

INTERHABITAT MOVEMENTS BY SANDERLINGS IN RELATION TO FORAGING PROFITABILITY AND THE TIDAL CYCLE

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ABSTRACT.—Sanderlings (*Calidris alba*) wintering near Bodega Bay, California move between outer coast sandy beaches and nearby harbor sandflats on a regular tidal schedule. Birds forage on outer beaches at high and mid-level tides, switching to the protected sandflats as the tide recedes; Sanderling density fluctuations measured along transects were complementary in these two habitats. The habitat time budget of the local Sanderling population varied between days with different tidal regimes, averaging 45% of daylight hours spent on beaches during November 1976. Some Sanderlings defended territories on the beaches, while others foraged in flocks; both groups moved to the lagoon tidal flats at low tide.

The density of Sanderling prey in the two habitats changed through the tidal cycle in foraging sites used by Sanderlings. On harbor sandflats, energy density increased sharply with falling tide level. On outer beaches, energy density was highest at middle and upper tidal levels, decreasing at low and at very high tides. These results suggest that Sanderlings switch feeding sites on a tidal schedule to maximize foraging efficiency. We offer a simple graphical model based on tide-related changes in foraging efficiency to explain the shifts in habitat use. Sanderling behavior under seasonally varying prey conditions and behavioral comparisons of territorial and nonterritorial birds are consistent with the model. *Received 16 April 1980, accepted 29 July 1980.*

"There are birds everywhere, but not always."—Edward Howe Forbush (1921)

SHOREBIRD populations wintering in coastal areas exploit a habitat mosaic dominated by the tidal cycle. Numerous studies document shorebirds' choices of foraging habitats (see papers in Pitelka 1979 and references therein). Furthermore, within habitats shorebirds respond to spatial variations in prey density and the relative profitability of using different foraging sites (Goss-Custard 1970, 1979; Goss-Custard et al. 1977; Myers et al. 1979a). Few studies, however, address the temporal effects of tides directly. This is unfortunate because of the clear importance of tides for wader feeding (Ehlert 1964, Heppleston 1971, Prater 1972, Burger et al. 1977).

In this paper we examine movements by Sanderlings (*Calidris alba*) in response to the strong and complex tidal cycle at Bodega Bay, California. More specifically, we consider the proportion of the day spent by local Sanderlings on sandy beaches and harbor sandflats and their timing of movement between these habitats. We then develop a simple model based on changing profitabilities of foraging that summarizes the patterns of movement. Finally, we explore two predictions based on changes in the model's parameters.

STUDY AREA

Sanderlings forage principally on sand beaches and tidal sandflats within the Bodega Bay area (Fig. 1). Salmon Creek Beach and Doran Beach, 4.2 km and 3.2 km in length, respectively, are wide sand beaches backed by low dunes covered by dune grass (*Ammophila arenaria*). The tidal flats within Bodega Harbor occupy approximately 200 ha at mean lower low water, roughly 60% of the harbor surface area (Standing et al. 1975). Sediments consist largely of well-sorted medium and fine sand. At tides above +5.5 ft (1.7 m), virtually all of the tidal flats are water-covered.

Tides are of the mixed, semi-diurnal type, with two unequal high and two unequal low tides occurring

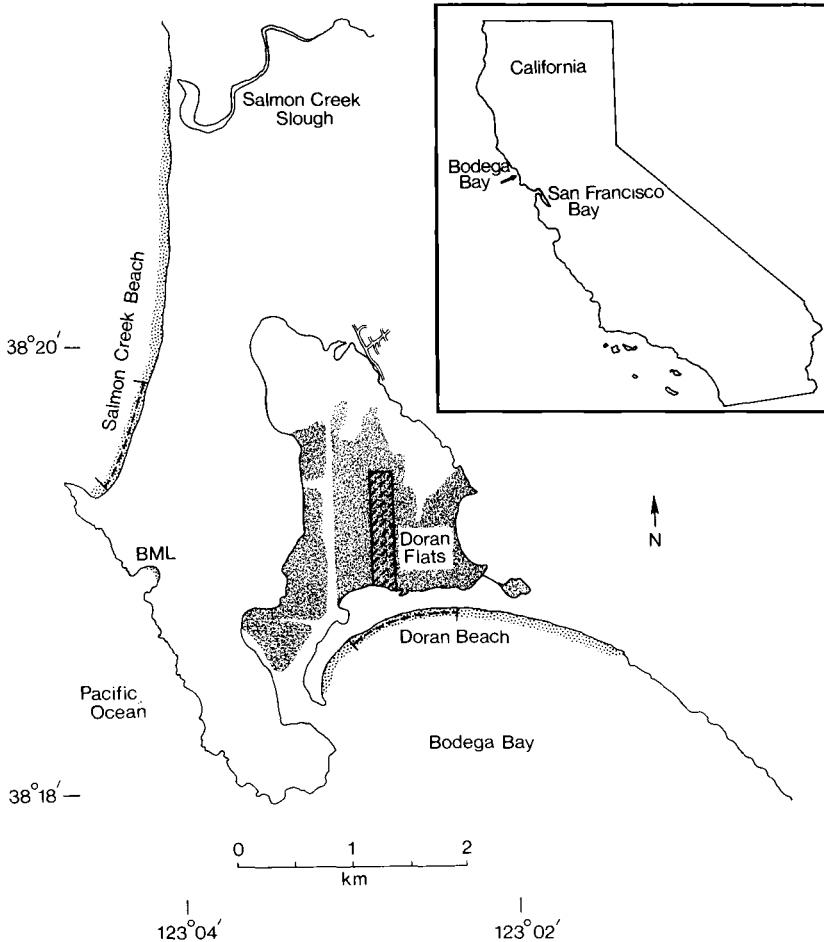


Fig. 1. Map of the study area showing the location of census transects on Salmon Creek Beach, Doran Beach (dashed lines enclosed by brackets), and Doran Flats (oblique barring). Stippled areas are beaches; uneven shading is harbor sandflat. Road network at northeast corner of harbor is the town of Bodega Bay. Inset shows the position of Bodega Bay within California.

on most days (Standing et al. 1975). During the years of this study, the highest and lowest values recorded were +6.8 ft (+2.1 m) and -1.7 ft (-0.5 m), respectively. Daily tidal ranges vary between 8.8 ft (2.7 m) and 4.0 ft (1.2 m) at the mouth of the harbor, but they decrease somewhat inside. High and low tides occur several minutes later within the harbor than outside the harbor (Barbour et al. 1973).

