tidal movements relative to a known tide height, not the actual height of the tidal flat.

Sediment particle size. Yates, Jones et al. (1993) demonstrated the ability to use satellite

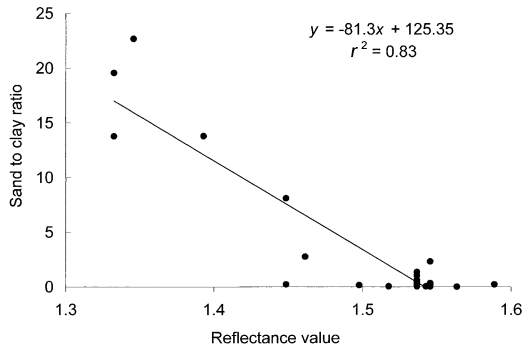


FIGURE 2. Relationship between sediment particle size in Humboldt Bay, California, and reflectance values from Landsat imagery. The ratio of percent sand to percent clay from 31 sediment samples taken from survey sites was significantly predicted by the log of Landsat TM band 4 (near infrared) reflectance values at those locations.

imagery to describe estuarine substrates. We used a Landsat Thematic Mapper (TM) satellite image to analyze relationships between sediment particle size and Landsat reflectance values. We used the most recent cloud-free image available, acquired on 15 July 1994, and assumed the pattern of sediment deposition had not changed significantly and that organic content did not influence reflectance values. Landsat sensors record reflectance in seven wavelength bands, and create an image composed of pixels 30 m on a side. Each pixel consists of a series of reflectance values that correspond to the amount of brightness sensed in each of the seven bands. We classified the satellite image into 11 substrate classes using bands 4, 5, and 7 (the near infrared band and two shortwave infrared bands; Danufsky 2000). To ground truth these data, we quantified 31 surface sediment samples collected from the bay according to percent sand ($>63 \mu\text{m}$), silt ($2\text{--}63 \mu\text{m}$), and clay ($<2 \mu\text{m}$) by mass, using standard wet sieve and pipette techniques (Kramer et al. 1994). Next, we regressed particle size percentages on the mean reflectance values of the Landsat substrate classes that corresponded to the location where each sediment sample was collected. The best regression model used the log of band 4 reflectance (near infrared) as the independent variable, and the ratio of percent sand to percent clay as the dependent variable (Fig. 2, $r^2 = 0.83$, $P < 0.001$). Given the strength of this relationship, we used GIS to calculate a weighted mean reflectance value based on the

proportion of a site in each of the substrate classes. We used the regression model to calculate the ratio of sand to clay for each site (Danufsky 2000).

Substrate heterogeneity. We used the particle size classification from the Landsat image to quantify substrate heterogeneity. For each site, we calculated a standard deviation of mean reflectance values for substrate classes weighted by the proportion of a site in each of the eleven substrate classes.

STATISTICAL ANALYSES

For each species, we estimated use of a site as the highest of the 4–6 counts during each survey. For each site, we calculated each species' abundance as the mean of these high counts for the four surveys. We calculated densities by dividing a species' mean maximum abundance by the mean length of the tideline for each site. We defined incidence as the presence of a species during one or more counts at a site. We calculated species richness as the total number of species observed at a site during all four surveys. We did not analyze species density as the number of species per unit area because the limited number of species available to occupy sites of increasing size created a strong negative correlation between species density and area, which overshadowed any other habitat effects.

We analyzed bird densities for the eight species present at more than 15 sites. We used multiple linear regression to analyze relationships between habitat variables and bird densities. We applied Box-Cox transformations to dependent variables as needed, determined by model diagnostic plots. We used multiple logistic regression to analyze relationships between species incidences and habitat variables. For both analyses, independent variables consisted of the following: tidal flat width, channelization, standing water, ebb timing, and sediment particle size. In addition, we added length of tideline to the incidence analyses. We used multiple linear regression to analyze the relationship between habitat variables and species richness. We included all the above independent variables in the analysis with the addition of sediment heterogeneity, since we expected habitat heterogeneity to affect species richness (Recher 1966).

