EFFECTS OF TIDE CYCLES ON HABITAT SELECTION AND HABITAT PARTITIONING BY MIGRATING SHOREBIRDS

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ABSTRACT.—We studied assemblages of feeding shorebirds in three intertidal habitats on the coast of New Jersey during August to document how species segregate spatially both among and within habitats and to determine the effects of tidal cycles on these patterns. The habitats were a sandy beach facing the ocean proper (outer beach), a sandy beach on the mainland side of a barrier island (inner beach), and a small mudflat adjacent to a *Spartina alterniflora* salt marsh. We were able to identify several microhabitats on the outer beach and mudflat.

Most species fed in more than one habitat, but only two, *Charadrius semipalmatus* and *Calidris canutus*, used all three habitats regularly. Within habitats, most species exhibited strong preferences for the wettest areas, but we found differences among species in degrees of preference. The least amount of partitioning occurred on the inner beach, where birds crowded into a small zone near the water's edge and had frequent agonistic encounters suggesting intense competition. Shorebird feeding activity was partly a function of tide time: each habitat had a characteristic temporal pattern of use by shorebirds related to tide time rather than diel time; within habitats, we found species-characteristic feeding activity rhythms that were also a function of tide time. Feeding by most species peaked during the first 2 hours after low tide on the outer beach and mudflat. The results are discussed in terms of feeding strategies and interspecific competition.—*Department of Biology, Livingston College, Rutgers University, New Brunswick, New Jersey 08903* (Burger, Chase); *National Fish and Wildlife Laboratory, National Museum of Natural History, Washington, D.C. 20560* (Howe); and *Institute of Animal Behavior, Rutgers University, Newark, New Jersey 07102* (Hahn). *Present address of* Chase: *Department of Biology, Barnard College, New York, N.Y. 10027*. Accepted 11 March 1977. (This paper was subsidized by the Migratory Bird Program, U.S. Fish and Wildlife Service.)

ALTHOUGH usually solitary on their breeding grounds, migrating shorebirds (Charadrii) often form large, mixed-species aggregations that feed along coastal beaches, mudflats, and marshes. These concentrations of shorebirds result in high population densities in prime feeding areas (Recher and Recher 1969). As these habitats are effectively two-dimensional, spatial segregation of flock members can only occur in a horizontal plane. Increased density may lead to more intense competition for space, resulting in more frequent aggressive interactions and/or niche partitioning. Moreover the cyclic tidal inundation of mudflats and beaches causes changes both in the available feeding space and in the diversity and availability of prey items. Shorebirds respond to these changes by moving continually from one foraging area to another.

Studies of ecology of migrating and wintering shorebirds have dealt primarily with feeding methods and rates (Goss-Custard 1969, Ashmole 1970, Burton 1972, Baker and Baker 1973, Baker 1974), feeding dispersions (Goss-Custard 1970a), prey densities (Bengtson and Svensson 1968, Brooks 1967, Goss-Custard 1970b), feeding ecology (Recher 1966, Thomas and Dartnall 1971, Holmes 1966, Holmes and Pitelka 1968), and aggressive behavior (Hamilton 1959, Recher and Recher 1969). Most of these studies stress behavior and diet as related to prey availability or broader ecological considerations. Collectively, most data suggest that shorebird species overlap broadly in their diets and feeding habitats.

Competitive exclusion may be avoided because species move from point to point without fully exploiting the available food reserves (Recher 1966). Some studies have also identified patterns of niche partitioning with respect to foods, feeding methods,

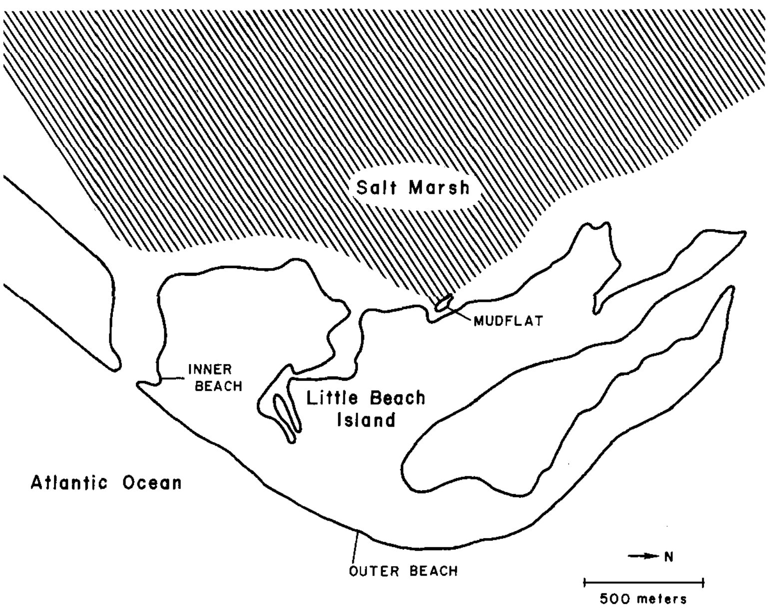

Fig. 1. Map of Little Beach Island, showing the locations of the mudflat, outer beach, and inner beach.

timing, and spacing. Recher (1966) examined microhabitat utilization by shorebirds in tidal environments on the east and west coasts of North America and found that each species had definable microhabitat preferences that varied with flock composition. Species segregated both spatially and by the depth from which food items were extracted from the mud. Although Recher noted changes in bird abundances and behavior as a function of tide levels, he did not examine these relationships in detail. Instead, he tried to minimize the effects of tidal variations by making his observations only after a large percentage of the tidal flat was exposed. Ehlert (1964) reported that feeding times and amounts of food taken by Dunlins (*Calidris alpina*) varied in relation to both tidal and daily rhythms, but he did not investigate patterns of habitat use as functions of tidal fluctuations.