On the two beaches, Sanderlings forage regularly in the surf zone, where the main prey species during most of the winter are small crustaceans, chiefly the isopod *Excirolana linguifrons* (Richardson) and the sand crab *Emerita analoga* (Stimpson) (P. G. Connors, J. P. Myers, and S. E. Smith, unpublished data). To a lesser extent, Sanderlings feed in the upper beach zone above the high tide line, where they take mainly insects and talitrid amphipods, often from sites in and around beach wrack (Yaninek 1980). Our knowledge of diet on the harbor tidal flats is limited, by comparison, chiefly because the diversity of the potential prey base there is much greater and more collecting for stomach contents remains to be done. Detailed analyses of Sanderling food habits in the Bodega Bay area will be presented elsewhere.

The general zonation of the invertebrate fauna across the intertidal area of both habitats is already well known (Hedgpeth 1957, Barbour et al. 1973). On outer beaches at Bodega Bay, *Excirolana linguifrons* occupies a position immediately below the high tide line, comparable to other cirrolanid isopods elsewhere (cf. Dahl 1952, Jones 1970, Klapow 1971). *Emerita analoga* occurs just below the isopod zone

and ranges down to the subtidal region (Barnes and Wenner 1968). Additional information on the zonation of beach and harbor prey will be presented in Results.

The Bodega Bay region is utilized by 400–600 Sanderlings each winter. They arrive between August and October and depart in April and May. From October to April most birds remain within the local vicinity, with some individuals temporarily wandering up to several kilometers along the coast. The extent of wandering, in numbers and in distance, varies between years. During the years dealt with in this paper, wandering was not extensive. Of banded adults, 70% return the year after banding, suggesting that most, if not all, surviving birds are strongly winter philopatric. While some individuals defend feeding territories during a portion of the tidal cycle, most forage in flocks (Myers et al. 1979a, b).

METHODS

Interhabitat movements.—Three study plots were chosen to span the range of habitats used by Sanderlings at Bodega Bay (Fig. 1). Each plot was marked with permanent stakes: (1) a 1,000-m × 200-m strip on Doran Flats extending perpendicular to the high tide shoreline and divided into 100-m × 100-m subunits, (2) a 1,000-m strip on Salmon Creek Beach, and (3) a 1,000-m strip on Doran Beach. Both beach transects were divided into 50-m linearly sequenced subunits. They ranged in width from 50 m to 100 m due to variations in beach topography and were censused from the surf zone to the dunes.

Three observers simultaneously censused all study plots at 1-h intervals throughout daylight hours on four separate days in November 1976. Sampling dates were chosen to include a range of tidal regimes within a single lunar cycle. During each hourly census we recorded: (1) the number of birds within each flock within each subunit; (2) the number of territorial and otherwise aggressive birds within each subunit; (3) the location of all territory boundaries, which usually changed very little between censuses; and (4) the identity of individual birds from color-bands. We distinguished territorial and nonterritorial individuals on the basis of their responses to other birds approaching their foraging sites and on their use of particular displays (Myers et al. 1979a, b).

We repeated the census procedure on Doran Beach on 5 and 14 April 1978 to examine the effect of altered prey conditions (see below). To compare population responses to tidal level changes, we used the Wilcoxon signed ranks test, after computing mean Sanderling densities in tide intervals of 0.5 ft. This permitted tide-related behavior comparisons between beaches, between seasons, between territorial and nonterritorial groups, and between rising and falling tides.

During the winters of 1974–1976 we had captured 265 Sanderlings and banded them with unique combinations of colored leg-bands, permitting individual identification. In addition to recording such individuals along our transects during the November 1976 censuses, we periodically searched for banded birds over the Bodega Bay area throughout the 1976–1977 and 1977–1978 winters. For each resighting we recorded the identity, date, time, and position on a grid system of 200-m × 200-m unit resolution.

Invertebrate distribution: beaches.—We measured prey abundance on the beaches using two sampling schemes. The first provided a broad picture of the variation in prey density at different tidal levels and in peak density along the length of the beach. The method is described more fully elsewhere (Myers et al. 1979a). Briefly, we sampled prey on 27 parallel cross-tidal transects 50 m apart along 1,300 m of Salmon Creek Beach, including the 1,000-m bird study plot, and on 25 cross-tidal transects along 1,200 m of Doran Beach (Fig. 1). We sampled for the three species comprising the main surf zone prey of Sanderlings on these beaches, the isopods *Excirolana linguifrons* and *E. kincaidi* and the sand crab *Emerita analoga* (megalops and juvenile stages). Distributions of these prey were determined on Salmon Creek Beach during the weeks of 21 September, 24 October, 6 December, 17 January, 7 March, and 19 April 1977–1978, and on Doran Beach during the weeks of 28 February and 28 March 1978. Additional sampling for *Emerita* alone was conducted on Salmon Creek Beach during the weeks of 30 March and 20 April 1977.

The sampling procedures for *Excirolana* and *Emerita* differed in order to maximize our efficiency in this extensive sampling scheme. Both species were sampled at low tide. To determine *Excirolana* abundance along each cross-tidal transect, we cored along two parallel lines 2 m apart, locating samples every 5 m from high tide to low water. The cores (101 mm in diameter × 78 mm deep) were sieved through a 1-mm screen, were counted separately in the field, and were used to identify the peak *Excirolana* zone. At this peak we took 3 additional replicates, separated horizontally by up to 2 m, to a total of 5 per peak sampling location.

We sampled *Emerita analoga* along the same cross-tidal transects by taking a 0.07-m² slab to a depth of 4 cm every 5 m. We controlled sampling depth by placing runners on each side of the sampler (a scoop) to prevent it from penetrating beneath 4 cm, and we forced it to this depth. We washed samples through

a 2-mm sieve, and, based on the initial run, we identified the peak of the *Emerita* zone. At the peak we took four additional replicates, with each sample at the same cross-tidal position but separated by 5 m along the beach.

During the week of 2 February 1977 we conducted a variation of this sampling scheme for *Excirolana* only on Salmon Creek Beach, pooling 3 cores at each tidal height in our initial cross-tidal transects and sampling 4 additional replicates at the peak. At this time, approximate tidal heights of each sampling station were calculated from measured beach profiles and distances using standard trigonometric relationships.

The second sampling scheme was designed to examine changes in prey density within the wave-washed zone (the major microhabitat used by foraging Sanderlings) at different tidal levels. At low tide on 6 December 1976 we established four cross-tidal transects on Salmon Creek Beach running from the previous high water mark to low water. As the tide came in, we sampled all transects at four different tidal levels (Fig. 7A), taking six samples at each level on each transect distributed in a random array within 2.5 m of the center of the wave-washed zone. Each sample consisted of five pooled cores (101 mm in diameter \times 50 mm deep) washed through a 0.7 mm sieve. We measured individual *Excirolana linguifrons* and *Emerita analoga* to the nearest millimeter. Based on bomb calorimetry of each species, caloric values were estimated from their lengths (J. P. Myers and S. E. Smith unpubl. data). From these figures we calculated the energy density of prey (calories/m²) at different tidal levels.