To select independent variables for inclusion in the models we performed all possible regressions, and based selection of the best model on

MSE, adjusted R^2 , F -value, collinearity, and outliers. We present adjusted R^2 to control for effects of multiple independent variables and small sample size (SAS Institute Inc. 1999).

We performed logistic regressions on species present at 5–15 sites. Two species showed complete (dowitchers) and quasi-complete (Whimbrel) separation of sample points in their best incidence models. This occurs when it is impossible to calculate a maximum likelihood estimator due to lack of overlap (complete separation), or insufficient overlap (quasi-complete separation) between presences and absences (Hosmer and Lemeshow 1989). In these cases, we removed variables to get the next best model that did not have complete or quasi-complete separation. We used NCSS 2000 (Hintze 1999) for all possible and multiple regression analyses and SAS v.8 (SAS Institute Inc. 1999) for Box-Cox transformations and logistic regressions. We considered results significant at $P < 0.05$.

RESULTS

HABITAT CHARACTERISTICS OF SITES

Physical features of the 19 study sites varied greatly from wide mudflats characterized by small particle size, extensive channelization, and standing water, to narrow, sandy flats with no standing water or channelization (Appendix). There were significant correlations between habitat characteristics (Table 2). Tidal flat width, channelization, standing water, substrate composition, and heterogeneity were all significantly correlated. Despite these correlations, regression diagnostics (variance inflation factors < 10 and condition numbers < 30 ; Hocking 1996) indicated multicollinearity was not a problem in the analyses.

SHOREBIRD OBSERVATIONS

We observed 19 species of shorebird (Table 1), ranging from single observations of Spotted Sandpiper and Ruff to 56 115 Dunlin (total of high counts). The number of species observed at sites ranged from 8–16 (Appendix). Six species occurred at all sites and two occurred at single sites. There was a strong relationship between species abundance and incidence ($y = 1.845 \ln(x) + 4.095$, $R^2 = 0.82$, $P < 0.001$) indicating that the most abundant species were the most widespread.

Species incidences. Of the seven species that occurred at 5–15 sites (Appendix), four had sig-

TABLE 1. Common and scientific names and total observations of shorebird species surveyed at Humboldt Bay, California, from November 1998–January 1999. Total observations are calculated as the high count (of 4–6 half-hour counts at each site on a single day) summed over 19 sites and four surveys at each site.

Common name	Scientific name	Observations
Dunlin	<i>Calidris alpina</i>	56 115
Least Sandpiper	<i>Calidris minutilla</i>	36 046
Western Sandpiper	<i>Calidris mauri</i>	30 168
Marbled Godwit	<i>Limosa fedoa</i>	10 869
Willet	<i>Catoptrophorus semipalmatus</i>	2817
Black-bellied Plover	<i>Pluvialis squatarola</i>	1752
Semipalmated Plover	<i>Charadrius semipalmatus</i>	1216
American Avocet	<i>Recurvirostra americana</i>	618
Long-billed Curlew	<i>Numenius americanus</i>	609
Sanderling	<i>Calidris alba</i>	596
Short- and Long-billed Dowitcher	<i>Limnodromus griseus</i> and <i>L. scolopaceus</i>	511
Greater and Lesser Yellowlegs	<i>Tringa melanoleuca</i> and <i>T. flavipes</i>	100
Black Turnstone	<i>Arenaria melanocephala</i>	91
Killdeer	<i>Charadrius vociferus</i>	59
Whimbrel	<i>Numenius phaeopus</i>	20
Ruddy Turnstone	<i>Arenaria interpres</i>	6
Red Knot	<i>Calidris canutus</i>	2
Spotted Sandpiper	<i>Actitis macularia</i>	1
Ruff	<i>Philomachus pugnax</i>	1

nificant incidence models (Table 3). American Avocet incidence correlated negatively with sediment particle size. Whimbrel presence correlated negatively with mudflat width, and positively with standing water and earlier ebbing. Dowitcher presence correlated negatively with standing water. Sanderling had positive correlations with sediment particle size and ebb timing.