We studied mixed-species assemblages of shorebirds in southern New Jersey in three habitats exposed to tidal inundation: a sandy beach facing the ocean, a sandy beach on the mainland side of a barrier beach, and a small intertidal mudflat adjacent to a salt marsh. Our objectives were to determine how shorebirds distribute themselves spatially among and within habitats and to determine the effects of tidal fluctuations on these patterns.

STUDY AREA AND METHODS

This study was conducted on Little Beach Island, Brigantine National Wildlife Refuge, on the Atlantic coast of southern New Jersey (38°28′N, 74°21′W). Little Beach is a barrier island consisting of sandy beach and dunes on the ocean side and bordering expansive salt marshes (primarily *Spartina alterniflora*) on the mainland side (Fig. 1).

The area of most intensive study, an intertidal mudflat of less than 2 ha at maximum exposure adjacent to the marsh, contained four microhabitats: 1) an area of soft mud and some standing water covered extensively with large blades of the marine alga, sea lettuce (*Ulva lactuca*), 2) an area of drier mud mixed with smaller and more widely dispersed blades of *U. lactuca*, 3) an area of wet sand with large visible concentrations ($\bar{x}$ = 324/m^2) of periwinkles (*Littorina littorea*), and 4) an area of drier sand with fewer visible periwinkles ($\bar{x}$ = 94/m^2). We refer to these areas as 1) algae, 2) mixed, 3) sand A, and 4) sand B. As

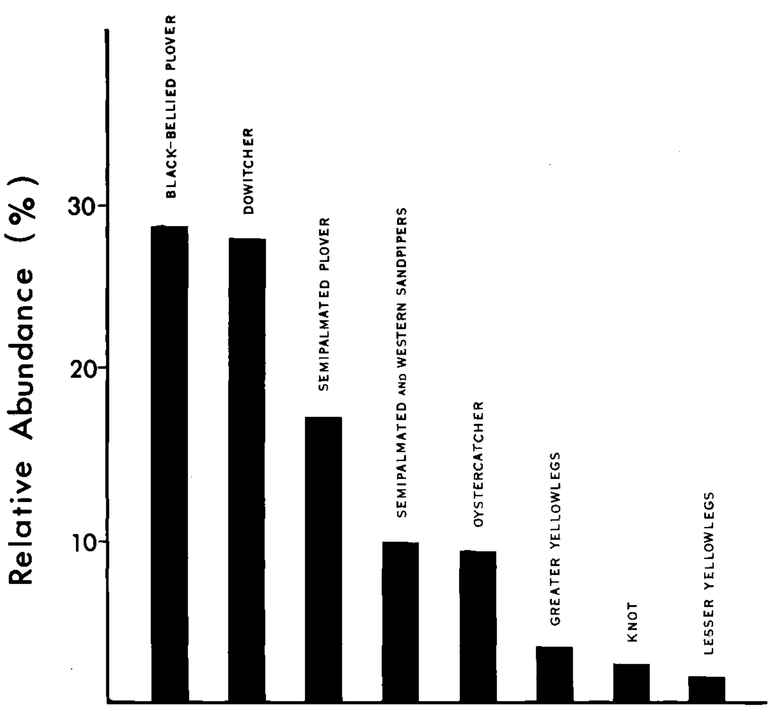

Fig. 2. Relative abundances of shorebirds on the mudflat, averaged over the period 13–27 August.

wet sand dries, periwinkles burrow beneath the surface and sand A becomes sand B. The transition between these zones is quite abrupt.

The other habitats we investigated were two sandy beaches, one on the ocean side and one on the mainland side of the barrier island (Fig. 1). The outer beach, which received direct surf action from the Atlantic Ocean, had a gentle slope and an average intertidal exposure of 50 m. The inner beach, which received negligible surf action, was considerably steeper with an average intertidal exposure of 15 m.

The study period was from 15 July to 10 September 1974, during which time we were able to sample in all three habitats during most daylight hours and under all tide conditions. Because we found that shorebirds did not use all areas equally with respect to tide time, we collected most data during peak periods of use for each habitat. Hence, after determining the general pattern of use for each habitat, we usually made observations on the mudflat during the entire 6-hour period it was above water and on the inner beach for 3 hours after high tide. We devoted the remainder of the day to observations on the outer beach.

We censused shorebirds on the mudflat in the following manner. A meter stick was driven vertically in the water near the edge of the mudflat at low tide. This enabled us to document water levels and determine when tide reversal occurred. Next we established a primary transect consisting of numbered stakes at 10 m intervals along the highest ridge of the mudflat. Two parallel transects, 20 m apart, were laid perpendicular to the primary transect. We then used the stakes as references points to compute the changes in total area of the mudflat and its component microhabitats as the water reached each numbered stake along the primary transect.

Every 15 min from the time the receding tide exposed the mudflat until the rising tide fully covered it we made a complete census of all species in each of the four microhabitats, recording the time of day and position of the water in relation to the stakes and meter stick. At the end of each tide cycle we recorded the exact time that tide reversal had occurred. While censusing, we remained at one site near the edge of the mudflat for the entire period it was exposed. We sometimes had difficulty distinguishing Semipalmated Sandpipers (*Calidris pusilla*) from Western Sandpipers (*C. mauri*), so for some analyses we pooled these species.