Invertebrate distribution: harbor sandflats.—Compared to outer coast beaches, the benthic invertebrate community of the harbor sandflats offers an extensive array of prey species for Sanderlings. Sanderlings feeding here take small crustaceans, molluscs, and worms (Couch 1966; Recher 1966; unpubl. data, this study). This makes assessing prey densities on the flats difficult, because it prevents sampling one or a few key species selectively. We chose therefore to sample densities of the three major taxa mentioned above and to convert to energy densities (calories/m²) in order to obtain a common currency for comparison. This approach gives a maximum energy density at each sampling station. We believe the true energy density usable by a foraging Sanderling to be less than this, as it would be decreased by the density of species that are not Sanderling prey and by the portion of potential prey unavailable because of prey depth, prey behavior, and substrate conditions.

We collected samples on the Doran Flat transect at eight tidal levels between +6.0 ft (1.8 m) and +1.2 ft (0.4 m) (Fig. 6) as the tide receded on 13 November 1977. At each tidal level we sampled six different locations spaced at 60-m intervals along 300 m of the water's edge. Each sample consisted of five cores (54 mm diameter \times 25 mm deep) spaced 3 m apart along the water's edge; cores at each sample site were pooled and washed through a 0.7-mm sieve.

Differences between beach and sandflat areas in substrate characteristics and in species, densities, and dispersions of invertebrates necessitated different sampling procedures for the two habitats. In particular, our greater uncertainty concerning prey species on the tidal flats required a conservative approach, using shallower cores to sample only animals within reach of Sanderlings and using a smaller mesh sieve to include more potential prey species. Because we will use these data only to suggest the general relationship between available energy density and tidal height in both habitats, the differences in sampling procedures do not compromise our results.

We preserved the sieved samples in 70% ethanol and sorted all specimens into three categories: crustaceans, molluscs, and worms (phoronids were included with polychaetes in this latter category). For a simple estimate of biomass, we weighed each subsample after 5 min of air drying to approximate a fresh condition. Conversion to caloric values allowed us to combine the categories for an index of available energy density at each sampling site. We used conversion values taken from Tyler (1973): crustaceans, 448 cal/g fresh weight (mean of 2 species of amphipod); molluscs, 284 cal/g fresh weight (5 clams); and worms, 835 cal/g fresh weight (2 polychaetes).

RESULTS

SANDERLING MOVEMENTS IN RELATION TO TIDAL LEVEL

Population movements.—Sanderling numbers fluctuated throughout each day on the transects. Minima recorded on each study plot on most days approached 0 birds, while maxima ranged from 38 to 323 birds. Density was clearly related to tidal level. Figure 2 shows changes in Sanderling abundance on Doran Beach on census days in 1976 and compares those changes with fluctuations in tidal level. On each day

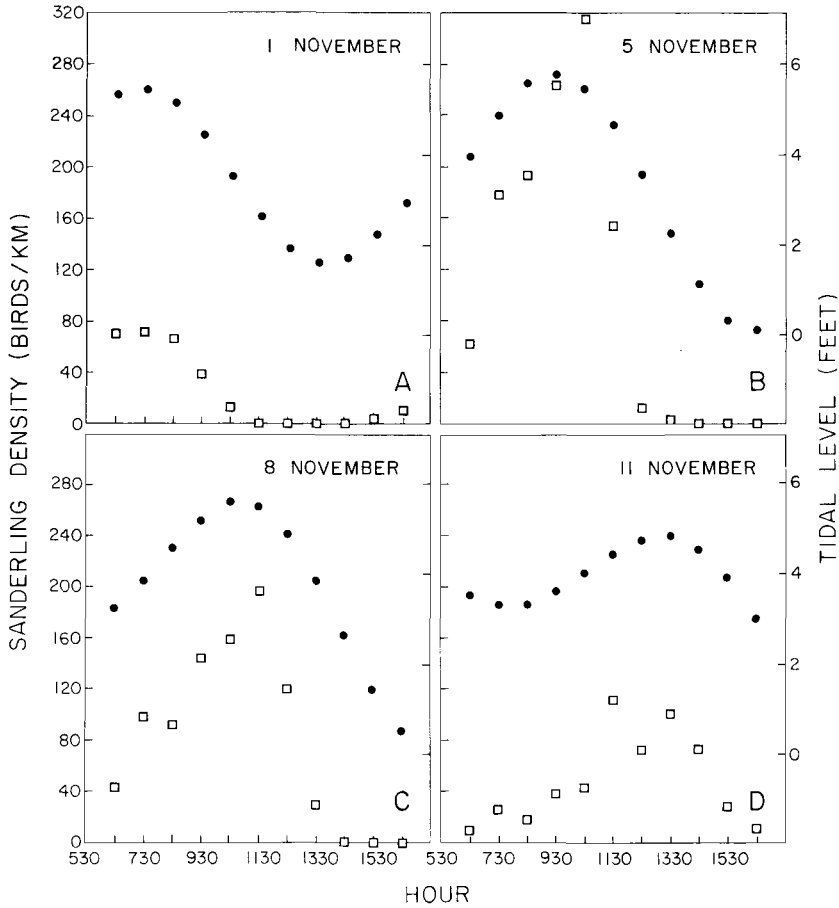


Fig. 2. Changes in Sanderling density on Doran Beach during daylight hours on four sampling days in November 1976. Open squares: Sanderling density (birds/km). Closed circles: tidal level (ft).

the time of maximum density corresponds with the period around high tide, even though the time and height of high tide vary among days.

Figure 3 combines the census data for all four days for each of the beach study plots. The ordinate, Sanderling relative density, expresses each census total as a percentage of the daily maximum recorded for the transect. This procedure normalizes each census to the same relative peak density (100%) to emphasize the consistency of timing of abundance relative to tide height. On both beach study plots the pattern was similar, with higher relative densities recorded at higher tidal levels, but birds remained on Salmon Creek Beach even at low tide, albeit at very low density. The two beaches also differed in the density of territorial birds: none defended sites along Doran Beach, while daily maxima of 26–31 territorial birds were recorded on Salmon Creek Beach. These two differences were probably related, because territorial birds remained on Salmon Creek Beach at lower tidal levels than did nonterritorial birds (see below).

