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Shorebird use of an exposed sandy beach in southern California

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Abstract

Frequent morning surveys of birds were conducted on 1 km of beach in southern California to investigate shorebird use of an exposed sandy beach. The overall mean abundance (98.6 individuals km^{-1}), estimated biomass (9.6 kg km^{-1}), and species richness (5.5 species km^{-1}) of shorebirds observed were very high for a sandy beach in the temperate zone. Eight species, sanderling (*Calidris alba*), semipalmated plover (*Charadrius semipalmatus*), marbled godwit (*Limosa fedoa*), black-bellied plover (*Pluvialis squatarola*), western sandpiper (*Calidris mauri*), willet (*Catoptrophorus semipalmatus*), surfbird (*Aphriza virgata*), and whimbrel (*Numenius phaeopus*), occurred in overall mean abundances >1 bird km^{-1} and accounted for 97% of the abundance and biomass of shorebirds. Sanderlings were the most abundant shorebird every year (64% of individuals and 35% of the biomass). Different species of abundant shorebirds exhibited distinct patterns of use of beach habitat, including fall, spring, and winter peaks in abundance. Temporal variation in shorebird use on seasonal and interannual scales was associated with migration patterns, and also with habitat availability and condition. Seasonal variation in monthly mean abundance and estimated biomass of shorebirds varied over more than an order of magnitude and followed a similar pattern in each year, reaching maxima in the fall or winter (161–280 individuals km^{-1} and 15.4–23.9 kg km^{-1}) and minima in May or June (3–11 individuals km^{-1} and 0.8–2.2 kg km^{-1}). A minor peak in shorebird abundance and biomass coinciding with spring migration was observed in April of most years. The number of species of shorebirds observed in individual surveys ranged from 0 to 11 species km^{-1} and was positively and significantly correlated with abundance. Monthly mean species richness and the total species observed monthly followed similar seasonal patterns, ranging from annual maxima of 7.4–9.1 and 12–17 species km^{-1} between August and October to minima of 0.8–2.1 and 2–8 species km^{-1}, respectively, during June. In contrast, species turnover was lowest (1.1–1.7) in October and November, and generally highest (2–4) during early summer (June). The amount of sandy intertidal habitat available to shorebirds on the transect was estimated using sand elevations and predicted tide heights. In the fall and winter, the abundance of shorebirds was significantly and positively correlated with tide height, possibly reflecting feeding opportunities and high tide refuge effects during the highest tides. In the spring when sand levels were low, the abundance of shorebirds was negatively correlated with tide height. Prey availability, beach condition and the local availability, and condition of alternative foraging habitats may influence those relationships. Interannual variations in shorebird use and beach condition were observed in the course of the study. During an El Nino Southern Oscillation (ENSO) event (1997–1998), the extent of sandy habitat was greatly reduced and intertidal habitat was mostly converted to rocky substrate. The overall abundance of shorebirds and the mean abundance of some common species (e.g. sanderling) were depressed, and an uncommon species (surfbird, *A. virgata*) was unusually abundant during the ENSO event. In summary, the results suggest that sandy beaches are important habitat for many species of shorebirds, particularly in areas where alternative coastal foraging habitats, such as coastal wetlands, have become scarce. Understanding the dynamics of and threats to exposed sandy beaches may be increasingly important for shorebird conservation in many coastal regions.

Keywords: sanderling; plover; godwit; sandpiper; willet; whimbrel; El Nino Southern Oscillation

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1. Introduction

Populations of many species of shorebirds are declining in North America (Howe & Geissler, 1989; Morrison et al., 2001). Factors affecting shorebirds, such as loss of habitats important for breeding, staging, and non-breeding season foraging, and exposure to contaminants are important concerns for conservation and restoration of shorebird populations (Brown, Hickey, Harrington, & Gill, 2001; Burger, Niles, & Clark, 1997; Hothem & Powell, 2000; McCrary & Pierson, 2000; Powell & Collier, 2000).

Strong seasonal variation in shorebird abundance in California is driven primarily by migration patterns (DeSante & Ainley, 1980; Shuford, Page, Evens, & Stenzel, 1989). The majority of shorebird use of southern California intertidal habitats occurs during migration and over-wintering periods, July through May (Garrett & Dunn, 1981). Shorebird distributions in the region have been categorized generally as: (1) breeding (May and June), (2) fall migration (from July to October), (3) over-wintering (from November to February), and (4) spring migration (from March to May; Lehman, 1994; Paulson, 1993). Some shorebird species may be present in the region for only a few days per year (Lehman, 1994), making a complete description of shorebird use challenging.

The majority of research on shorebirds in marine systems has been conducted in protected habitats, such as bays and estuaries (e.g. Goss-Custard et al., 1991; Piersma, Degoeij, & Tullp, 1993; Recher, 1966; Shuford et al., 1989). The loss of coastal wetlands suitable as shorebird habitat has been severe in southern California with <10% of historic levels remaining today. The regional loss of protected habitats may be increasing the importance of exposed coastal habitats, such as sandy beaches, for shorebirds. Relatively little information exists on shorebird use of exposed sandy and rocky intertidal shores (Bradley & Bradley, 1993; Burger et al., 1997; Colwell & Sundeen, 2000; DeSante & Ainley, 1980; Dinsmore, Collazo, & Walters, 1998; Lopez-Uriarte, Escofet, Palacios, & Gonsalez, 1997; McLachlan, Wooldridge, Schramm, & Kuhn, 1980). Many bird species, including shorebirds, use exposed shores for roosting or loafing (pelicans, cormorants, gulls, and terns), nesting, and chick rearing (snowy plovers and least terns). More than 25 species of migrating, wintering, and breeding shorebirds use exposed sandy beaches on the California coast (Colwell & Sundeen, 2000; Dugan, Hubbard, & Wenner, 2001; McCrary & Pierson, 2002).

Exposed sandy beaches comprise approximately three-quarters of the world's shorelines (Bascom, 1980), including much of the California coast (Smith et al., 1976). Beaches are the least understood and least studied intertidal habitat on the California coast, despite their importance as a major component of the coast, ecological, recreational, and economic resources, and potential impacts from both marine and terrestrial pollutant sources. In southern California, exposed sandy beaches support diverse and abundant invertebrate macrofaunal communities (Dugan et al., 2000; Dugan, Hubbard, McCrary, & Pierson, 2003). Invertebrate macroinfauna can attain an abundance of >80,000 individuals and biomass of >10 kg m^{-1} of shoreline on southern California beaches (Dugan et al., 2000, 2003). Such macrofauna may be increasingly important as prey resources for shorebirds, as the function, quality, and availability of coastal wetlands decrease regionally.

Exposed sandy beaches are dynamic habitats that exhibit strong temporal variation in many characteristics, this is particularly evident in southern California (e.g. Dugan, 1999; Dugan, Hubbard, & Wenner, 1998a,b). Factors important in seasonal and long-term changes in beach morphology include: movement of sand between intertidal and subtidal zones; episodic inputs of sand from watershed and coastline sources; high rates of longshore transport; and loss of sand from the nearshore zone. Sand levels vary seasonally on California beaches (Inman, Elwany, & Jenkins, 1993), along with beach slope, widths, and sand texture. Exposed sandy beaches often reach maximum widths and elevations in the fall, and erode to minimum levels (even exposing bedrock and large cobble) in the winter and spring on the coast of southern California (Bascom, 1980).

The southern coast of Santa Barbara County is composed mostly of bluff-backed perennial or ephemeral beaches perched on bedrock platforms (Dugan et al., 1998a,b). In the area, seasonally varying wind and wave regimes drive beach morphology through annual cycles in which beaches retreat during periods with frequent erosive wave episodes (from November to March), and accrete during summer and fall. This seasonal cycle results in changes in the extent and nature of intertidal habitats exposed for shorebird feeding. During periods of low wave energy, the sandy intertidal habitat is relatively wide, fine-textured, and flat, with a gentle swash climate. With the seasonal movement of sand to the subtidal zone, beaches become narrower, coarser, steeper, and substantial areas of cobble or bedrock may be exposed, drastically changing the nature of the habitat and altering the distribution of food resources.