In the final compilation of mudflat species, we summed the counts for each 15-min sample over the total period of observation each day and converted the number of each species observed per 15-min sample to a

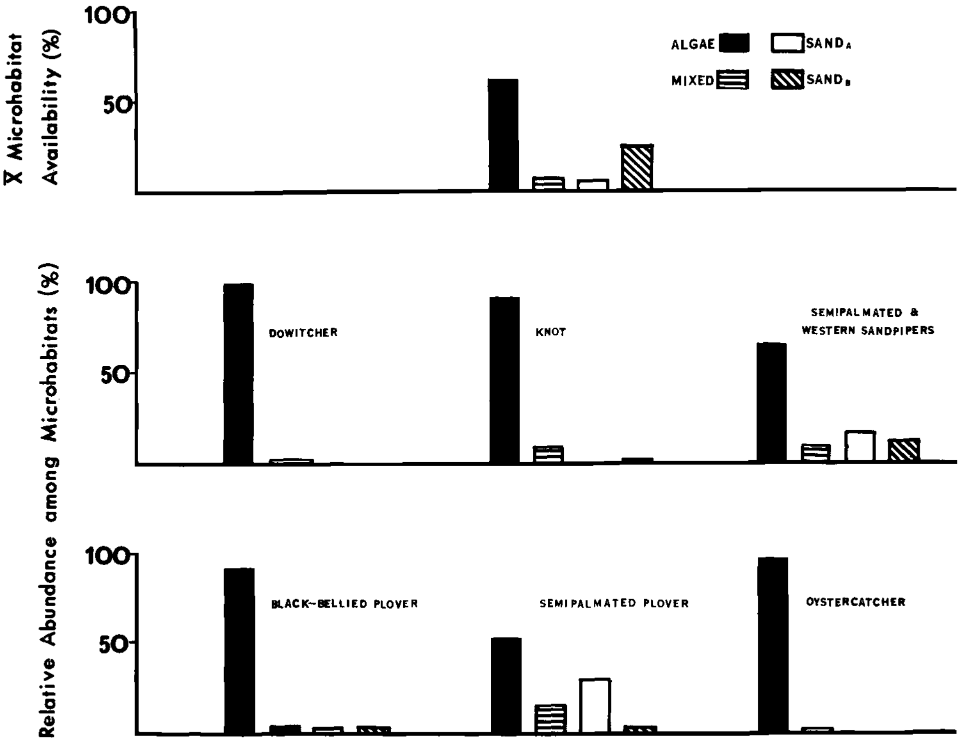

Fig. 3. Top: Average relative areas of the four microhabitats on the mudflat, based on area measurements every 15 minutes over one 6-hour cycle. Bottom: Within-species summaries of relative abundance among microhabitats, averaged over 13 6-hour cycles.

percentage of the daily sum for that species. We called this value the "abundance index." This procedure minimized the effect of a sudden large influx of a species for a short time. We then averaged the percentage figures over the entire period of the study, standardized by water levels, in order to present the data graphically (Fig. 6).

On the outer beach we recorded densities of each species per 100 m shoreline. We divided the beach into functional feeding zones with respect to wave coverage (see below), and recorded the number of each species feeding in these zones. On the inner beach the birds fed in a restricted area, so we made complete censuses of each species at 15-min intervals during the period of use. We recorded whether each species fed on the sand, at the edge of the receding tide, or in the shallow water at the edge of the wave.

RESULTS

Mudflat.—The mudflat supported the greatest number of species of shorebirds, including Black-bellied Plover (*Pluvialis squatarola*), Dowitcher (*Limnodromus griseus*), Semipalmated Plover (*Charadrius semipalmatus*), Semipalmated Sandpiper, Western Sandpiper, Oystercatcher (*Haematopus palliatus*), Greater Yellowlegs (*Tringa melanoleuca*), Lesser Yellowlegs (*T. flavipes*), and Knot (*Calidris canutus*). Between 13 and 27 August, the total population reached an average maximum of 84 individuals during each period of exposure. The mean relative abundances of the most regular species are shown in Fig. 2. Black-bellied Plovers and Dowitchers comprised over 50% of the birds present. The relative abundance of species did not change markedly during the study period.

The mudflat habitat was not uniform but contained zones of algae, mixed, sand A, and sand B (see Methods). We computed the areas of each microhabitat at 15-min

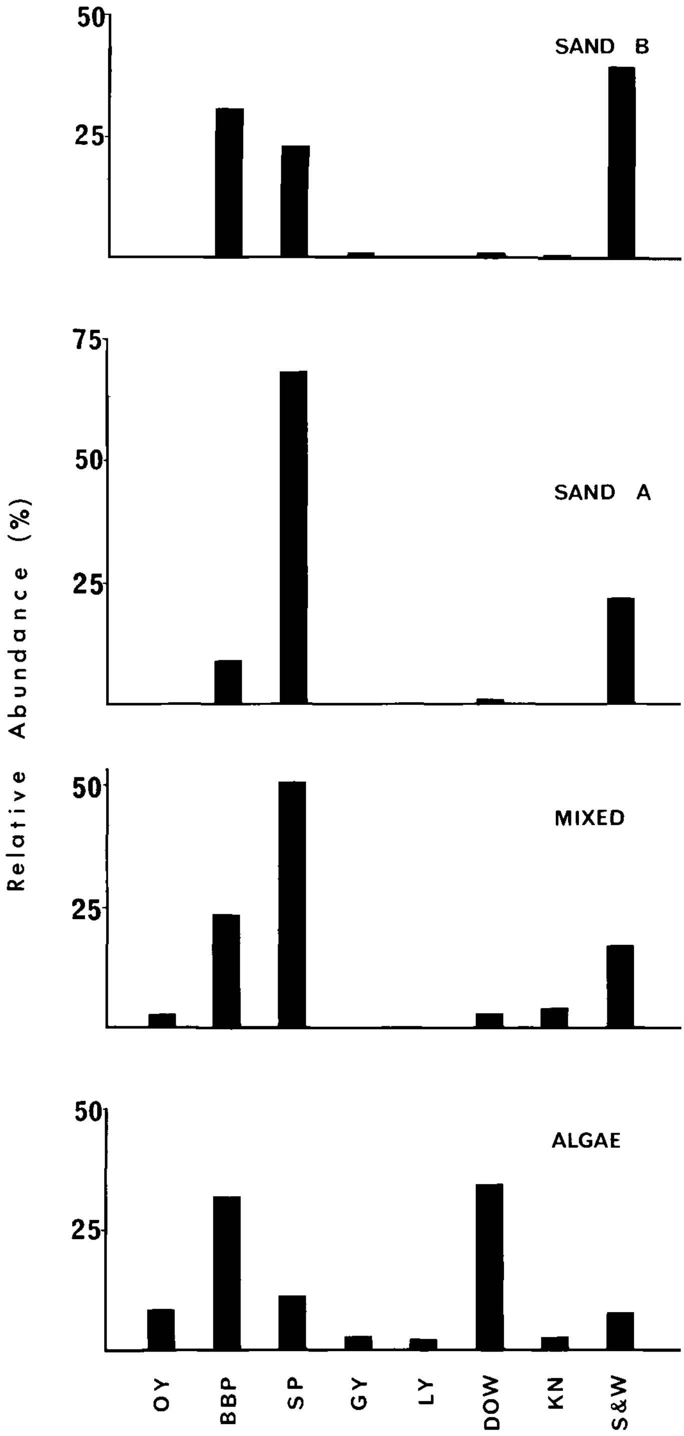

Fig. 4. Relative abundances of species within microhabitats on the mudflat, averaged over 13 6-hour cycles.