Species densities. Species abundances and densities varied greatly among sites (Appendix), but only yellowlegs (adjusted $R^2 = 0.39$, $P < 0.01$) and Long-billed Curlew (adjusted $R^2 = 0.34$, $P = 0.01$) had significant density models (Table 4). Yellowlegs densities were higher at later-ebbing sites. Curlews occurred at higher densities at sites with more channelization and earlier ebbing. The weakest relationships be-

tween species densities and habitat characteristics were seen in Marbled Godwit and Dunlin, two of the most abundant species.

Species richness. The best regression equation for species richness was: $y = 10.48 + 0.46x$ (model adjusted $R^2 = 0.22$, $P = 0.03$), where y = species richness and x = sediment heterogeneity. This equation indicated that species richness increased with substrate heterogeneity (partial $R^2 = 0.26$, $P = 0.03$). None of the other habitat variables correlated significantly with species richness.

DISCUSSION

SPECIES PATTERNS

Analyses identified varied relationships between shorebird distributions and habitat variables. We

TABLE 2. Spearman correlation coefficients for habitat characteristics measured at 19 shorebird survey sites on Humboldt Bay, California. Correlations are significant at $P < 0.05$ when $|r_s| \geq 0.46$. Significant correlations are displayed in boldface.

	Length of tideline	Tidal flat width	Channelization	Standing water	Ebb timing	Sediment particle size
Tidal flat width	-0.24					
Channelization	0.26	0.54				
Standing water	-0.30	0.50	0.46			
Ebb timing	0.13	-0.24	0.11	-0.03		
Sediment particle size	0.09	-0.70	-0.63	-0.65	0.16	
Substrate heterogeneity	0.33	-0.64	-0.58	-0.65	0.22	0.89

TABLE 3. Best regression models for logistic regression analyses on incidence (presence/absence) of shorebird species at sites in relation to habitat characteristics.

Species	Variables in model	Coefficients				Model		
		Coefficient	SE	χ^2	<i>P</i>	<i>R</i> ²	χ^2	<i>P</i>
Semipalmated Plover	Length of tideline	<0.01	<0.01	1.2	0.28	0.07	1.4	0.24
Killdeer	Channelization	<0.01	<0.01	1.4	0.24	0.09	1.7	0.19
American Avocet	Sediment particle size	-0.95	0.52	3.4	0.07	0.35	9.2	<0.01
Whimbrel	Tidal flat width	-0.01	0.01	1.8	0.18	0.41	10.3	0.02
	Standing water	0.58	0.43	1.8	0.18			
	Ebb timing	17.54	9.22	3.6	0.06			
Black Turnstone	Channelization	0.01	0.01	1.3	0.25	0.24	5.0	0.08
	Sediment particle size	0.66	0.45	2.2	0.14			
Sanderling	Ebb timing	9.94	5.40	3.4	0.07	0.45	13.0	<0.01
	Sediment particle size	1.6	0.73	2.5	0.11			
Dowitchers	Standing water	-0.74	0.42	3.1	0.08	0.36	9.5	<0.01

detected strong associations between sediment particle size and two species distributions: particle size correlated negatively with occurrence of American Avocet and positively with Sanderling. These results corroborate findings of others. For instance, Page et al. (1979) showed that Sanderlings were most abundant in habitats characterized by coarse (sandy) sediments. By contrast, foraging American Avocets use habitats with fine sediments, a finding supported by experimental work (Quammen 1982). The relationship between avocets and particle size makes ecological sense given the avocet's foraging behavior (Hamilton 1975). Avocets scythe the bill through water and substrate, and fine sediments offer less physical impediment than coarse substrates. Moreover, at Humboldt Bay, the baywide distribution of avocets at low tide is decidedly nonrandom, with birds occurring nearly exclusively in areas of fine sediment (Evans and Harris 1994, Colwell et al. 2001).