Interannual variation in coastal conditions can be associated with episodic El Nino Southern Oscillation (ENSO) events in the study region (e.g. 1982–1983 and 1997–1998). ENSO winters are characterized by strong storms, extreme waves, high sea levels, coastal flooding, and beach erosion (Flick, 1998). The 1997–1998 ENSO event resulted in record sea levels in La Jolla and San Francisco, CA, with a maximum at 0.9 ft above the seasonal average (Flick, 1998). Storm conditions associated with El Nino events may greatly increase rates of change and erosion in coastal habitats (Flick, 1998) and leave a lasting signal in morphology, macrophyte wrack input, and invertebrate communities of exposed sandy beaches (Dugan & Hubbard, unpublished data).

To investigate the importance of exposed sandy beaches to shorebirds in southern California, and to assess the influence of survey frequency on seasonal variation and annual trends of shorebird abundance, biomass density, and species richness, frequent surveys of shorebirds on an exposed sandy beach were conducted over 6 years. The hypothesis that shorebird abundance is related to the amount of available habitat, which predicts there should be higher abundances of shorebirds when more habitat is exposed during low tide was also examined. The study period included a strong California ENSO event, which produced warm sea surface temperatures, elevated local sea level, heavy rain, energetic storm waves, and extensive coastal erosion between November 1997 and April 1998 (Flick, 1998), and allowed investigation of the response of sandy beach habitat and shorebirds to a strong disturbance event.

2. Study site and methods

2.1. Study site

The 1 km survey transect extends generally east to west across a bluff-backed intertidal shoreline in the western portion of Isla Vista, Santa Barbara County, CA (west end of transect at latitude 34°24.45′ north, longitude 119°52.76′ west). The transect is isolated from adjacent sandy intertidal habitats during high tides. Physical and ecological aspects of this site have been investigated in several other studies (Dugan & Hubbard, 1996, unpublished data; Dugan et al., 1998a,b).

Like much of the shoreline of southern Santa Barbara County, the Isla Vista transect is on the protected outer coast, partially sheltered from prevailing west and north-west wind and ocean swell by the east–west orientation of the coast, and by the California Channel Islands to the south. With the exception of the westernmost 100 m of the transect, this site is further protected by its location in the lee of Coal Oil Point. The habitat is composed of perennial beach, ephemeral beach, and rocky shore with pools at low tide. The beach is chronically exposed to hydrocarbon contamination by its proximity to nearshore petroleum seeps.

Physical characteristics of the study beach were measured monthly on low tides from November 1998 to January 2001, as part of a concurrent study (Dugan & Hubbard, unpublished data). The width of the beach (bluff base to low swash level) ranged from 29 to 72 m. Mean sediment size at the water table outcrop ranged from 0.18 to 0.40 mm. The modal morphodynamic state of the beach was low intermediate, with Dean's parameter values ranging from 0.7 to 3.8. The study beach receives large subsidies of macrophyte wrack from adjacent intertidal and subtidal rocky habitats and is ungroomed. The standing crop of macrophyte wrack was estimated as mean cover and varied from 1.29 to 7.90 $m^2 m^{-1}$ of shoreline. The beach supports a very rich community of intertidal macroinvertebrates (39 species in a single survey) with extremely high abundance (up to 91,000 individuals m^{-1}) and biomass (up to 3060 $g m^{-1}$) (Dugan & Hubbard, 1996, unpublished data). That community includes wrack-associated and suspension-feeding species, all of which may serve as prey for shorebirds (Dugan et al., 2003). The beach is subject to regular use by humans and dogs.

2.2. Methods

To characterize shorebird use of the site, birds were surveyed between February 1995 and January 2001. For each survey, two indicators of available habitat were also recorded: 1) the predicted tide height (to the nearest 0.15 m Mean Lower Low Water), and 2) the height of the sand surface at a concrete stair landing at the east end of the transect (nearest 2 cm).

All birds were counted along a standard 1 km length of coast during morning hours (mostly between 7:00 and 9:00 a.m.). Typically, birds were counted while walking through upper beach habitat on the outward leg and from the lower shore on the return, with an elapsed time of about 25 min. Birds were counted only when they occurred on intertidal sand, rock, or macroalgal wrack, in pools, or wading in the nearshore zone (not in flight). Surveys were conducted in all weather, tide, and swell conditions encountered during the morning survey window. When possible, at least three surveys were conducted in each 10-day period. Shorebirds were identified to species whenever possible, but dowitchers could not always be reliably identified. Long-billed dowitchers (*Limnodromus scolopaceus*) and short-billed dowitchers (*Limnodromus griseus*) were both observed during the study, but combined counts for both species into one category, dowitcher spp., in the analysis.

Descriptive statistics for shorebirds and environmental parameters were calculated on three time scales: (1) single survey observations are used to describe extreme values during the study (maximum values); (2) monthly means are used to describe seasonal patterns (tide height, sand level, shorebird abundance biomass, and species richness, and abundance of individual species); and (3) standard years are used to compare shorebird abundances among years (mean abundance between February and January of the following year between 1995 and 2001). To estimate the biomass of shorebirds on the transect, monthly mean abundance of shorebirds was multiplied by values of mass given for each species in Paulson (1993). The turnover of shorebird species was estimated among the surveys in each month by dividing total monthly richness by mean monthly richness. Hypotheses concerning variation in abundance and species richness of shorebirds were investigated using regression analyses and ANOVA. To investigate patterns of shorebird abundance relative to tide level and extent of available habitat, ordinary least squares regressions were calculated for the abundance and species richness of shorebirds as a function of predicted tide heights. Data were also pooled from each calendar month across years of the study to reduce seasonal effects, and were then tested for significant correlations between daily shorebird abundance and tide height at survey time.

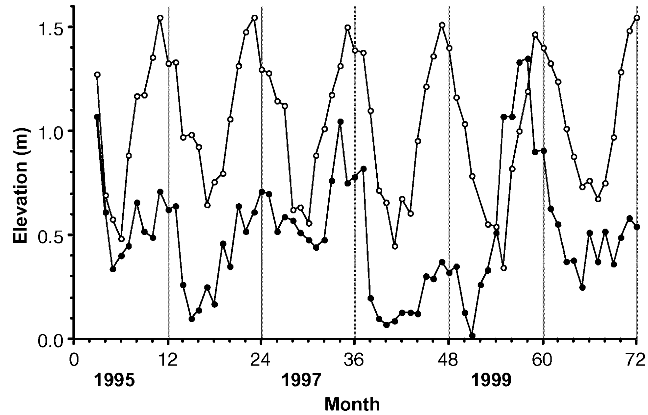

Fig. 1. Mean monthly predicted tide level during surveys (open circles, meters above MLLW) and elevation of sand surface above bedrock platform (solid circles) between February 1995 and January 2001.

3. Results

3.1. Habitat

The extent of beach habitat available for shorebirds at the study site was affected strongly by the amount of sand accumulated (sand elevation) and the tide level. The estimated extent of the intertidal habitat varied by an order of magnitude among surveys, from <1 ha during spring high tides in the winter to ~10 ha during spring low tides in the summer months.

Predicted tide levels during the morning survey window varied seasonally, with generally higher tide levels for October through February and lower tide levels from May through July. Predicted tide levels ranged over 2.6 m and varied from −0.30 to 2.30 m MLLW during the shorebird surveys. Mean predicted tide levels for the survey periods for the 72 months of the study ranged from 0.35 to 1.45 m MLLW (Fig. 1). In southern California during the 1997–1998 ENSO event, mean sea level was elevated by an average of 0.3 m with higher peaks (Flick, 1998), and predicted tide levels underestimated actual values for that period.