intervals during the 6-hour period the mudflat was above water (Fig. 3 top). On the average, algae covered over 60% of the area and sand B over 25%. The relative abundance of species among microhabitats differed from the proportion of microhabitats available (Fig. 3). Dowitchers, Knots, Black-bellied Plovers, and Oystercatchers showed significant preferences for the algae zone (Chi-squared test: $P < 0.001$ for all species). Pooled for this analysis, Semipalmated and Western Sandpipers showed a preference for the sand A and mixed zones ($\chi^2 = 124$, d.f. = 3, $P < 0.001$). When these two species could be identified accurately, Western Sandpipers seemed to prefer the wet algae and mixed zones, whereas Semipalmated Sandpipers fed in the drier sand B zone. These impressions agree with the findings of Ashmole (1970) for these species. Semipalmated Plovers preferred the sand A zone ($P < 0.001$). Hence, the larger species of shorebirds preferred the muddier algae zone and the smaller species the drier microhabitats, although all species spent considerable time feeding in the algae zone.

We next determined the relative abundance of shorebird species within each microhabitat (Fig. 4). Oystercatchers, Semipalmated Sandpipers, and Western Sandpipers were the most abundant species in sand B; Semipalmated Plovers predominated in sand A and mixed; and Dowitchers and Black-bellied Plovers predominated in the algae zone. Greater Yellowlegs sometimes fed in the shallow water of the ebbing tide in addition to our four designated microhabitats. The number of shorebird species using a microhabitat correlated positively with microhabitat area ($r = 1.0$); and the variation of species abundances within microhabitats tended to decrease as the number of species increased. Thus one or two species tended to be disproportionately represented in the smaller microhabitats.

Because the mudflat had discrete boundaries, we were able to consider the area exposed as a function of tide time. Tide time refers here to the number of hours before (− values) or after (+ values) dead low tide (= 0). An average of 3.5 hours was required for the mudflat to be exposed completely and 2.5 hours to be covered. We superimposed the mean number of individuals of all species present upon an area-tide time curve (Fig. 5). The number of birds increased faster than the area of the mudflat for the first 1½ hours, but after 2 hours the number of birds remained constant until after dead low, when tidewaters began to cover the mudflat. The maximum number of birds occurred 1 hour after low tide. The pattern suggests that limiting food resources or other constraints during the 2 hours before low tide prevented further increases in the number of birds, despite a continuing increase in the area available. With the incoming tide, the uncovered area decreased at a faster rate than the number of birds. In the hour before complete inundation, many birds fed in shallow water as a thin film covered the algae zone.

On an individual species basis, similar patterns of population change in relation to tide occurred for Oystercatcher, Black-bellied Plover, and Dowitcher, with one peak near the midpoint of the ebbing tide and a higher peak near the midpoint of the rising tide (Fig. 6). Knots used the area most intensively during the 2nd hour after dead low. Semipalmated Plovers, the only species not showing a bimodal pattern, peaked between the 1st and 2nd hour after low tide. It was the only species for which we were able to show a preference for sand A. We had too few data to permit preference tests for the less common species.

The changes in area of each microhabitat during the course of a cycle apparently affected the patterns of microhabitat use. Figure 7 shows the relative areas of microhabitat exposed during two equal time periods before low tide and two equal time

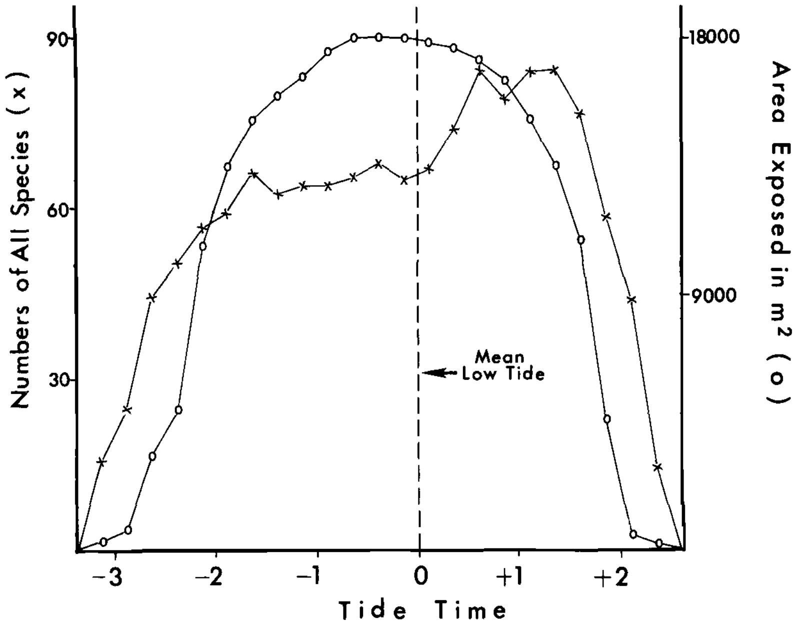

Fig. 5. Temporal changes in the area of mudflat (circles) and the numbers of individuals of all shorebird species (X's) present on the mudflat, averaged over 13 6-hour cycles. Tide time is measured in hours before (− values) and after (+ values) low tide (= 0).