Reasoning that higher elevation sites (exposed earlier on an ebbing tide) would be available sooner to foraging birds, and, hence, would attract more individuals, we predicted a positive correlation between species distributions and ebb height. Indeed, three of four species (Whimbrel, Sanderling, yellowlegs, and Long-billed Curlew) had higher incidences and densities at earlier-ebbing sites. The positive relationship between site elevation and shorebird use is noteworthy given that we conducted our study during winter. Early-exposed sites may attract more birds because shorter days place a premium on maximizing foraging time. Therefore, individu-

als move to the first available sites to forage during ebbing tides. Comparisons to fall and spring would be valuable, especially given the high frequency of nocturnal foraging at Humboldt Bay during the autumn (Dodd and Colwell 1996), and the availability of flooded pastures as alternative feeding sites in winter and spring.

We cannot rule out that other unmeasured landscape-level habitat features may contribute to shorebird use of higher elevation tidal flats. For example, Long-billed Curlews occurred in greater numbers at earlier-ebbing sites, and this may be related to the proximity of some sites to high-tide roosts. As the tide ebbed, curlews moved directly from roosts to tidal flats to feed, and then dispersed to territories as more foraging area became available (Colwell and Mathis 2001). We observed as many as 63 curlews (~20% of the Humboldt Bay winter population; Mathis 2000) leaving a roost and feeding at an adjacent site (site 1, Fig. 1).

Contrary to our predictions, yellowlegs densities correlated negatively with ebb height. Earlier work on yellowlegs at Humboldt Bay (Gerstenberg 1979) showed that yellowlegs used high and low elevation mudflats with nearly equal frequency. Lower elevation sites may be preferred because they are wetter, offering more prey, offsetting the advantage of earlier exposure. Indeed, both Greater and Lesser Yellowlegs typically take prey from the water column while standing in water (Elphick and Tibbitts 1998, Tibbitts and Moskoff 1999), suggesting that lower, wetter sites should be favored.

TABLE 4. Best regression models for multiple regression analyses on densities for shorebird species at Humboldt Bay, California, sites in relation to habitat characteristics. Where necessary, data for individual species were transformed using a Box-Cox procedure to achieve normality.

Species	Variables in model	Coefficients				Model		
		Coefficient	SE	<i>P</i>	Part. <i>R</i> ²	Adj. <i>R</i> ²	<i>F</i>	<i>P</i>
Black-bellied Plover	Channelization	<0.01	<0.01	0.17	0.12	0.15	2.1	0.15
	Ebb timing	0.36	0.19	0.07	0.20			
Yellowlegs	Sediment particle size	0.02	0.01	0.10	0.17	0.39	12.5	<0.01
	Ebb timing	-0.20	0.06	<0.01	0.42			
Willet	Standing water	<0.01	<0.01	0.09	0.17	0.13	2.4	0.12
	Ebb timing	0.07	0.04	0.12	0.14			
Long-billed Curlew	Channelization	<0.01	<0.01	0.12	0.15	0.34	5.7	0.01
	Ebb timing	1.86	0.61	0.01	0.37			
Marbled Godwit	Sediment particle size	0.01	0.01	0.32	0.06	<0.01	1.0	0.32
Western Sandpiper	Channelization	<0.01	<0.01	0.11	0.18	0.18	2.0	0.15
	Standing water	0.03	0.02	0.19	0.12			
	Ebb timing	0.64	0.39	0.12	0.16			
	Sediment particle size	0.07	0.03	0.03	0.30			
Least Sandpiper	Standing water	0.06	0.03	0.08	0.17	0.12	3.6	0.08
Dunlin	Sediment particle size	0.05	0.09	0.54	0.02	0.00	0.4	0.54

One methodological facet of our study may have influenced the patterns we obtained. Shorebirds following the ebbing tide become increasingly difficult to view from shore. For this reason, we placed all of our 19 study sites immediately adjacent to shore. Therefore, our conclusions about bird-habitat relationships are limited to periods early in the ebbing tide or when neap (high low and low high) tides create tidal conditions similar to those when we surveyed.