Sanderling abundance on the harbor sandflat transect varied inversely with tidal level (Fig. 4A) in a pattern complementary with the outer beach data. The imperfect

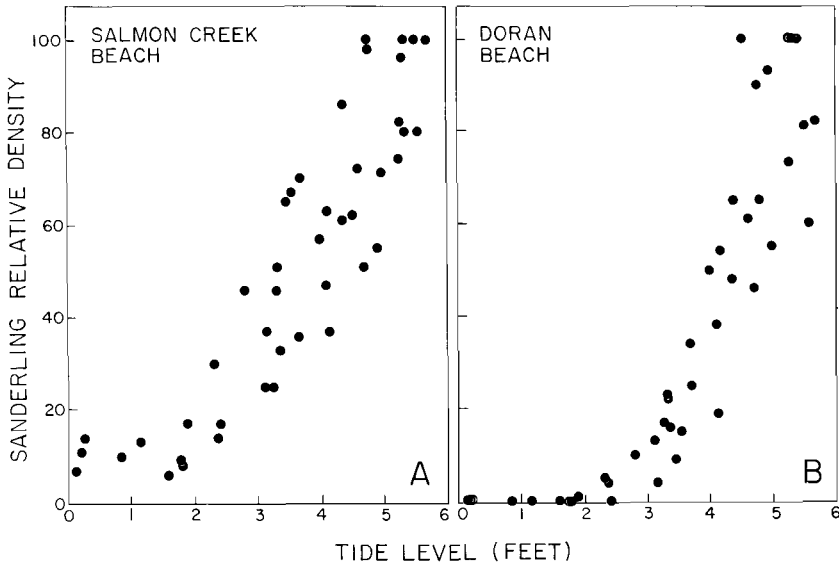


Fig. 3. Changes in Sanderling relative density on outer beach transects as a function of tidal level. Each census count is normalized as a percentage of the daily maximum census recorded for the transect for a given day.

symmetry between density changes on the outer beach transects and on the Doran Flat site arises from local variation in elevations and drainage patterns of the harbor tidal flats. As tides begin to recede, Sanderlings leaving the beaches fly immediately to areas first exposed on the flats; most of these occur off the transect. As tides continue dropping, birds move onto the census area, and their numbers rise until the tide falls to approximately +2 ft (0.6 m). Below this level, Sanderlings begin moving away to other sandflat foraging sites freshly exposed by the ebbing tide. Figure 4B relates area of exposed tidal flats on the transect, estimated during every census, to predicted tidal level during the census. The form of this curve is quite similar to the general pattern of Sanderling use of the Doran Flat transect. The scatter in these data points arises from differences between predicted and actual tides, from wind effects, and from drainage patterns on and near the transect. Tidal phase differences between the outer beach transects and the sandflats amount to only a few minutes' delay in the harbor and did not strongly affect the timing of Sanderling movements.

Individual movements.—The complementary abundance patterns in the two habitats indicate that Sanderlings move from one habitat to the other as the tidal levels change. Direct observations of three kinds confirm this interpretation. First, we regularly observed individuals and small groups departing one area and flying in the direction of the other. On Doran Beach, the two habitats are separated by only a 200+-m-wide spit (Fig. 1), which Sanderlings traverse regularly. Similarly, birds on Salmon Creek Beach frequently fly east from the beach in the direction of the harbor at times consistent with the schedule of their use of the sandflats.

Second, individual birds identified from unique combinations of colored leg-bands repeatedly foraged in both habitats (Table 1). Of 84 individuals with five or more records in 1976–1977, and of 97 in 1977–1978, only 3 and 11, respectively, were

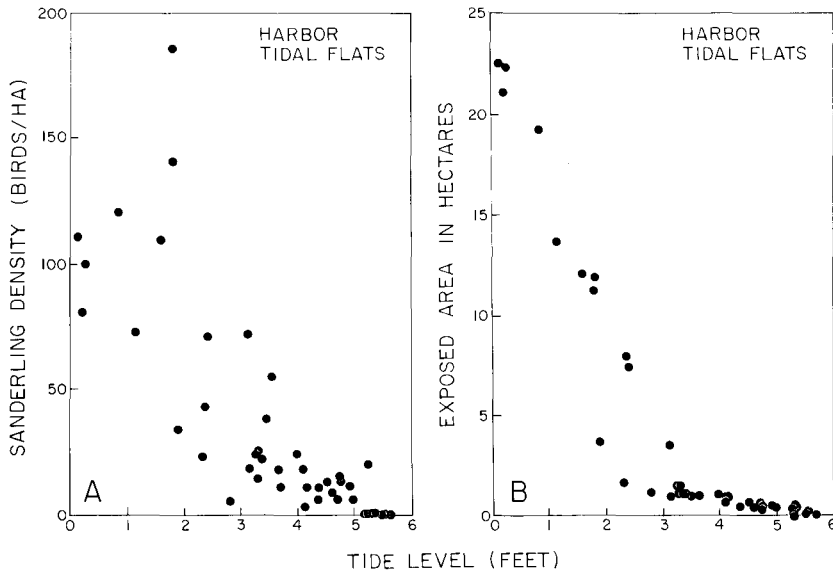


Fig. 4. A. Sanderling density (birds/ha) at different tidal levels on the Doran Flat transect. B. Exposed surface area (ha) on the Doran Flat transect at different tidal levels.

seen in only beach or only sandflat habitat. Approximately 40% used the sandflats and both beaches, while the rest used the sandflat plus one of the two beaches.

Third, and most conclusively, on 47 occasions during the winters of 1976–1977 and 1977–1978 we observed a color-banded individual first in one habitat at one tidal level and then, on the same day, in the other habitat at a second tidal level. In all cases the switch was consistent with low-tide use of sandflats and high-tide use of beaches. We would have recorded this pattern more frequently except that searches for banded birds usually concentrated on one habitat during any given day.

Habitat time budgets.—During census days in November 1976, Sanderlings spent an estimated 45% of daylight hours on outer beaches. This figure is based on the total beach bird-hours (sum of birds recorded each hour over all hourly censuses) compared with the potential maximum beach bird-hours (assuming the daily maximum of birds remained on the beach all day).

Sanderlings vary their allocations of time according to tidal regime (Fig. 5). As more of the day is given over to low tidal levels, both territorial and nonterritorial Sanderlings spend more time on harbor sandflats, which is consistent with the movement patterns discussed above. Differences between territorial and nonterritorial birds will be examined below.