periods after low. Relative changes of the algae and sand B zones account for most of the variation. These data can be compared with microhabitat use patterns averaged over the same time periods for seven species (Fig. 8). Knots, Dowitchers, Black-bellied Plovers, and Oystercatchers did not undergo any major shifts in microhabitat use during the course of a tide cycle. Strong preferences for algae were evident in all cases (Chi-squared test: $P < 0.001$ except for Knots in period 4, for which $\chi^2 = 6.9$, $P < 0.05$). Semipalmated and Western Sandpipers, despite an overall preference for the mixed and sand A zones (Fig. 3), occurred more frequently in sand B during period 1 and in algae during period 3 ($P < 0.001$). This pattern may not indicate a true shift of preference, but could simply be a result of rising water levels forcing smaller species feeding in algae to move to shallower places. Generally most species preferred to feed in algae in the hour before and the hour after dead low. At this time the sand areas are the driest, while the mud of the algae zone retains moisture and may harbor more accessible prey items (Green and Hobson 1970).

Outer beach.—On the outer beach we recognized three microhabitats, each approximately 6 m wide, paralleling the water's edge. The area between the minimum and maximum extents of the waves constituted the water-covered zone. Above this zone was an area of sand dampened by unusually high waves or left wet by the receding tide. We called this the wet sand zone. Above the wet sand was the dry sand zone. For the purpose of describing microhabitat use by feeding birds, those individuals that used both the wet and water-covered zones were categorized as using both.

Sanderlings (*Calidris alba*), Knots, Semipalmated Plovers, Piping Plovers (*Charadrius melodus*), and Black-bellied Plovers fed regularly on the outer beach. Sanderlings, by far the most abundant species, reached peak densities of 1–3 per

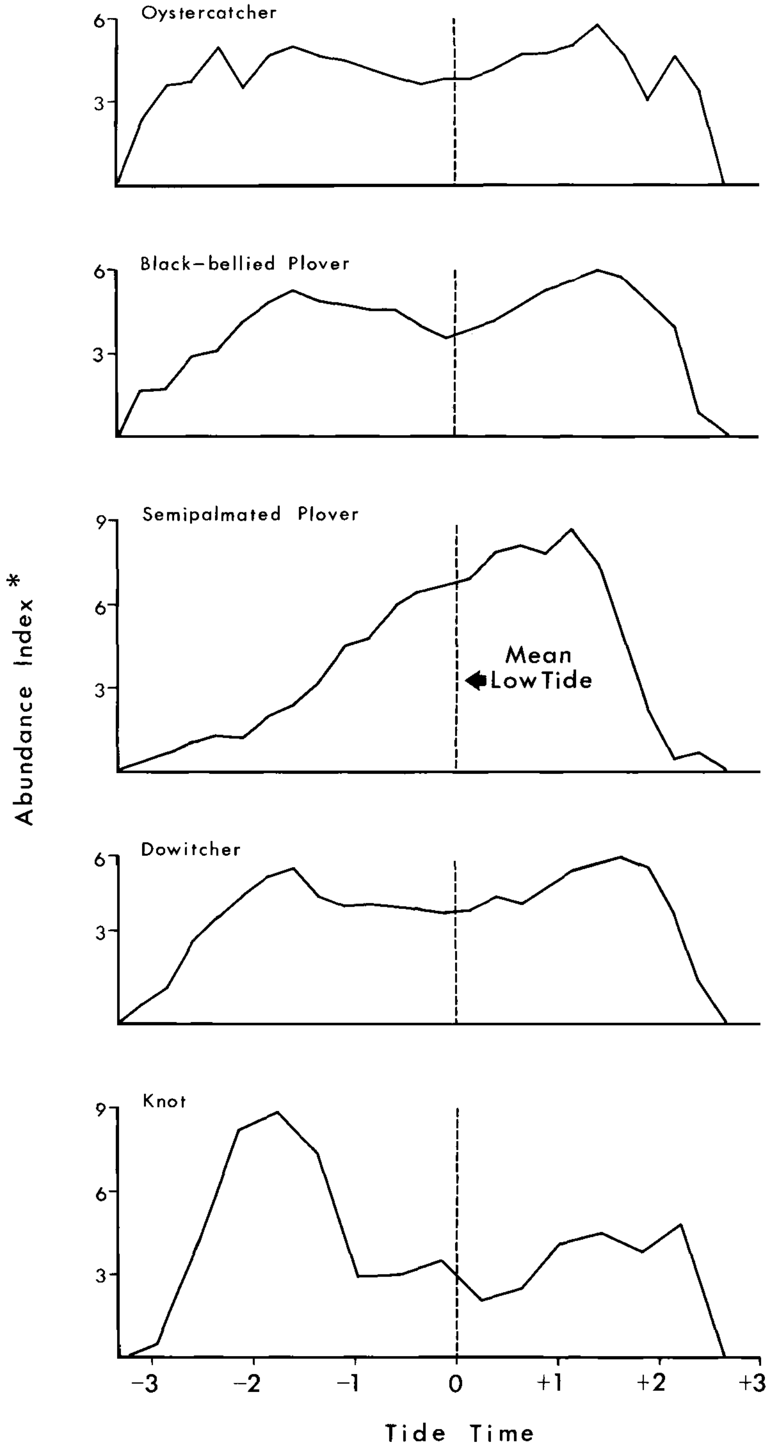

Fig. 6. Changes in abundance of five species of shorebirds on the mudflat in relation to tide time. The data are averaged over 13 6-hour cycles. Tide time is measured in hours. The abundance index is a percentage measure proportional to actual abundance and allows different species to be compared on the same scale (see Methods).