A larger proportion (4 of 7 less common taxa) of the species incidence models rather than analyses of density (2 of 8 more common taxa) detected meaningful shorebird-habitat relationships. This suggests that a species' presence may be a more reliable metric of bird use of a site. Density models may produce fewer relationships because of the substantial variation (within and among sites) in bird densities of the most abundant species. We did not sample the entire bay, and as birds moved across boundaries of individual sites, their abundances on the site varied greatly. This affected densities (as a response variable) to a greater extent than incidences. Moreover, we obtained the weakest habitat relationships for two of the most abundant species wintering at Humboldt Bay, Marbled Godwit and Dunlin (Colwell 1994). None of the habitat variables contributed significantly to density models for these species. Gerstenberg (1979) reported that godwits and Dunlins used a wide va-

riety of habitats at Humboldt Bay; Page et al. (1979) found these taxa to be most abundant in areas with substrates of intermediate texture.

Finally, our conclusions about species responses to habitat characteristics may have been influenced by the manner in which we estimated density. We used mean tideline to estimate density because most shorebirds forage along the tide edge rather than on entire exposed flats (Recher 1966). However, some species, notably plovers and curlews, do not follow the ebbing tide (Recher 1966, Townshend et al. 1984). Black-bellied Plovers and Long-billed Curlews are often territorial on winter foraging grounds (Colwell 2000); as a result, individuals tend to be evenly spaced within intertidal habitats (Goss-Custard 1985). Results of analyses for one of these species (curlew) using density calculated from the tideline did show some significant correlations. However, a better approach for territorial species may be to calculate density based on area of tidal flat rather than tideline.

COMMUNITY PATTERNS

Two well-established ecological patterns are the relationships of species richness to area and habitat heterogeneity. The first of these, the species-area relationship (Connor and McCoy 1979, Wiens 1989), predicts increasing diversity with greater area surveyed. The number of species at 19 sites around Humboldt Bay varied from 8–

16 and correlated significantly with substrate heterogeneity; species richness was not associated with area or tideline. This positive correlation suggests that tidal flats with more microhabitats (as represented by variation in substrate differences) support more taxa. Therefore, our findings provide quantitative support for general statements that diversity of nonbreeding shorebird communities is related to heterogeneity of substrates in the intertidal habitats where they forage (Recher 1966).

CONSERVATION IMPLICATIONS

Habitat loss and degradation are principal causes of population decline for many shorebird species (Senner and Howe 1984, Page and Gill 1994). Therefore, improved understanding of shorebird-habitat relationships is vital to effective conservation (Brown et al. 2001). Additionally, large numbers of nonbreeding shorebirds concentrate at a few estuaries like Humboldt Bay (Myers et al. 1987), making conservation of these sites imperative (Bildstein et al. 1991).

We showed that physical features of tidal flats influence the distribution patterns of wintering shorebirds at Humboldt Bay. These habitat characteristics correlated with species distributions for a number of species we analyzed. A reasonable extension of these findings is that alterations to habitats that affect these physical characteristics are likely to impact shorebirds and should be carefully considered in development plans. For example, a report assessing effects of proposed (completed in 2000) dredging of navigational channels (U.S. Army Corps of Engineers 1995) predicted no net loss of foraging habitat for shorebirds. Yet, the report defined habitat homogeneously as "mudflat." Although tidal flat habitat was not lost as a result of this project, it is not known if dredging altered distributions of sediment particles of different sizes, which could affect shorebird habitat. For example, if deposition of large, sandy sediment particles increases in the vicinity of dredged channels (owing to increased current velocities, for example), then these flats may no longer be suitable foraging habitat for American Avocets. The information gained in this study of smaller-scale heterogeneity in tidal flats and its relationship with shorebird use (incidence and density) should be taken into account in future assessments of this kind. Lastly,

given the strength of relationships between Landsat imagery, sediment particle size, and distributions of some shorebird species (Yates, Goss-Custard et al. 1993, Yates, Jones et al. 1993), we encourage others to investigate this remote sensing tool to monitor long-term habitat changes, especially in coastal estuaries where land use contributes sizeable sediment loads to estuaries where nonbreeding shorebirds concentrate (Myers et al. 1987).