Sand elevations at the reference point varied seasonally with maxima in the late fall and winter months and minima in the late winter and spring months (Fig. 1). Sand elevations for individual surveys ranged from 0.0 m (exposed rock platform) to 1.54 m at the reference point on the upper beach. Mean monthly sand elevations ranged from 0.0 to 1.3 m (Fig. 1). Changes in sand level were smaller seaward from the reference point where thinner sections of sediments accumulated on the bedrock platform. The extent and width of sandy intertidal habitat increased rapidly with increasing sand levels because overall beach slopes became shallower as sand accreted at the site. Monthly mean tide heights during the morning survey window and sand levels were strongly and positively correlated ($p < 0.01$, $n = 72$). During the 1997–1998 El Nino, mean monthly sand levels dropped to <0.2 m in the winter and remained low (<0.4 m) until the fall of 1999 (Fig. 1). During that period, a large amount of formerly sandy intertidal habitat was converted to exposed rock. The interaction of low sand levels, record sea levels, and storm surges during the 1997–1998 ENSO led to inundation of the shore all the way to the bluff on numerous occasions, eroding high intertidal sand and removing wrack deposits and upper beach macrofauna.

3.2. Shorebirds

A total of 97,750 shorebirds of 26 species were observed in 994 surveys on the 1 km transect between February 1995 and January 2001 (Table 1; Fig. 2a, b). Standardized common names are used throughout the text (refer to Table 1 for species names). There were 34 occasions (3.4% of surveys) when no shorebirds were observed; most of these being in the late spring and early summer (12 in late May, 16 in June, and three in early July). Shorebirds were present on the transect in all weather, tide, and swell conditions. Most common shorebirds typically occurred in flocks, often composed of mixed species. Two species, whimbrels and black-bellied plovers, often occurred singly.

The majority of shorebirds observed during the surveys were actively foraging in the intertidal zone of the beach. Few individuals were observed roosting or loafing on the transect. Shorebirds were observed foraging at all intertidal levels, including the swash zone, saturated, damp and dry sand, in and around macrophyte wrack, in pools, and on and around exposed rocks. Shorebirds were observed probing in the sand and wrack, pecking on the sediment surface, gleaning wrack, and catching flies. Shorebirds were observed to capture a variety of prey species on the transect including: sand

Table 1
Mean abundance, maximum abundance, and occurrence of shorebirds in 994 surveys of 1 km of shoreline, Isla Vista, CA, from February 1995 to January 2001

Common name	Species	Mean abundance	Maximum abundance	Number of times observed
Sanderling	*Calidris alba*	62.8	840	703
Semipalmated plover	*Charadrius semipalmatus*	8.2	54	669
Marbled godwit	*Limosa fedoa*	6.3	63	535
Black-bellied plover	*Pluvialis squatarola*	5.7	41	728
Western sandpiper	*Calidris mauri*	4.9	710	250
Willet	*Catoptrophorus semipalmatus*	3.9	62	723
Surfbird	*Aphriza virgata*	1.8	456	29
Whimbrel	*Numenius phaeopus*	1.8	18	747
Least sandpiper	*Calidris minutilla*	0.7	50	122
Black turnstone	*Arenaria melanocephala*	0.6	13	196
Greater yellowlegs	*Tringa melanoleuca*	0.6	8	315
Killdeer	*Charadrius vociferus*	0.5	10	190
Ruddy turnstone	*Arenaria interpres*	0.2	6	111
Snowy plover	*Charadrius alexandrinus*	0.14	7	71
Dowitchers	*Limnodromus* spp.	0.12	44	37
Red-necked phalarope	*Phalaropus lobatus*	0.09	2	7
Dunlin	*Calidris alpina*	0.06	33	21
Spotted sandpiper	*Actitis macularia*	0.06	3	53
Wandering tattler	*Heteroscelus incanus*	0.03	3	24
Long-billed curlew	*Numenius americanus*	0.00	2	18
Red knot	*Calidris canutus*	0.00	1	2
Lesser yellowlegs	*Tringa flavipes*	0.00	1	2
American avocet	*Recurvirostra americana*	0.00	1	1
Black oystercatcher	*Haematopus bachmani*	0.00	1	1
Baird's sandpiper	*Calidris bairdi*	0.00	1	1
Total shorebirds		98.6	886	960

crabs (*Emerita analoga*), talitrid amphipods (*Megalorchestia* spp.), polychaetes (*Euzonus mucronata*, *Scolelepis* spp.), and flies (*Coelopa vanduzei* and *Fucellia* sp.). Intensive feeding activity was observed for many species of shorebirds during incoming spring tides when the beach face was eroding rapidly.

The abundance of shorebirds varied among seasons and years (Fig. 2a). The mean abundance of shorebirds observed in the survey was 98.6 birds km^{-1} (Table 1). The maximum number of shorebirds observed in a single survey was 886 birds on 10 November 1996. Monthly mean abundance of shorebirds varied by more than an order of magnitude with season (Fig. 2a) and varied significantly among months (one-way ANOVA, $F = 30.105$, df $= 11$, $p < 0.001$). Monthly mean abundance of shorebirds peaked in the fall months (from October to November, between 161 and 280 birds km^{-1}) and declined in the winter (from December to March) (Fig. 2a). It was generally lowest in May or June (3–11 shorebirds km^{-1}), then rose in July, August, and September as fall migrants arrived (Fig. 2a). Secondary peaks in shorebird abundance occurred during spring migration (April, 70–217 birds km^{-1}) except in 1999 (Fig. 2a).

The annual mean abundance of shorebirds ranged from 79.4 to 118.7 birds km^{-1} (Fig. 2a). The overall abundance of shorebirds declined during the ENSO event and remained lower than pre-ENSO levels (1995–1997) through the end of 2000 (Fig. 2a). The lowest annual mean abundance was observed in 1998–1999 (79.4 birds km^{-1}) during the ENSO event. Shorebird abundance increased slowly through 1999–2000 (90.3 birds km^{-1}) and 2000–2001 (97.4 birds km^{-1}; Fig. 2a).

Overall, the estimated mean biomass of shorebirds on the transect was 9.6 kg km^{-1}. Mean monthly biomass of shorebirds decreased from annual maxima between October and April (15.4–23.9 kg km^{-1}) to minima in May or June (0.8–2.2 kg km^{-1}; Fig. 2b). The biomass of shorebirds was depressed following the ENSO (1998–1999) and recovered slowly through January 2001 (Fig. 2b).

The species richness of shorebirds varied seasonally (Fig. 3a) and significantly among months (one-way ANOVA, $F = 34.582$, df $= 11$, $p < 0.001$). Mean species richness of shorebirds was 5.5 species km^{-1} during the study. The number of shorebird species observed in individual surveys ranged from 0 to 12 species. In each year, the mean monthly number of shorebird species ranged from annual maxima (7.4–9.1 species km^{-1}) between August and October to minima (0.8–2.1 species km^{-1}) during June (Fig. 3a). The total number of shorebird species observed monthly showed a pattern similar to the monthly mean number of species (Fig. 3a). The monthly total number of shorebird species observed was