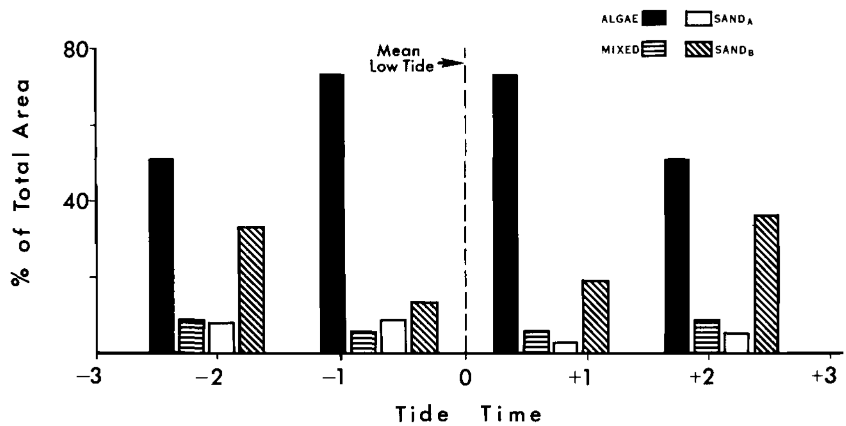

Fig. 7. Relative areas of the four microhabitats on the mudflat as a function of tide time (in hours). The data are averaged over each of two equal time periods before low tide and two equal periods after low tide. Each group of four bars represents one of the four time periods.

linear meter of shoreline. Sanderlings usually fed in the water-covered zone. Knots were relatively scarce and fed in small groups in the water-covered zone. Semipalmated and Piping Plovers were fairly common, more widely spaced than Sanderlings and Knots, and fed in the wet, dry, and water-covered zones. Black-bellied Plovers were the least common regular member of the outer beach assemblage and fed solitarily in the wet and dry sand zones.

During the 5-hour period after high tide, we made a series of 1-min observations on feeding behavior of randomly selected Sanderlings, Semipalmated Plovers, and Piping Plovers, noting the microhabitat(s) used. Because birds were not marked, some individuals may have been sampled more than once, but as we took these observations over several days on different segments of the beach, we believe most individuals were sampled only once. Chi-squared tests showed that all species were distributed nonrandomly among the outer beach microhabitats (Fig. 9). Sanderlings fed in the water-covered zone exclusively ($\chi^2 = 144$, d.f. $= 3$, $P < 0.001$). Piping Plovers fed in the wet sand but showed a secondary preference for the water-covered zone ($\chi^2 = 8.7$, d.f. $= 3$, $P < 0.05$). Semipalmated Plovers also preferred the wet sand, but individuals of that species were more likely to move between wet and water-covered sand during the course of a 1-min sample than were Piping Plovers ($\chi^2 = 20.7$, d.f. $= 3$, $P < 0.001$). Dry sand received greatest use by Semipalmated Plovers but was not a preferred feeding zone for any species. On the outer beach Sanderlings exhibited two peaks of abundance during a complete cycle. Greatest numbers occurred after low tide, with a secondary peak after high tide (Fig. 10). Between the peaks Sanderlings were generally scarce or absent. Occasionally we found them roosting high up on the beach during these lulls in feeding activity. Piping and Semipalmated Plovers, although much less common, seemed to show similar patterns of change in abundance with respect to tide time.

Inner beach.—The inner beach feeding assemblage consisted of Dowitchers, Ruddy Turnstones (*Arenaria interpres*), Semipalmated and Western Sandpipers, Knots, Sanderlings, Semipalmated Plovers, Piping Plovers, Black-bellied Plovers, and Willets (*Catoptrophorus semipalmatus*). Most species fed in a narrow zone from the water's edge to about 3 m into the water over a 50-m segment of shoreline.