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APPENDIX. Physical characteristics measured at 19 study sites on Humboldt Bay, California, and densities of shorebird species observed. Densities for each species at each site are calculated as mean of the daily high count from each of the four surveys at each site divided by the mean length of the tideline (m). Site numbers correspond to those mapped in Figure 1.

	Site number							
	1	2	3	4	5	6	7	8
Habitat variables								
Area (ha)	24.2	20.7	9.3	21.9	24.7	32.3	11.7	3.5
Length of tideline (m)	951	1170	1574	1035	1025	1017	711	796
Tidal flat width (m)	387	415	225	350	230	489	237	45
Channelization (m ha ⁻¹)	225	49	267	192	219	137	0	0
Standing water	1	0	0	4	1	0	0	0
Ebb timing (m)	1.3	0.9	1.3	1.1	1.2	1.0	0.7	1.1
Sediment particle size	0.6	1.0	3.5	0	0.8	0.7	8.6	4.5
Substrate heterogeneity	2.6	3.8	7.8	2.3	3.0	3.4	4.9	4.0
Species								
Black-bellied Plover	0.10	0.01	0.03		0.02	0.001	0.04	0.01
(SD)	(0.08)	(0.01)	(0.01)		(0.003)	(0.001)	(0.02)	(0.002)
Semipalmated Plover	0.02	<0.001	0.06		<0.001		0.17	<0.001
(SD)	(0.03)		(0.02)				(0.02)	
Killdeer				0.003				
(SD)				(0.005)				
American Avocet	0.03	0.01			0.01	0.03		
(SD)	(0.03)	(0.01)			(0.004)	(0.02)		
Yellowlegs	0.001	0.004	<0.001	0.004	<0.001	<0.001	0.01	0.002
(SD)	(0.001)	(0.003)		(0.002)			(0.004)	(0.001)
Willet	0.04	0.01	0.004	0.06	0.07	0.03	0.02	0.01
(SD)	(0.02)	(0.01)	(0.002)	(0.04)	(0.01)	(0.01)	(0.01)	(0.01)
Spotted Sandpiper								
(SD)								
Whimbrel	0.001				0.002			
(SD)	(0.001)				(0.002)			
Long-billed Curlew	0.07	<0.001	0.003	0.01	0.01	<0.001	0.004	0.002
(SD)	(0.08)		(<0.001)	(0.005)	(0.002)		(0.001)	(0.001)
Marbled Godwit	0.40	0.16	0.14	0.07	0.19	0.15	0.46	0.05
(SD)	(0.18)	(0.22)	(0.06)	(0.05)	(0.07)	(0.14)	(0.36)	(0.02)
Ruddy Turnstone			<0.001				<0.001	
(SD)								
Black Turnstone			0.002		0.001		0.01	
(SD)			(0.002)		(0.002)	<0.001	(0.004)	
Red Knot								
(SD)								
Sanderling	<0.001		0.02		0.005		0.02	0.01
(SD)			(0.001)		(0.008)		(0.01)	(0.01)
Western Sandpiper	0.33	0.07	1.06	0.001	0.14	<0.001	0.66	0.21
(SD)	(0.35)	(0.11)	(0.34)	(0.002)	(0.05)		(0.59)	(0.17)
Least Sandpiper	1.31	0.28	0.43	0.11	0.13	0.07	0.61	0.31
(SD)	(0.35)	(0.13)	(0.20)	(0.13)	(0.12)	(0.09)	(0.40)	(0.11)
Dunlin	0.73	0.23	0.83	0.24	0.32	0.005	1.60	0.75
(SD)	(0.39)	(0.12)	(0.48)	(0.33)	(0.15)	(0.01)	(0.54)	(0.34)
Ruff								
(SD)								
Dowitchers	0.001	0.03	0.001		<0.001	0.04	0.003	<0.001
(SD)	(0.003)	(0.02)	(0.002)			(0.03)	(0.006)	

APPENDIX. Extended.