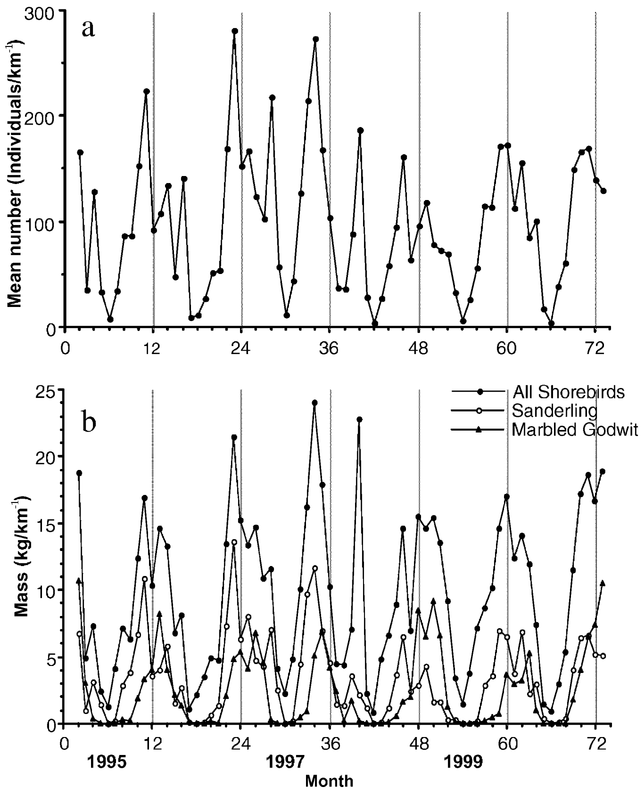

Fig. 2. (a) Mean monthly shorebird abundance (individuals km^{-1}), (b) estimated mean monthly biomass (kg km^{-1}) of all shorebirds (solid circle), sanderlings, *Calidris alba* (open circle), and marbled godwits, *Limosa fedoa* (triangle) on the study transect between February 1995 and January 2001.

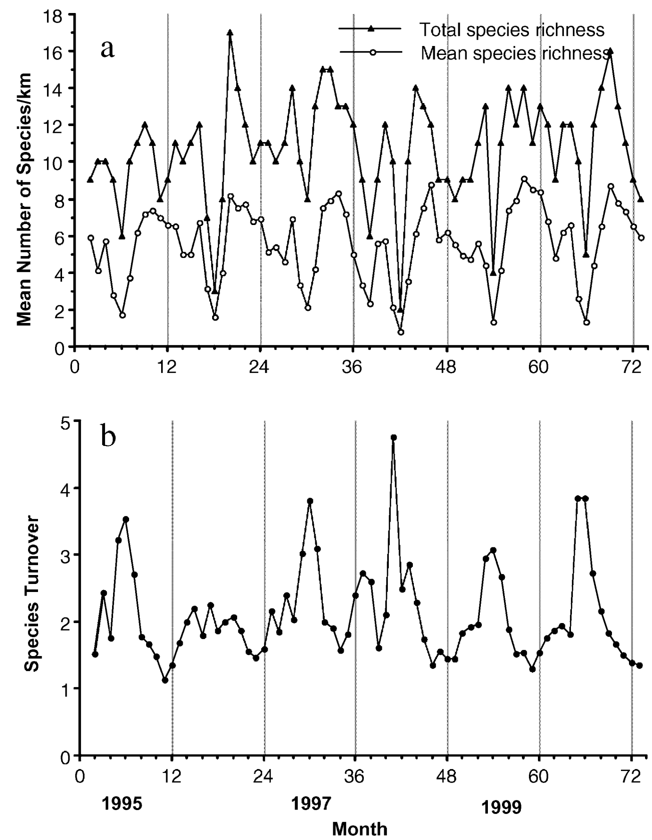

Fig. 3. (a) Total monthly richness and mean monthly richness of shorebird species, (b) turnover of shorebird species (total number of shorebirds observed in month divided by the mean number of species observed in month) on the study transect between February 1995 and January 2001.

highest between August and October (12–17) and lowest during June (from two to eight species) in each year (Fig. 3a). Species richness appeared to be less affected by the ENSO event than abundance.

The high frequency of surveys in this study also allowed estimation of turnover of shorebird species (total monthly species richness/mean monthly species richness) and its variation across seasons. The turnover of shorebird species among the surveys in each month varied seasonally in each year (Fig. 3b). Estimated turnover of species reached minima between October and December (1.1–1.6) and was generally highest during June (2.2–4.7) (Fig. 3b).

The mean monthly species richness of shorebirds was positively and significantly correlated with the abundance of shorebirds (Fig. 4). Peaks in the abundance and species richness of shorebirds occurred in the fall migration period, while minima occurred in the early summer (June). Conversely, species turnover was greatest when shorebird abundance was low and least when abundance was high.

Although 26 species were observed during the study, the shorebird assemblage was dominated by a relatively small number of species. Six species accounted for >90% of shorebird abundance and 87% of shorebird biomass (sanderling, semipalmated plover, marbled godwit, black-bellied plover, western sandpiper, and willet). Eight species of shorebirds occurred in overall mean abundances greater than 1 individual km^{-1} and accounted for 97% of the total abundance and biomass (sanderling, semipalmated plover, marbled godwit, black-bellied plover, western sandpiper, willet, surfbird, and whimbrel). Some species of shorebirds were present for only a few days per year (e.g. red-necked phalarope) or occurred in only one or two surveys (red knot, lesser yellowlegs, American avocet, black oystercatcher, and Baird's sandpiper) during the study (Table 1).

Patterns of total and mean abundance, and of occurrence differed considerably among the 26 species that were observed (Table 1; Figs. 5 and 6). The total number of individuals observed for each species ranged from one (e.g. American avocet) to 62,382 sanderlings during the study (Table 1). Six species of shorebirds occurred frequently and were observed in >50% of the surveys (sanderling, semipalmated plover, marbled godwit, black-bellied plover, willet, and whimbrel). Frequency of occurrence of a species did not always coincide directly with total or average abundance (Table 1).

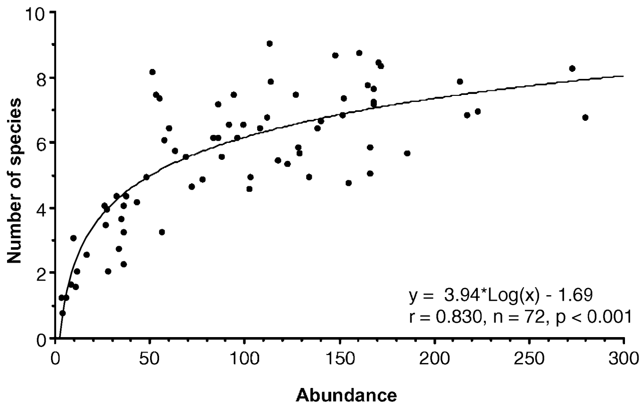

Fig. 4. Mean monthly shorebird species richness as a function of mean monthly shorebird abundance on the study transect between February 1995 and January 2001.

Some species were observed frequently as scattered individuals, while others occurred rarely but sometimes in large flocks (Table 1). For example, whimbrels occurred in mean abundance of 1.8 individuals km^{-1},