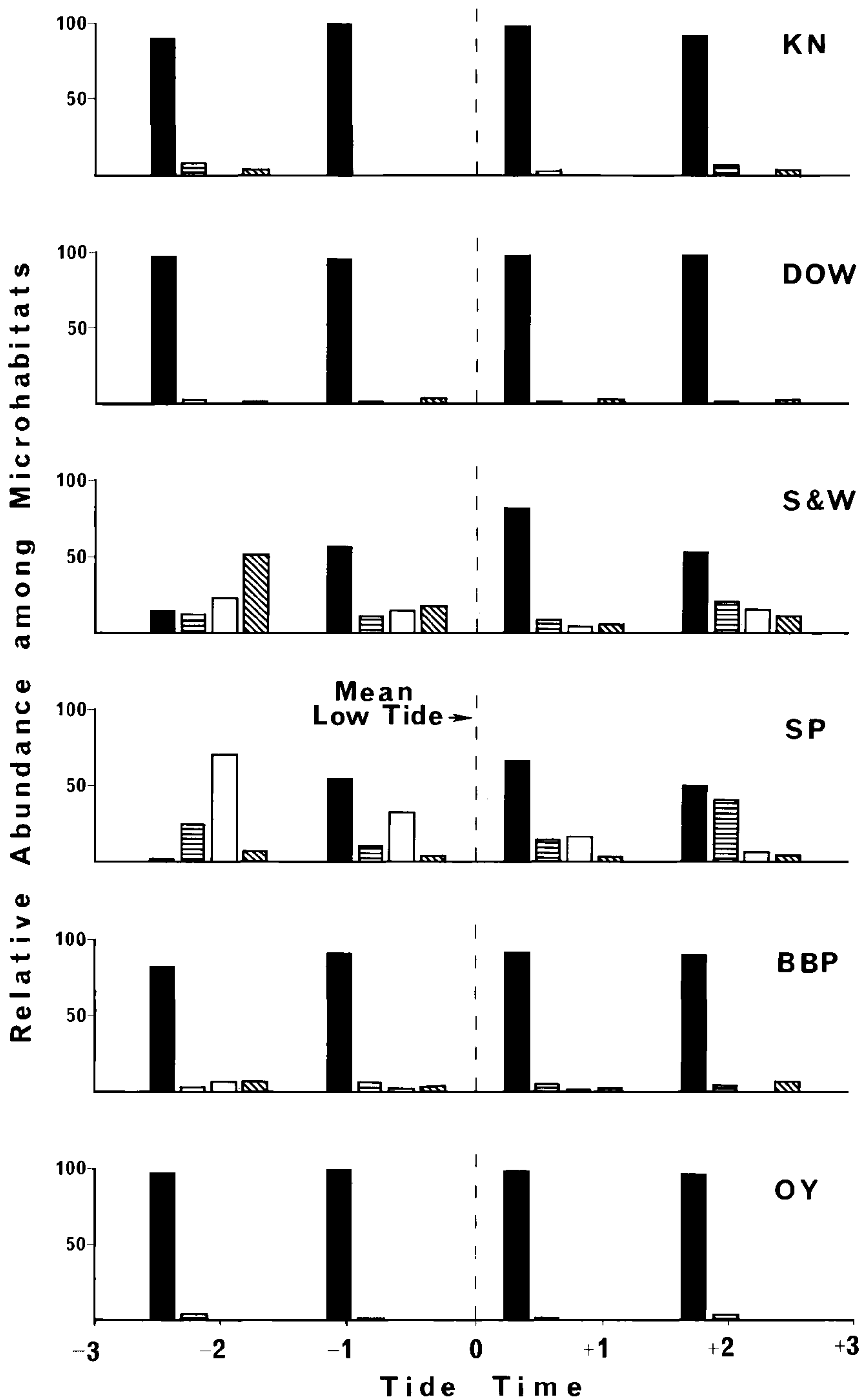

Fig. 8. Within-species summaries of relative abundance among microhabitats on the mudflat as a function of tide time. Data for each species are averaged over each of two equal time periods before low tide and two equal time periods after low tide. Data should be compared with the relative areas of microhabitats available (Fig. 7). Microhabitat designations as in Fig. 7.

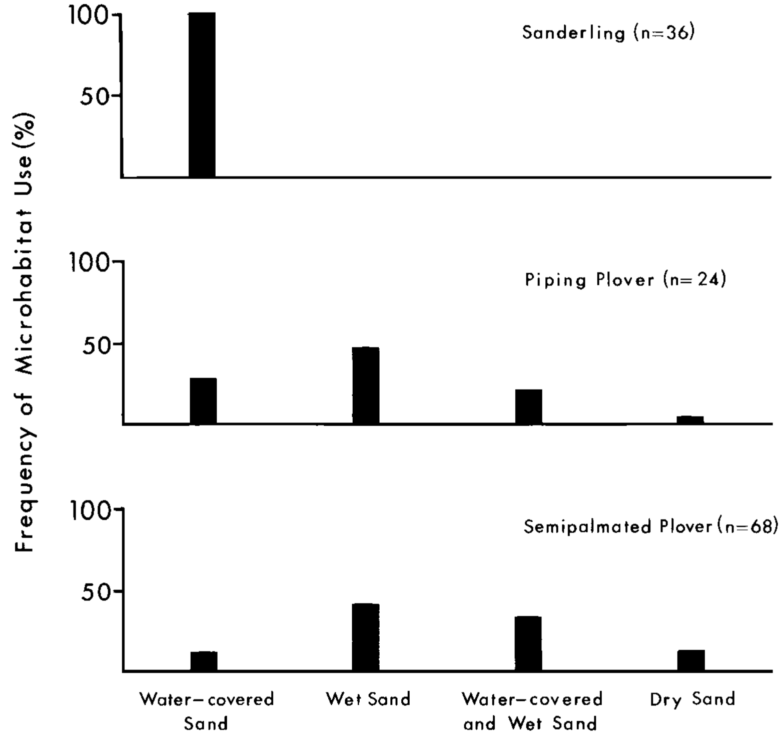

Fig. 9. Within-species summaries of microhabitat use by feeding shorebirds on the outer beach, based on 1-min observations of randomly selected individuals. N represents the number of 1-min samples.

Semipalmated and Piping Plovers fed mainly on the sand above the water line, as on the outer beach. Ruddy Turnstones and Sanderlings frequently fed on the beach up to 10 m from the water's edge. Numbers of feeding birds in this limited zone occasionally reached 150, resulting in higher densities than on either the mudflat or the outer beach. Nearest neighbor distances usually averaged less than 0.6 m except for

TABLE 1

Summary of Habitat Use and Microhabitat Preferences by Feeding Shorebirds[1]

	Mudflat				Outer Beach				Inner Beach	
Species	Algae[2]	Mixed	Sand A	Sand B	Water-covered	Both[3]	Wet	Dry	Water's edge	Sand
Oystercatcher	X	–	–	–	–	–	–	–	–	–
Black-bellied Plover	X	–	–	–	?	?	X	?	X	–
Semipalmated Plover	x	X	X	–	x	X	X	x	–	X
Piping Plover	–	–	–	–	X	x	X	–	–	X
Greater Yellowlegs	X	–	–	–	–	–	–	–	–	–
Willet	–	–	–	–	–	–	–	–	X	–
Dowitcher	X	–	–	–	–	–	–	–	X	–
Ruddy Turnstone	–	–	–	–	–	–	–	–	–	X
Knot	X	x	–	–	X	–	–	–	X	–
Semipalmated Sandpiper	x	x	x	X	–	–	–	–	X	–
Western Sandpiper	X	X	x	x	–	–	–	–	X	–
Sanderling	–	–	–	–	X	–	–	–	X	x

[1] Large X's indicate the most preferred microhabitats and small x's indicate secondary preferences. A dash indicates negligible use. Preference for a microhabitat here implies that birds are disproportionately abundant in that microhabitat relative to microhabitat area.
[2] See Methods for microhabitat descriptions.
[3] Water-covered and wet (see text).