Invertebrate distribution: tidal flats.—Total energy density (cal/m^2) in Sanderling

TABLE 1. Numbers of color-banded Sanderlings recorded in different combinations of foraging sites around Bodega Bay, California.^a

Winter	SCB only	DB only	HSF only	SCB + DB	SCB + HSF	DB + HSF	SCB + DB + HSF
1976–1977	2	0	1	0	28	18	35
1977–1978	6	2	0	3	41	13	32

^a Minimum of five sightings per individual. SCB, Salmon Creek Beach; DB, Doran Beach; HSF, Harbor sand flats.

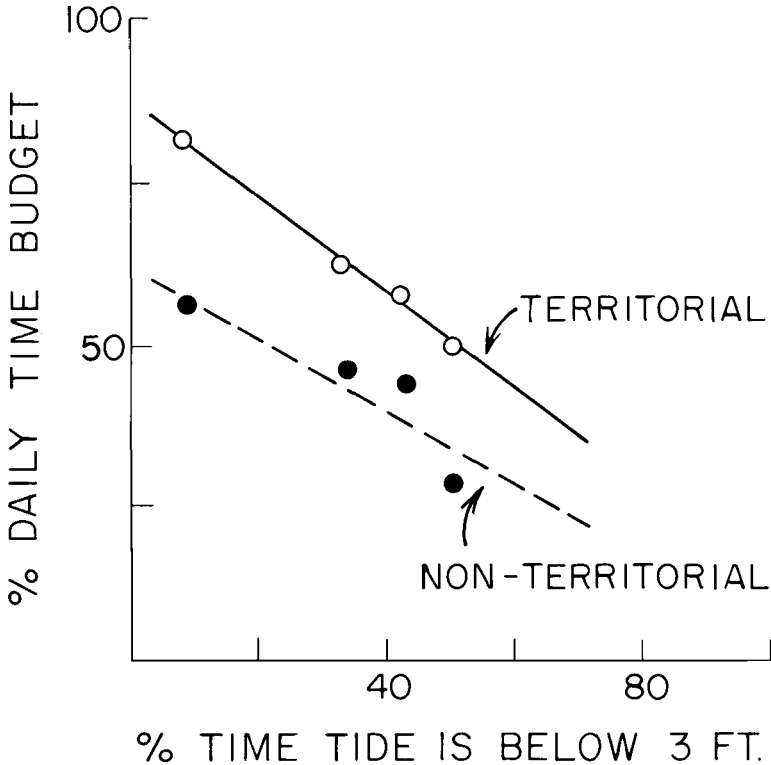


Fig. 5. Percentage of daily time budget spent by Sanderlings on the outer beach at Bodega Bay for different days in a lunar cycle. Abscissa calculated as the percentage time of daylight hours that tidal level is below 3 ft. See text for explanation of daily time budget calculation.

foraging habitat varied inversely with tidal height in the harbor (Fig. 6; $P < 0.001$, Spearman rank order correlation). This pattern resulted from the horizontal displacement of the water's edge—where Sanderlings feed—to lower tidal levels. At lower levels, densities of all prey taxa increased (crustaceans $P < 0.05$; molluscs $P < 0.001$; polychaetes and phoronids $P < 0.001$). Differences in zonation patterns among groups, however, led to changes in the relative importance of the three invertebrate categories across the intertidal zone as the tide receded. Crustaceans, particularly cirrolanid isopods, predominated at tidal levels between +3 and +5 ft (0.9 and 1.5 m). Molluscs, polychaetes, and phoronids became progressively more important at lower levels. From this limited sampling, we conclude that available energy density for Sanderlings on the tidal flats increases with falling tidal level. Because of problems in relating available prey to measured prey (Myers, Williams, and Pitelka 1980), Fig. 6 does not necessarily represent either the absolute magnitude of energy density or the precise form of the relationship with tidal level.

Invertebrate distribution: beaches.—Energy density on the beach on 6 December 1976 was highest at +5 ft (1.5 m), where it averaged approximately 1,000 cal/m² (Fig. 7A), and decreased both above and below this tidal level. Most of the calories recorded were in *Excirrolana linguifrons*; only three *Emerita analoga* were counted in the samples. A low *Emerita* density in December is typical for this area (Myers, Connors, and Pitelka 1980). Thus, the pattern of energy distribution in relation

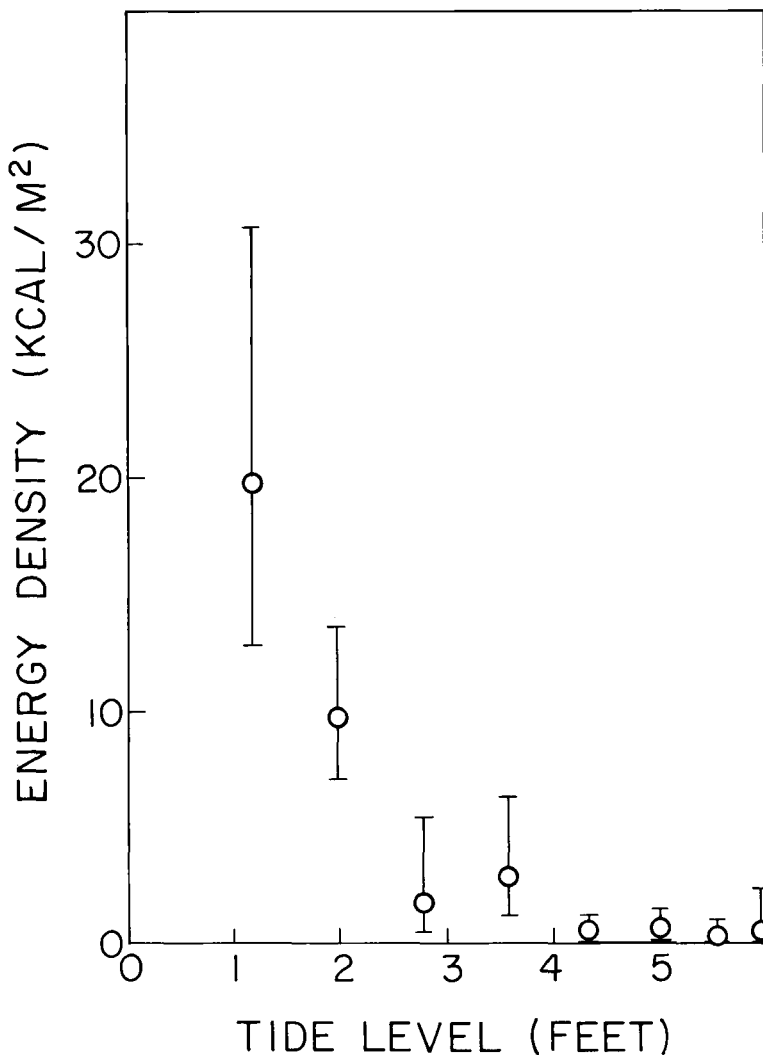


Fig. 6. Energy density of Sanderling prey at different tidal levels on the harbor sandflat. Mean density (kcal/m²) with 95% confidence interval (calculated from natural logarithm transformation of data).

to tidal level closely resembles the average zonal distribution of *Excivrolana* along 1,300 m of Salmon Creek Beach (Fig. 7B). Peak *Excivrolana* densities typically occur between +4.5 and +5 ft (1.4 and 1.5 m).