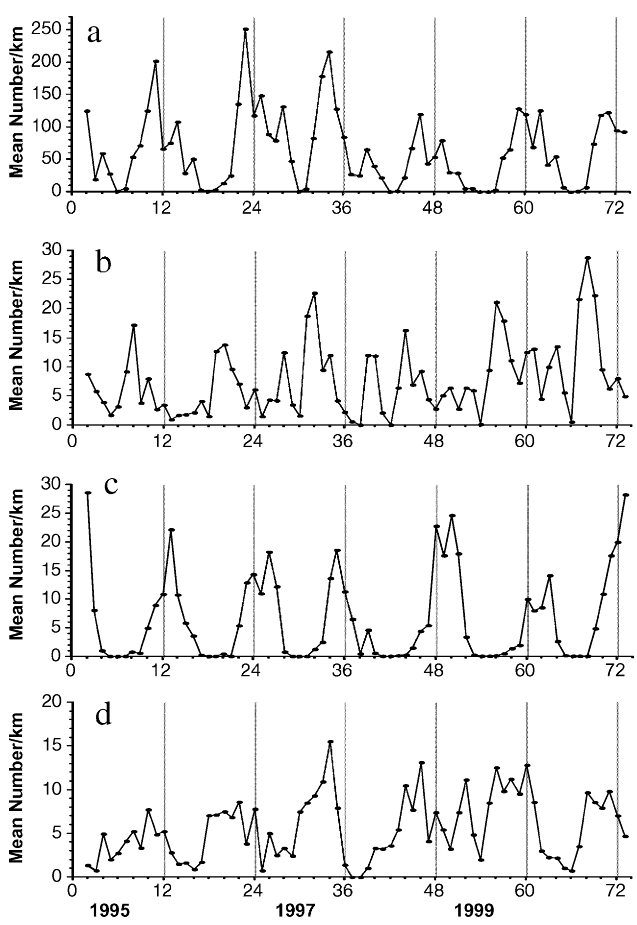

Fig. 5. Mean monthly abundance of shorebird species on the study transect between February 1995 and January 2001: (a) sanderlings, *Calidris alba*; (b) semipalmated plovers, *Charadrius semipalmatus*; (c) marbled godwits, *Limosa fedoa*; and (d) black-bellied plovers, *Pluvialis squatarola*.

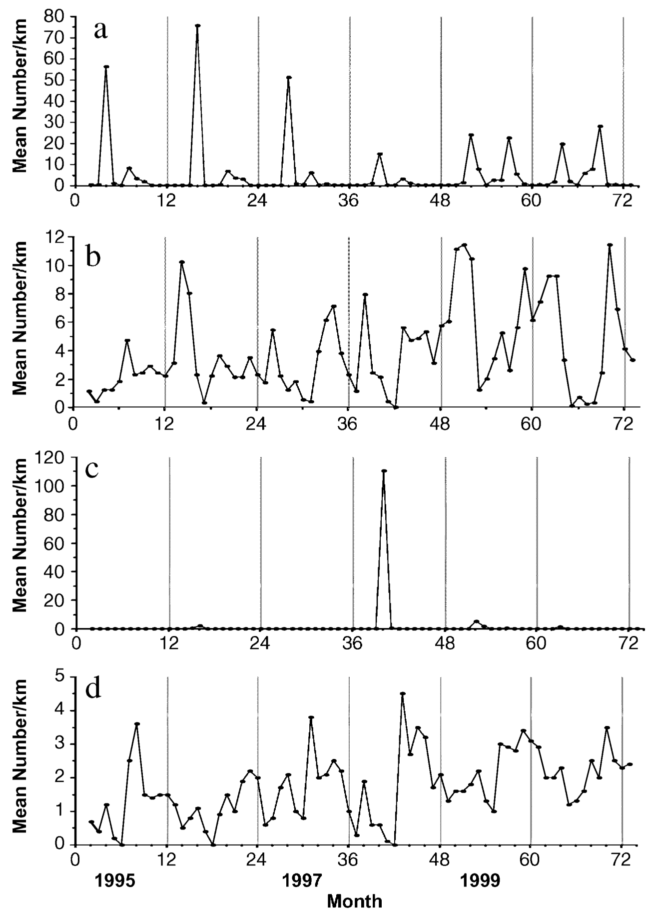

Fig. 6. Mean monthly abundance of shorebird species on the study transect between February 1995 and January 2001: (a) western sandpipers, *Calidris mauri*; (b) willets, *Catoptrophorus semipalmatus*; (c) surfbirds, *Aphriza virgata*; and (d) whimbrels, *Numenius phaeopus*.

but were observed on 747 surveys. The mean abundance of surfbirds was 1.9 individuals km^{-1}, but they were observed in only 29 surveys.

Seasonal variation in the abundance and occurrence of shorebird species in these surveys appeared to be associated with different migration patterns. Sanderlings peaked in abundance during fall migration, but occurred in large numbers for several months of each year during the non-breeding season. Many species of shorebirds, including the plover species (semipalmated plovers, snowy plovers, black-bellied plovers, and killdeer) and greater yellowlegs also reached their peak abundance in the fall migration period (from July to October). Peaks in abundance (highest mean monthly values) of the four plover species observed on the transect occurred in a distinct sequence each year. The abundance of semipalmated plovers peaked on the transect in July–August, followed by snowy plovers in August–September, black-bellied plovers in September–October, and killdeer in October–November. Other species, such as the marbled godwit, reached peak numbers in the winter. Species that typically exhibited peak abundance during spring migration include western sandpipers, surfbirds, black turnstones, and ruddy turnstones. Species with peaks in mean abundance during spring and fall migrations included least sandpipers and the dowitcher species. Some species of larger shorebirds, such as black-bellied plovers, willets, and whimbrels occurred nearly year-round, but in low average abundances. They were the most likely species to occur through the summer months, including June.

The magnitude and duration of declines in abundance associated with the 1997–1998 ENSO event varied among species of shorebirds (Figs. 5 and 6). Abundance decreased in some common species of shorebirds (sanderling, western sandpipers) and remained depressed for over a year after the ENSO event (Figs. 5a and 6a). The lowest annual average abundance observed for the dominant species of shorebird, sanderlings, occurred between 1998 and June 1999, immediately following the 1997–1998 ENSO (Fig. 5a), and abundance did not increase to pre-ENSO levels during subsequent years. The abundance of other species of shorebirds (marbled godwit, black-bellied plover, whimbrel) decreased to the lowest levels observed, but rebounded more quickly after the ENSO event (Figs. 5c, d and 6b, d). The abundance of at least one relatively uncommon species, surfbird, increased during and immediately following the 1997–1998 ENSO event (Fig. 6c).

3.3. Accounts of common species

Sanderlings, *Calidris alba*, were the most abundant shorebirds in each year of the study, averaging 63 birds km^{-1} and comprising 64% of the total abundance and 35% of biomass of shorebirds (Table 1; Fig. 2b). Sanderlings were observed frequently on the transect, occurring in 704 of 994 surveys (71%) and three shorebird species occurred more frequently (Table 1). The mean abundance of sanderlings, when present, was 89 birds km^{-1}. They were the most abundant shorebirds in 54 of the 72 months (between August and May). They were typically observed feeding in dense single species flocks in the swash zone or around stranded wrack on the upper beach at all tide levels on the transect. They were not observed maintaining individual feeding territories, or leaving the beach for alternate habitats (e.g. coastal lagoons or estuaries) at higher tide levels. The abundance of sanderlings varied significantly among months (one-way ANOVA, $F = 8.732$, df $= 11$, $p < 0.001$). They were relatively scarce in summer and were not observed on the transect in June, but occurred in all other months during the study (Fig. 5a). Their abundance increased from June to October or November and decreased between April and June in each year. Maximum monthly mean abundance of sanderlings ranged between 120 and 251 birds km^{-1}, and occurred in the fall each year (October and November). Peak abundance observed was 840 individuals on 10 November 1996. Abundance of sanderlings in the winter and spring was lower than in the fall, with maximum values between January and March ranging from 65 to 147 birds km^{-1}. Their highest annual abundances occurred in the first 3 years of the study. The maximum annual abundance (71 birds km^{-1}) occurred between February 1996 and January 1997. The lowest annual average abundance observed was 53 birds km^{-1} (1999–2000, the year following the 1997–1998 ENSO event). Peak abundances of this species did not reach pre-ENSO levels by fall 2000.