Site number										
9	10	11	12	13	14	15	16	17	18	19
8.2	51.0	13.1	7.5	12.0	33.7	36.2	31.5	40.1	5.4	27.1
810	641	924	1089	719	591	680	600	1094	632	904
240	780	183	70	197	602	466	640	458	99	258
96	385	7	16	10	125	87	144	827	50	168
0.1	11	0.1	0	9	7	1	1	2	0	0.2
1.3	0.8	1.1	1.1	1.1	1.0	1.2	1.3	1.0	1.0	0.8
1.6	0.5	2.3	8.4	1.9	0.4	2.4	0.7	0.7	2.6	0.4
3.2	0.3	6.1	6.2	3.7	0	4.9	1.2	2.0	3.6	0
0.02	0.003	0.02	0.01	0.01		0.18	0.02	0.04	<0.001	0.01
(0.01)	(0.004)	(0.01)	(0.003)	(0.002)		(0.08)	(0.02)	(0.03)		(0.01)
		0.004	0.02	0.03	0.02		0.01	0.003		0.001
		(0.006)	(0.01)	(0.01)	(0.02)		(0.01)	(0.002)		(0.002)
				0.002		<0.001		0.01		0.001
				(0.003)				(0.02)		(0.003)
<0.001	0.004	0.001		0.02	0.003	0.03	0.04	0.01	0.01	0.003
	(0.004)	(0.001)		(0.02)	(0.005)	(0.03)	(0.04)	(0.01)	(0.003)	(0.003)
<0.001	0.002	<0.001		<0.001	0.003	<0.001	0.001	0.001	0.002	0.004
	(0.002)				(0.005)		(0.001)	(0.001)	(0.001)	(0.003)
0.07	0.06	0.01	0.06	0.09	0.02	0.05	0.13	0.03	0.02	0.06
(0.03)	(0.03)	(0.01)	(0.06)	(0.08)	(0.01)	(0.02)	(0.03)	(0.01)	(0.003)	(0.03)
					<0.001					
<0.001		<0.001		0.001						
				(0.002)						
0.02	0.003	0.003	0.001	0.006	0.002	0.03	0.01	0.01	<0.001	0.003
(0.02)	(0)	(0.001)	(<0.001)	(0.002)		(0.005)	(0.01)	(0.004)		(0.001)
0.15	0.09	0.23	0.03	0.20	0.05	0.34	0.04	0.10	0.13	0.13
(0.11)	(0.03)	(0.17)	(0.04)	(0.07)	(0.06)	(0.26)	(0.02)	(0.07)	(0.22)	(0.11)
		<0.001								
0.002	0.004	0.003	<0.001	0.004				0.002	<0.001	
(0.001)	(0.006)	(0.003)	<0.001	(0.003)				(0.001)		
		<0.001	<0.001							
0.002		0.01	0.05	0.01		0.003		0.001		
(0.002)		(0.003)	(0.03)	(0.01)		(0.003)		(0.002)		
0.96	0.70	0.06	0.33	0.96	0.01	1.72	0.16	0.73	0.01	0.32
(0.59)	(1.11)	(0.10)	(0.20)	(0.31)	(0.01)	(0.99)	(0.21)	(0.54)	(0.01)	(0.56)
1.08	0.98	0.08	0.27	0.89	1.33	1.31	0.12	0.99	0.30	0.25
(0.79)	(1.53)	(0.14)	(0.16)	(0.37)	(0.60)	(0.64)	(0.20)	(0.57)	(0.14)	(0.37)
0.74	0.57	0.47	0.49	1.50	0.02	3.88	1.10	1.68	0.02	1.43
(0.50)	(0.57)	(0.17)	(0.08)	(1.22)	(0.02)	(2.03)	(1.21)	(0.81)	(0.02)	(0.34)
			<0.001							
<0.001		0.03	<0.001			0.003	0.01	0.005		
		(0.02)				(0.005)	(0.03)	(0.009)		