The energy densities shown in Fig. 7A are averages of values from four transects placed without reference to bird foraging. As a result, while the form of the distribution in Fig. 7A is representative of conditions exploited by the birds, absolute values measured may not be, as Sanderling feeding is concentrated in areas of high *Excivrolana* density (Myers et al. 1979b). The transects sampled on 6 December averaged 156 *Excivrolana* per m² at +5 ft (1.5 m), but densities encountered along Salmon Creek Beach ranged from 0 to over 1,300 *Excivrolana* per m². The variable *Emerita* densities can contribute up to 30 kcal/m² of additional energy at seasonal peaks.

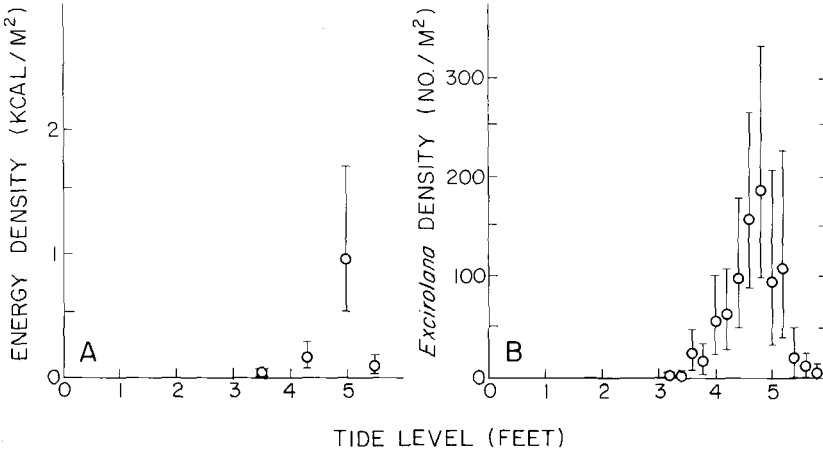


Fig. 7. Distribution of Sanderling prey at different tidal levels on the beach. A. Mean energy density (kcal/m²) with 95% confidence interval (calculated using natural logarithm transformation). B. Mean density of *Excirologa linguifrons* (animals/m²) with 95% CL (using ln transformation).

A MODEL AND TWO PREDICTIONS

When viewed in relation to invertebrate zonation patterns on the beach and in the harbor, it is clear that within the Bodega Bay system Sanderlings switch habitats in order to exploit the most profitable foraging locations. This can be summarized in a simple graphical model (Fig. 8A): a Sanderling should forage where its foraging efficiency (FE), the net energy intake per unit time, is greatest. As tidal levels change, prey availability and therefore Sanderling FE change because of invertebrate zonation patterns.

The patterns of energy density (Figs. 6 and 7) suggest that, compared to sandflat FE, beach FE decreases with the receding tide. Provided that the energetic cost of flying between habitats is small, Sanderlings should switch to the sandflat as beach FE becomes less than sandflat FE, which is consistent with the observed pattern of interhabitat movements. The FE curves in Fig. 8 are, of course, only rough approximations due to the complex relationship between energy density and actual energy availability to foraging Sanderlings. Availability may vary with changing tidal height even at constant prey density because of changes in prey species, prey behavior, and foraging substrate characteristics, especially water content and penetrability (Goss-Custard 1970, Jones 1970, Evans 1976). It suffices now to represent the sandflat FE relationship (X) in a simple linear form and the beach FE curve (Y) with a maximum at moderate to high tides. The only requirement of the model is that the FE curves cross, with the sandflat FE curve (X) increasing at low tide levels relative to the beach FE curve (Y). Within these limitations, the model leads to two predictions:

Prediction 1: Changes in resource conditions.—A change in relative profitability of foraging in one habitat should be accompanied by a change in the tidal level at which a Sanderling switches between habitats. In fact, a striking increase in beach prey densities occurs each year in late March and April when large numbers of megalops (post-larval stage) of *Emerita analoga* settle out of the plankton onto the beaches. *Emerita* megalops occupy a position [approximately +1 ft (0.3 m) to +4

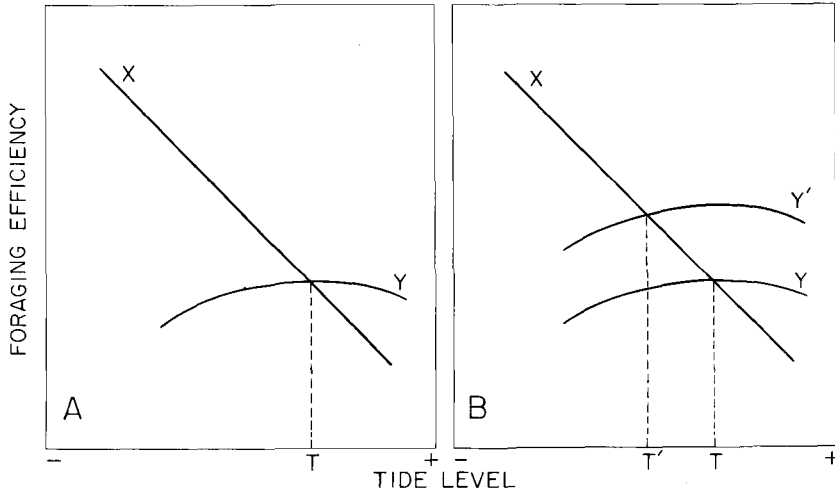


Fig. 8. Hypothetical relationships between foraging efficiency (FE) and tidal level in two habitats. A. The basic model. Curve X = FE on the harbor sandflats. Curve Y = FE on the beach. B. The basis for two predictions. Curves X and Y as in A. Curve Y' = the increased beach FE due to (Prediction 1) increased beach prey density because of seasonal settling patterns in prey species, or (Prediction 2) increased beach prey due to territorial behavior by Sanderlings.

ft (1.2 m)] immediately below the *Excirolana* zone and are usually stranded above the water line on outgoing tides. Their settling produces as much as a 10-fold increase in the density of a preferred food item (Table 2). Sanderling beach FE at these tidal levels may not increase by the same factor, but an appreciable increase is likely. *Emerita* do not occur on harbor sandflats, and the results from a seasonal monitoring of invertebrate densities on Doran Flats show no comparable increase in prey densities in April within Bodega Harbor (Smith 1977).