Semipalmated plovers, *Charadrius semipalmatus*, were the second most common shorebird species observed during the study and comprised 8.3% of the total abundance and 4% of total biomass of shorebirds observed (Table 1). They were the most common shorebird observed in 9 months during the study (between May and August). They were observed frequently (669 surveys or 67% of the surveys) and in every month of the study except February and June 1998 during the ENSO event. Their overall mean abundance was 8.2 birds km^{-1} (Table 1) and the mean abundance when present was 12.2 birds km^{-1}. Maximum abundance in a single survey on the transect was 54 individuals on 30 July 1998. They were typically observed in small flocks, feeding on wet, damp, and dry sand, and among rock outcrops. The abundance of semipalmated plovers varied significantly among months (one-way ANOVA, $F = 8.992$, df $= 11$, $p < 0.001$). Their abundance generally decreased from maxima in August to minima in the winter (from December to March). Maximum monthly mean abundance occurred in August throughout the study (14–29 birds km^{-1}) (Fig. 5b). Lowest mean monthly abundance generally occurred in May and June (0–1.7 birds km^{-1}). A minor peak in abundance usually occurred between March and May (Fig. 5b). Annual mean abundance was lowest in the first year of the study (5.2 birds km^{-1}), and highest in the last (12.6 birds km^{-1}).

Mean abundance of marbled godwits, *Limosa fedoa*, was 6.3 birds km^{-1} (Table 1) and their mean abundance when present was 11.6 birds km^{-1}. They comprised 6.4% of the total abundance and 25% of the total biomass of shorebirds (Fig. 2b). The highest count in a single survey was 63 individuals on 15 January 2001. Marbled godwits were observed frequently, occurring in 53.9% of the surveys (Table 1). The abundance of marbled godwits varied significantly among months (one-way ANOVA, $F = 9.843$, df $= 11$, $p < 0.001$). Peak mean abundances ranged from 14 to 29 birds km^{-1} and occurred in the fall or winter (from November to March), later than most other shorebird species reported in this study (Fig. 5c). This species was absent from the transect for several months each year, typically May, June, and July.

The mean abundance of black-bellied plovers, *Pluvialis squatarola*, was 5.7 birds km^{-1} (Table 1) and their mean abundance when present was 7.8 birds km^{-1}. This species comprised 5.8% of the total abundance and 12% of the total biomass of shorebirds. The maximum number of black-bellied plovers observed in a single survey was 41 individuals on 27 July 1997. They were observed frequently and occurred in >75% of the surveys. They rarely occurred in flocks, and their distribution often consisted of scattered individuals located far from conspecifics and birds of other species. They occurred in every month of the study except January and February 1998 (during the ENSO event) (Fig. 5d). Mean abundance of black-bellied plovers varied significantly among months (one-way ANOVA, $F = 6.004$, df = 11, $p < 0.001$) and generally reached maximum levels between August and December (Fig. 5d). Their annual mean abundance increased during the course of the study from a minimum of 3.9 birds km^{-1} in the 1995–1996 to a maximum of 8.6 birds km^{-1} in 1999–2000.

During the study, the mean abundance of western sandpipers, *Calidris mauri*, was 4.9 birds km^{-1} (Table 1) and that when present was 19.5 birds km^{-1}. This species comprised 5.0% of the total abundance and 1% of total biomass of shorebirds. The highest abundance observed was 710 individuals on 21 April 1996. They occurred moderately often, and were present in 25% of the surveys. They occurred on the transect only during spring and fall migration periods and were rarely observed in the winter or during June (Fig. 6a). Most of the western sandpipers recorded in the study occurred in dense flocks (often mixed with other species) during migration periods. Their mean abundance varied significantly among months (one-way ANOVA, $F = 11.929$, df = 11, $p < 0.001$) and peaked during both spring and fall migrations throughout the study (Fig. 6a). Maximum mean monthly abundance (15–75 birds km^{-1}) occurred in April in every year of the study except 2000, when a fall peak was observed. Annual mean abundance of western sandpipers ranged from 2 to 7 birds km^{-1}. The lowest spring and fall migration peaks occurred during the ENSO event, and spring migration peaks did not reach pre-ENSO levels by spring 2000.

The mean abundance of willets, *Catoptrophorus semipalmatus*, was 3.9 birds km^{-1} (Table 1), and their mean abundance when present was 9.5 birds km^{-1}. This species comprised 3.9% of the total abundance and 10% of total biomass of shorebirds. The highest single survey count of willets was 62 individuals on 25 February 1996. Willets were frequently observed and occurred in 73% of the surveys (Table 1). They were observed in every month of the study except June 1998 (ENSO event). Seasonal variation in the abundance of willets was less consistent than that observed in the other abundant species of shorebirds in this study (Fig. 6b). Generally, maximum abundance occurred in two periods: winter (February and March) and fall (August to November). Mean abundance of this species varied significantly among months (one-way ANOVA, $F = 2.912$, df = 11, $p < 0.01$). Their mean annual abundance ranged from 2.4 to 6.8 birds km^{-1}. No clear depression in willet abundance was evident during or following the ENSO event (Fig. 6b).

Surfbirds, *Aphriza virgata*, made up 1.9% of the total abundance and 3% of the total biomass of shorebirds. Their mean overall abundance was 1.9 birds km^{-1} (Table 1) and the mean abundance when present was 63 birds km^{-1}. However, this species had a very different pattern of occurrence than the other common species. They were observed in only 2.9% of the surveys (Table 1) and were present only in two seasons. The majority of individuals were observed during spring migration (from March to May) and the remaining few individuals were observed during fall migration (between August and September) (Fig. 6c). They were the most abundant shorebird, and we observed the highest single count of 456 individuals in April 1998 during the ENSO event (Fig. 6c). Mean annual abundance of this species varied from 0.0 to 9.7 birds km^{-1}, with the peak occurring in 1998 during the ENSO event.

Whimbrels, *Numenius phaeopus*, comprised 1.8% of the total abundance and 7% of the total biomass of shorebirds. Overall mean abundance of whimbrels on the transect was 1.8 birds km^{-1} (Table 1), and when present their mean abundance was 2.4 birds km^{-1}. Although they occurred in relatively low abundance, we observed them more frequently than any other species, and they occurred in 75% of the surveys (Table 1). They were present in all months except June of 1995, 1996, and 1998. Their highest single count was 18 individuals on 14 April 1996. They reached their highest monthly abundance (2–5 birds km^{-1}) during late summer and fall (from July to November) (Fig. 6d). A minor peak in the abundance of whimbrels occurred in each spring of the study (from February to May) (Fig. 6d). Their mean abundance varied significantly among months (one-way ANOVA, $F = 3.873$, df = 11, $p < 0.001$). Their mean annual abundance increased during the study, from 1.3 birds km^{-1} in 1995–1996 to 2.3 birds km^{-1} in 1999–2000.

3.4. Shorebirds and habitat

The influence of tide level (habitat availability) on the abundance and species richness of shorebirds was not consistent. Overall variation in the mean monthly abundance (Fig. 7) and species richness ($y = 1.32x + 1.40$, $r = 0.362$, $n = 72$, $p < 0.001$) of shorebirds was significantly correlated with tide height during the survey window. However, these results may be confounded by seasonal variation in abundance of shorebirds, tide level, and habitat extent. Shorebirds were most abundant in the fall and early winter, when

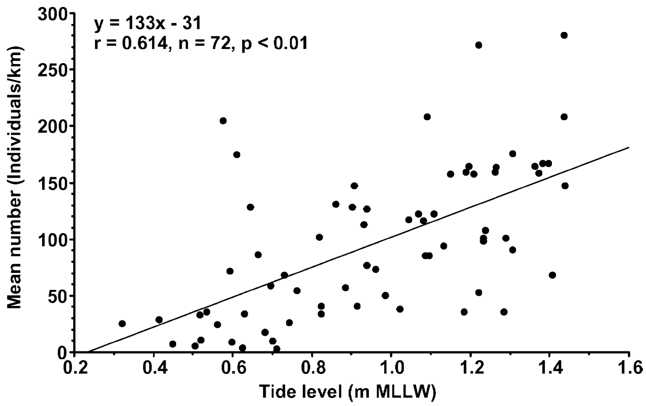

Fig. 7. Mean monthly abundance of shorebirds as a function of mean monthly predicted tide height during surveys on the study transect, February 1995 and January 2001.

sandy habitat was extensive, sand elevations were high, and the mean tide height during morning surveys was generally high (Figs. 1 and 2a). Shorebirds were scarcer in the late spring and early summer, when the beach was eroded, more rocky habitat was exposed, and sand elevations and morning tides were low (Figs. 1 and 2a).

When seasonal effects were reduced by pooling data from each calendar month across years of the study, correlations between shorebird abundance and tide height were: (1) significant and positive in 3 months during the fall (October, November, and December, more shorebirds present at higher tides); (2) significant and negative in 3 months (March, April, and June, consistent with the hypothesis that increasing habitat available at lower tides supports increasing numbers of shorebirds); and (3) not significant for 6 months (Fig. 8). The hypothesis that increased available habitat (lower tide levels) leads to increased shorebird abundance during the surveys was not generally supported. Results for March, April, and June were consistent with the hypothesis, but

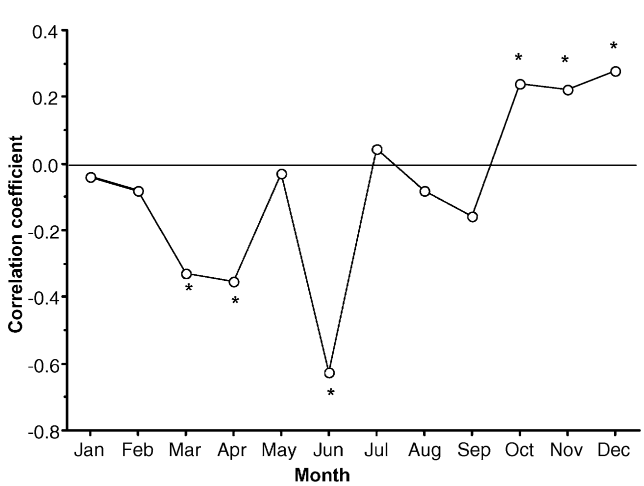

Fig. 8. Correlation coefficients for shorebird abundance and tide height during surveys by calendar month (*$p < 0.05$).

those for the fall months when shorebird density is highest, and the highest tides of the morning survey window make the lower shore habitat inaccessible to shorebirds, suggested that more birds concentrated onto the available habitat, even though it was at a minimum.

4. Discussion

These results indicate that exposed sandy beaches, even ephemeral, bluff-backed beaches subject to heavy human use and significant temporal changes in width and condition, can support high numbers of a diverse array of actively foraging shorebird species. Overall, shorebird abundance on the study transect was very high (1.3–11 times higher) compared with the results of the majority of other studies of shorebirds on exposed sandy beaches in California and elsewhere in the world (Table 2). This is particularly interesting, given the relatively narrow and bluff-backed nature of the beach on the study transect and the dramatic variation in habitat extent and condition observed over time during the study. Sand elevation changed by more than 1.5 m and the habitat available to shorebirds varied over an order of magnitude seasonally. The only study for which similarly high mean abundances of shorebirds were reported was also conducted on a relatively narrow beach with rocky outcrops and high inputs of macrophyte wrack on the west coast of South Africa (Griffiths, Stenton-Dozey, & Koop, 1983) (Table 2).

The average species richness of shorebirds using an exposed sandy beach was also high relative to other studies of beaches in California and elsewhere in the world (Table 2). The regional species richness of shorebirds appears to be high relative to other areas (Table 2). The high frequency counts of shorebirds likely generated comparable estimates of abundance and average species richness to less frequent surveys, but yielded higher estimates of total monthly and annual species richness. High species richness of shorebirds may be related to the high diversity of microhabitat and prey types available on the study beach, which contained exposed rocks, pools, washed sand, upper and mid-intertidal beach, and abundant macrophyte wrack. More than 39 species of infaunal and wrack-associated invertebrates were observed on the study beach in a single survey (Dugan & Hubbard, in preparation), all of which could be prey for shorebirds. A variety of rocky shore invertebrates are also available to shorebirds on the lowest tides.

Shorebirds have high metabolic rates and relatively high daily energy expenditures (Kersten & Piersma, 1987), hence rich and productive prey resources are critical to the survival of breeding and non-breeding individuals. Prey availability to shorebirds can vary with tidal height (Connors, Myers, Connors, & Pitelka, 1981)

Table 2
Results of shorebirds surveys on exposed sandy beaches for the study area and other regions

Abundance (individuals km^{-1})		Species richness (number)		Number of sites	Length of transects (km)	Total length (km)	Study region	Reference
Mean	Maximum	Mean	Total					
8.9	14.7	–	7	3	3–40	>60	S. Africa east coast	McLachlan et al. (1980)
98.1[a]	–	–	>6	1	1	1	S. Africa west coast	Griffiths et al. (1983)
50–68[b]	117[b]	–	21	5	3–34	123	USA, North Carolina Outer Banks	Dinsmore et al. (1998)
23.9	–	–	19	2	0.6–1.4	2	Mexico, Baja California	Lopez-Uriarte et al. (1997)
44.0[c]	124[c]	2.6	12	40	0.5	20	USA, N. California Humboldt Co. Del Norte Co.	Colwell and Sundeen (1998)
44.0	603	3.1	23	14	1	14	USA, S. California Ventura Co.	McCrary and Pierson (1999)
77.9	1200	4.0	28	20	1	20	USA, California Santa Barbara Co. San Luis Obispo Co.	Dugan et al. (2001)
98.6	886	5.5	26	1	1	1	USA, S. California Santa Barbara Co.	Present study

Abundance values are adjusted to 1 km if needed, but species richness values are not adjusted.
[a] Value is seasonally adjusted.
[b] Spring/fall migration only.
[c] Winter/spring only.

on sandy beaches. Tidal variation in prey availability depends in part on the macroinfaunal assemblage present on a beach. Optimal foraging strategies of shorebirds may include interhabitat movement as reported by Connors et al. (1981) for sanderlings. The high proportion of foraging individuals observed in this study suggests that the surveyed beach is particularly important as a feeding area for shorebirds. These results also suggest that prey availability and feeding of shorebirds could be enhanced on beaches during incoming tides and in swell conditions that actively erode the beach face, exposing buried infauna.

Wrack-associated invertebrates are available to avian predators on a wider range of tide levels than are most of the suspension-feeding invertebrates, and thus may represent an important prey resource for shorebirds of many species. Sandy beaches, such as the study beach, which receive large subsidies of macrophyte, support high diversity and abundance of wrack-associated fauna, which are prey for shorebirds. On the South African beach with high shorebird abundance studied by Griffiths et al. (1983), the abundance of wrack-associated invertebrates was very high and comprised 97% of the total macrofaunal biomass. Possible relationships between prey assemblages and availability to shorebirds are supported by the results of Tarr and Tarr (1987) who reported that total shorebird abundance was positively associated with the standing crop of wrack on beaches along the west coast of South Africa, and those of Dugan et al. (2003) who found that the abundance of two visually foraging plover species (black-bellied plover and the threatened western snowy plover) was correlated with wrack cover and the abundance of wrack-associated prey. High standing crops (abundance and biomass) of invertebrates occur on the study beach, wrack-associated fauna comprised 37–94% of the total macrofauna abundance (Dugan & Hubbard, 1996, unpublished data), and secondary production of invertebrates may be substantial. Prey availability and composition may thus be key to the heavy use of the study beach by shorebirds and the high level of feeding activity observed.