According to our model, the change in beach FE from Y to Y' should shift the switching point from tidal level T to a lower tidal level T' (Fig. 8B). This prediction was tested by repeating the bird censuses on Doran Beach in April 1978 during the high density period for *Emerita* megalops. We then compared these data with those obtained for nonterritorial birds on Doran Beach in November 1976 (Fig. 9). Sanderlings remained on the outer beach in April at lower tidal levels ($P < 0.01$, Wilcoxon signed ranks test). We fitted the data for each period by eye with sigmoid curves (Fig. 9) from which we estimated the mean tidal level at which 50% of the average maximum count of birds remained on the beach. This tidal level, approximately +4 ft (1.2 m) in November, shifted to less than +2 ft (0.6 m) in April.

Prediction 2: Differences among individuals.—Consider two individuals, one

TABLE 2. Seasonal changes in mean density of *Emerita analoga* on outer coast beach transects.

Season	Number of sampling periods		Mean density (animals/m ²)	Range
	Doran Beach	Salmon Creek Beach		
Winter (21 September–7 March)	1	5	20.2	2–38
Spring (28 March–20 April)	1	3	242	37–610

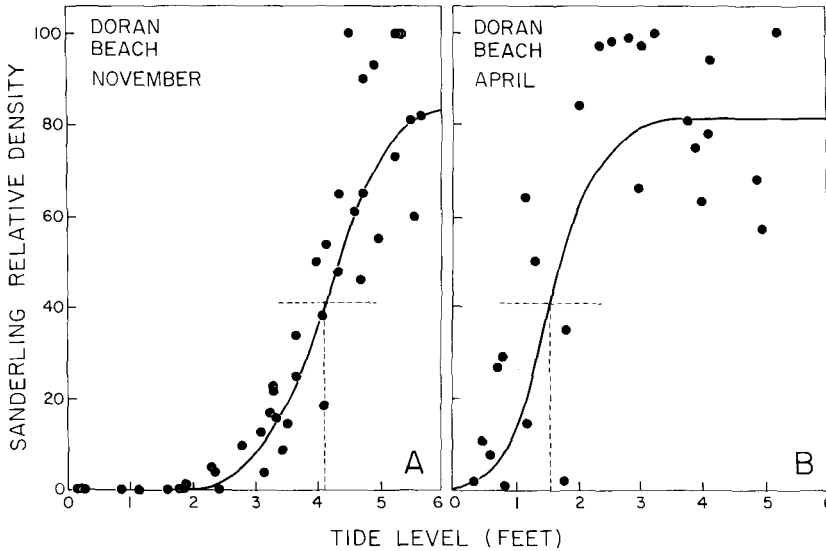


Fig. 9. Changes in Sanderling relative density on Doran Beach at different tidal levels. Sigmoid curves fitted by eye. The dashed line shows the tidal level at which 50% of the Sanderlings have moved to the harbor. A. November 1976, a period of low *Emerita* density. B. April 1978, a period of high *Emerita* density.

more efficient at beach foraging than the other. If they are equally adept at using sandflats, the bird that is more efficient on the beach should spend more time on the beach. This follows from the model, because the beach FE curve Y' for the more efficient beach bird will intersect the sandflat FE curve X at a lower tidal height T' (Fig. 8B). Thus, for this bird the beach will remain more profitable than sandflats over a longer portion of the tidal cycle.

Although we cannot test this prediction directly, we offer supportive evidence by comparing interhabitat movements of territorial versus nonterritorial birds. We assume that Sanderling wintering territoriality is food based (Myers et al. 1979a, b) and that a specific benefit of territorial defense is an increase in foraging efficiency for the territorial bird. This is consistent with analyses of food-based territoriality in other birds in which, by defending a site, the resident obtains exclusive use of the area's resources (e.g. Brown 1975 and references therein).

Based on the preceding assumptions, we expect territorial birds to remain on the beach at lower tidal levels than nonterritorial birds. This is in fact the case (Fig. 10): territorial birds move from beach to harbor at significantly lower tidal levels than do nonterritorial birds ($P < 0.01$). Returning from the harbor, however, their switching time is not significantly earlier than that of nonterritorial birds ($P > 0.05$). Thus territorial birds change their switching tidal level between incoming and outgoing tides by remaining later on outgoing tides ($P < 0.01$). Nonterritorial birds showed no such difference ($P > 0.05$).

The difference between territorial and nonterritorial switching times is consistent with the model for falling, but not rising, tides. This could indicate that the benefit of territoriality accumulates only over the period of one tidal cycle or, alternatively, that the benefit is not expressed on incoming tides because of differences in prey availability between rising and falling tides. For example, as the tide rises, water

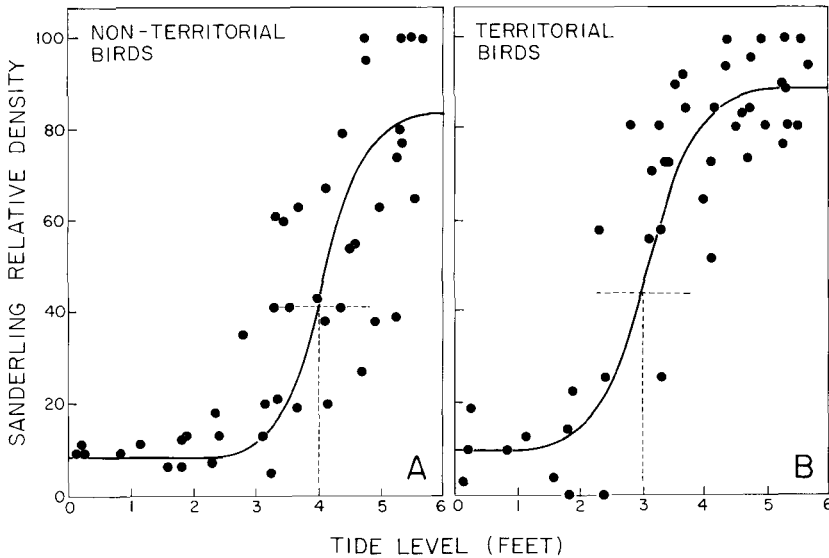


Fig. 10. Sanderling relative density at different tidal levels on Salmon Creek Beach. Sigmoid curves fitted by eye. The dashed lines show the tidal level at which 50% of the Sanderlings have moved to the harbor. A. Nonterritorial birds. B. Territorial birds.

content, substrate penetrability, or vertical distribution of prey may require time to recover to profitable foraging conditions. We favor the latter interpretation. It is our view that FE benefits for territorial birds on the beach extend over more than one tidal cycle. This is supported by the repeated return of marked individuals to their respective beach territories (Myers et al. 1979b). The asymmetry in switching time runs counter to the hypothesis that territorial birds spend more time on the beach simply to ensure successful defense of the territory. By this hypothesis, territorial birds should both arrive earlier and depart later than nonterritorial birds.