The role of avian predators in exposed intertidal communities is likely underestimated in many ecological studies. Shorebirds have been shown to have a large effect on invertebrate prey resources on exposed sandy beaches (McLachlan et al., 1980). High feeding rates of up to 20 and 19 individuals min^{-1} for hippid crabs and talitrid amphipods were observed on the study transect for several species of the most common large-bodied shorebirds (marbled godwit, willet, and whimbrel; see Table 1 for species) (Dugan & Hubbard, unpublished data). At these feeding rates and the high abundance observed, shorebirds could potentially deplete prey resources and affect invertebrate community structure during peak periods of use on the study beach.

Shorebirds exhibit large seasonal variability in abundance that is related to migration and their use of different habitats during breeding and non-breeding seasons (Desante & Ainley, 1980; Shuford et al., 1989). Our results indicate that different species of abundant shorebirds exhibit dramatically different patterns of use of an exposed sandy beach habitat in southern California. Much of this variation appears to be associated with species-specific migration and over-wintering patterns (Garrett & Dunn, 1981; Shuford et al., 1989), but a portion of it may also be associated with temporal changes in habitat availability and condition. Some species, such as sanderlings, peaked in abundance during fall migration, but occur in large numbers for several months of each year during the non-breeding season. Plovers, including the abundant semipalmated plover and black-bellied plover, as well as the less abundant snowy plover and killdeer, reached their peak abundance in the fall. Other abundant species, such as the marbled godwit, reached peak numbers in the winter. Other relatively abundant species, western sandpipers and surfbirds, typically exhibited peak abundance during spring migration. Species of larger shorebirds, such as black-bellied plovers, willets, and whimbrels occurred in low average abundances nearly year-round and were the most likely species to occur through the summer months as non-breeding individuals, suggesting that significant variation occurs in the life history of some species (e.g. Lehman, 1994).

Semi-decadal ENSO events in southern California alter physical dynamics of the coastal zone, affecting water temperatures, wave heights, productivity, storm tracks, and sea level (Flick, 1998). Such changes can affect the biotic communities of all marine habitats, from kelp forests to intertidal zones through direct effects on erosion and disturbance and indirect effects on growth, reproduction, condition, survival, food availability, and larval supply. Higher trophic levels including pinnipeds, seabirds, fishes, and shorebirds may be negatively affected by changes in prey availability and habitats. The study period included a strong California El Nino event that produced warmer sea surface temperatures, elevated local sea level, heavy rain, energetic storm waves, and extensive coastal erosion between November 1997 and April 1998 (Flick, 1998).

The response of shorebirds to the ENSO event was evident in both abundance and species composition. The overall abundance of shorebirds declined during the 1997–1998 ENSO event and remained lower than pre-ENSO levels through the end of 2000. The magnitude and duration of that decline varied among species of shorebirds. Abundance decreased in some common species of shorebirds (sanderling, western sandpiper) and remained depressed for over a year after the ENSO event. The abundance of other species of shorebirds decreased to the lowest levels observed, but rebounded more quickly after the ENSO event (marbled godwit, black-bellied plover, whimbrel). The lowest annual average abundance of the dominant species of shorebird, sanderling, was observed following the 1997–1998 ENSO. In contrast, a relatively uncommon species, surfbird, visited the transect in numbers unprecedented in Santa Barbara County (Lehman, 1994) during the ENSO event. That may be related to the increased availability of suitable habitat for some species, such as exposed rocks, relative to sandy shores, during that period and stormy conditions during spring migration. Most of the surfbirds observed in the study occurred in a single month, April 1998, when storm waves and elevated sea level associated with the 1997–1998 ENSO had reduced the cover of sand on the transect to the minimum observed during the 6 years of the study, converting it to primarily rocky substrate.

Shorebirds may respond to changes in both habitat characteristics and prey availability during an ENSO event. During the 1997–1998 ENSO event, the study beach and all the surrounding beach habitat experienced considerable alteration in sand elevations, beach width, tidal inundation, and wave regime. Prey availability for shorebirds on beaches was likely greatly reduced regionally, particularly for the lower beach invertebrates. Sand crabs, *Emerita analoga*, one of the major prey species available on the lower beach, exhibited very low over-winter survival of adults and depressed recruitment in the spring of 1998 in the study region (Dugan, personal observation). Kelp forest growth and viability were reduced and storm waves caused disturbance and damage to existing kelp beds during the ENSO event, altering wrack dynamics. On beaches, very large inputs of drift macrophytes were followed by reduced input through 1999 (Dugan & Hubbard, unpublished data), which likely affected prey availability on all beaches in the region.

The distribution of shorebirds among habitats has been linked to a variety of factors, including: habitat preferences of species, seasonal abundance, long-term population trends, use of habitats at night, and movement between habitats (Burger et al., 1997; Connors et al., 1981; Myers, Schick, & Hohenberger, 1984). Myers et al. (1984) documented movement of shorebirds between an estuary and a nearby beach, with changing tide levels exposing or covering intertidal habitats. Connors et al. (1981) reported positive relationships between the change in relative density of sanderlings and tide height on two exposed beaches adjacent to a protected tidal flat. Abundance of sanderlings on the tidal flat varied inversely with tidal level (Connors et al., 1981). No evidence was found of tidally mediated interhabitat movement in sanderlings in their study.

It was hypothesized that shorebird abundance might respond to the amount of intertidal habitat available on beaches. If shorebird abundance is related to the amount of available habitat, higher abundance would be expected when more habitat is exposed and available to birds, particularly at low tides, and also when there is more sand accumulated on the beach. On bluff-backed ocean beaches, the amount and type of exposed intertidal habitat available to shorebirds vary daily with tides, seasonally with tide regime, sand levels, and morphodynamic condition, and interannually with sand and sea levels. The results of the present study suggest that the overall relationship between shorebirds and the extent of available habitat (tide height) is positive, with higher numbers of shorebirds using the beach when less total habitat is available, in agreement with results reported by Connors et al. (1981) for sanderlings. However, that result may be confounded by seasonal variation in the abundance of shorebirds, morning tide levels (Flick, 2000), and habitat extent. When examined on a finer temporal scale, the direction of that relationship varied seasonally, with positive correlations in the fall and winter when sand levels are high, negative correlations in the spring when the beach is most eroded, and no relationship for half of the year, winter, and summer.

The results of this analysis suggest that in some coastal regions, local topography and the availability of alternative protected or exposed intertidal habitat may affect the relationship between shorebird densities, tide heights, and sand levels on exposed sandy beaches. Local availability of alternate foraging habitats for shorebirds is low in the study region. There is little remaining protected intertidal habitat and few tidal flats within 100 km of the study beach. Tidal influence is weak and inconsistent in nearby coastal wetlands, such as Goleta Slough. The upper intertidal zone of the beach studied here and similar areas may provide important refuges for shorebirds and some of their prey resources when the highest tides inundate the shore to the sea bluffs over much of the southern Santa Barbara County coast.

The results of the present study provide clear evidence that exposed sandy beaches can constitute important habitat for wintering and migrant shorebirds in southern California and should be considered in conservation and environmental planning for this region. As human population growth and development of the coastal zone continue, sandy beaches may become increasingly important to declining populations of shorebirds worldwide. The effects of human alteration of the shoreline and coastal processes may be very large, e.g. watershed and littoral cell scales (Nordstrom, 2000). The effects of large-scale and more local scale alterations may be particularly critical in the upper intertidal zone of exposed sandy beaches. For example, coastal armoring and reduced sediment supply can reduce high tide refuges and feeding opportunities for shorebirds on exposed beaches by converting the entire intertidal zone to a wave-swept reflective state. Beach grooming can significantly depress the abundance of wrack-associated fauna, reducing the prey available to shorebirds (Dugan et al., 2003), and the construction of emergency sand berms may defaunate both upper and lower intertidal zones (Peterson, Hickerson, & Johnson, 2000). Understanding the importance of exposed sandy beaches as habitat and sources of prey to shorebirds could potentially enhance coastal conservation efforts and provide much needed impetus for improving the management of exposed sandy beaches in many regions.

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