Because of the differences in their switching times, territorial and nonterritorial birds have different habitat time budgets (Fig. 5). While both sets adjust their daily habitat time budgets in response to changing tidal regimes, the territorial birds spend 48% more total time on the beach over the lunar cycle.

DISCUSSION

Combining a tidal cycle of habitat availability with a diurnal cycle of daylength can place severe limits on wader foraging time during the winter. Shorebirds circumvent these limits in several ways. Some increase nocturnal foraging, effectively lengthening the foraging day (Goss-Custard 1969, Heppleston 1971, Baker and Baker 1973). Others forage sequentially in habitats over which tidal exposures are not in phase, thereby expanding the range of utilized habitats within a tidal cycle (Goss-Custard 1969, Heppleston 1971, Burger et al. 1977). Still others simply roost less during daylight hours (Goss-Custard et al. 1977). Sanderlings at Bodega Bay display the second pattern, moving between two different habitats that have complementary patterns in profitability of foraging effort with respect to tidal height.

Sixteen other shorebird species winter commonly in the Bodega Bay lagoon system. Many of these birds spend much of the high-tide period roosting in multispecific

flocks adjacent to sandflats. Only Snowy Plovers (*Charadrius alexandrinus*) show interhabitat movements comparable in regularity and scale (in terms of the proportion of the local population involved) to those of Sanderlings. Other species often appear in a range of habitats. Individual Willets (*Catoptrophorus semipalmatus*), Black Turnstones (*Arenaria melanocephala*), Marbled Godwits (*Limosa fedoa*), and Black-bellied Plovers (*Pluvialis squatarola*) switch habitats on a tidal schedule, much like Sanderlings. These and other species also appear in several habitats, not because of tidally controlled movements but because different individuals specialize in different habitats. At times, large numbers of these and of several other species can be seen in habitats different from their usual haunts, most often as a result of temporary unfavorable environmental conditions such as winter periods of rain, cold weather, or high waves. This phenomenon, particularly with respect to use of upland fields at high tide, appears most pronounced during winters with severe storm conditions.

Why do individuals of more shorebird species not follow the Sanderling pattern, exploiting several habitats on a regular basis? Our data on energy densities suggest that, overall, the beach is relatively energy-poor compared to the harbor, especially at lower tidal levels. The morphological adaptations that permit Sanderlings to exploit beach resources successfully—a short stout bill and the lack of a hind toe—may interfere with their use of the most profitable sites in the harbor. Other species with longer bills and feet adapted for soft substrates may use harbor resources more effectively but roost during high tides.

Whether the pattern of shifting habitat use seen in Sanderlings exists among wader populations of other areas must depend upon a number of variables, most important the nature of local tides. Tidal regimes vary among geographic areas in absolute amplitude and also in whether they are semidiurnal or diurnal, or regular or irregular (King 1972). Strong shifts in profitability would seem most likely where amplitudes are highest, but access to usable nontidal areas can complicate this argument. Another complicating factor arises from phase shifts in the tidal cycle that occur between local sites because of variations in tidal drainage. Tidal lags within areas exploited by a single wader population can be quite large, especially when complex lagoon and spit systems are involved. These lags vary systematically with the type of tide and the time in the lunar cycle, as well as with lagoon volume, area, and mouth characteristics. Superimposed on these effects will be daily variations due to wind, wave, and current conditions. Pronounced phase differences within a local area might permit a wader to spend most of its foraging time within one habitat at approximately the same tidal level by moving from site to site. Alternatively, such differences could favor habitat switching if preferred invertebrates were to occur in habitats that were exposed on different schedules due to tidal lags.

Given this complex nexus of factors, it is not surprising that wader behavior varies regionally. For example, both Heppleston (1971) and Burger et al. (1977) found marked habitat shifts with the tidal cycle in species they studied. Some of the species that shift in this manner on the New Jersey study site (Burger et al. 1977) do not do so at Bodega Bay. The variable winter spacing systems of many species (Myers et al. 1979b), with changing emphases on flocking versus territoriality, site faithfulness versus vagility, may result ultimately from shorebirds' need to adjust facultatively to a wide range of spatiotemporal fluctuations in their environments. Clearly, a static interpretation of wintering shorebird behavior, undertaken without

explicit attention to tidal flow, would be mistakenly simplistic. Tides dominate the winter existence of coastal shorebirds. They are a prime factor in the evolution of wader behavior and wader ecology.

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A.O.U. Announcements

Fellows and Elective Members are reminded that nominations for Elective Member may be submitted to the Secretary on the prescribed form up until five months prior to the opening of the next Stated Meeting. The deadline for 1981 is **24 March**. Nominations for Fellow of the A.O.U. also must be received by that date. Nominations for Vice-President and Elective Councilors (3) may be made in writing to the Secretary at any time prior to the Annual Meeting.

The 99th Stated Meeting of the A.O.U. will be held at the **University of Alberta, Edmonton, Alberta, Canada** during the week of **August 24-27, 1981**.

The American Ornithologists' Union solicits applications for research grants from its **Josselyn Van Tyne** and **Alexander Wetmore Memorial Funds**. The Van Tyne awards will consider any aspect of avian biology; the Wetmore awards are limited to taxonomy/systematics. Grants are usually in amounts of a few hundred dollars. Preference is given to students and other persons without other sources of funds. Application forms may be obtained from **Dr. A. S. Gaunt, A.O.U. Committee on Research Awards, Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210**. Applications must be completed before **18 March 1981**.

Marcia Brady Tucker Travel Awards to aid in the travel expenses of students presenting papers at the AOU meeting in Edmonton in August 1981 are available. To apply, submit curriculum vitae, an expanded summary of the paper to be presented (maximum of three pages, double-spaced), a budget of anticipated expenses, and a letter of evaluation from your major professor. All material must be received by **18 April**. Send to **Douglas W. Mock, Department of Zoology, University of Oklahoma, Norman, OK 73019**. Students must make their own arrangements for a place on the scientific program.