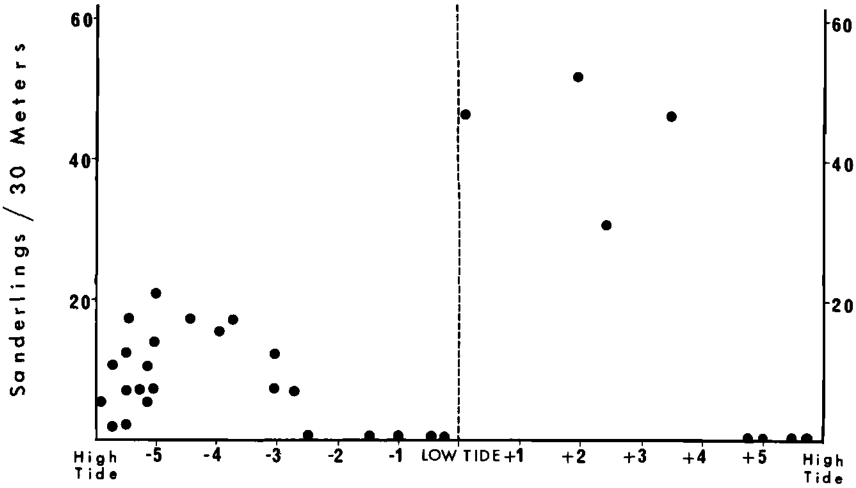

Fig. 10. Changes in the density of feeding Sanderlings on the outer beach as a function of tide time (in hours). Each point represents the average density over a 15-min observation period.

Sanderlings ($\bar{x}$ = 1.2 m). These values were smaller than on the mudflat, where nearest neighbor distances averaged from 1.7 to 4.6 m.

Birds congregated and fed on the inner beach only from 0.5 to 3 hours after high tide. Numbers increased rapidly for 0.5–1 hour after high, reaching a peak of up to 150 birds from 1 to 2 hours after high. By the third hour, most birds had left, and only scattered individuals remained for another few minutes. The spatial and temporal compression of feeding activity at this site suggested a highly localized food source available only near the water's edge during a brief period of time.

DISCUSSION

Habitats in this study showed obvious differences with respect to physical space (large to small), substrate type (sand to mud), vegetative cover (none to algae-covered), and moisture content. Moisture content was controlled mainly by tidal fluctuations and varied from dry, in areas not covered by tides for several days, to saturated, in areas covered by a film of water. Direct wave action was another important environmental factor in the outer beach habitat. All these parameters were either directly or indirectly related to the movements of the tides, which regularly and predictably exposed and covered feeding areas.

In this study we examined how migrating shorebirds use foraging space with respect to habitats, microhabitats, and tidal fluctuations. We found that species showed temporal patterns of foraging activity with respect to tidal fluctuations, and they segregated themselves to varying degrees both among and within habitats. These variations reflect niche specialization patterns among species as well as differential habitat selection.

Spatial segregation.—Our data showed species-specific differences in microhabitat selection as well as gross habitat selection by shorebirds (Table 1). The habitat in which the clearest spatial segregation among species occurred was the habitat with the greatest diversity of identifiable microhabitats, the mudflat. This was partly a by-product of low bird density (average maximum of 42 birds/ha) and intraspecific social attraction on the mudflat. Here we found that intraspecific nearest neighbor

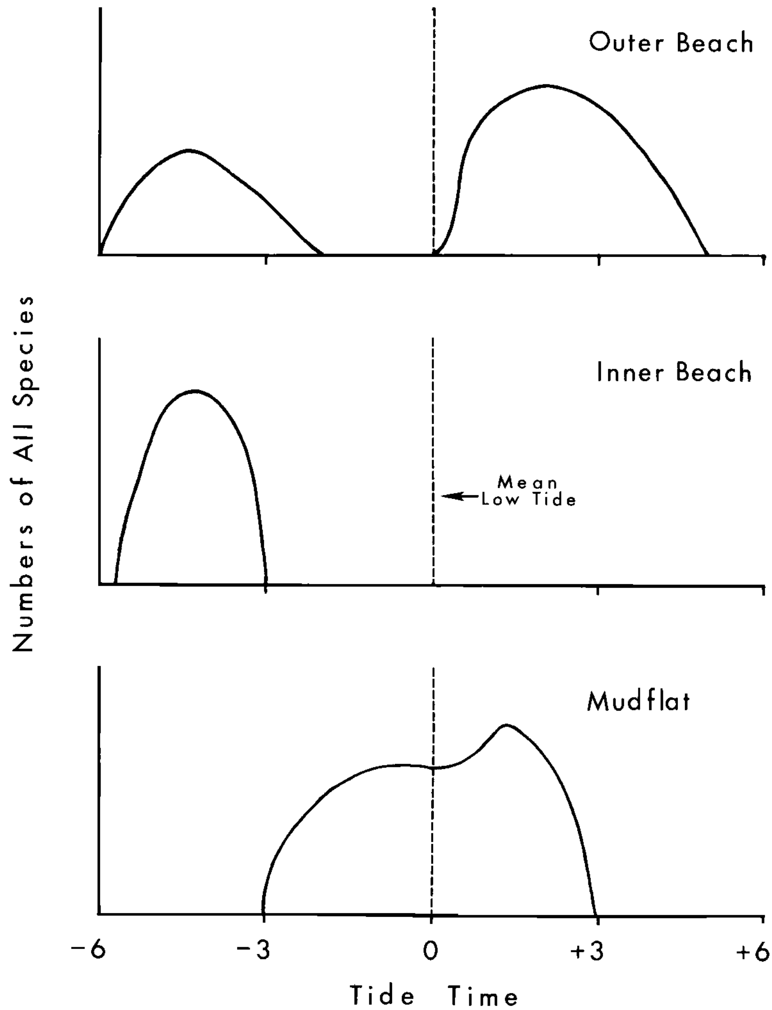

Fig. 11. Schematic summary by habitat of shorebird abundance as a function of tide time.

distances were smaller than interspecific distances, even within microhabitats. However, for most species, the data did indicate statistical preferences for one or more microhabitats (Fig. 3).

Although less segregated spatially, species foraging on the outer beach also showed microhabitat preferences, with plovers preferring damp sand and Sanderlings and Knots preferring water-covered sand. The latter two species showed further spatial segregation within the water-covered zone. Thomas and Dartnall (1971) reported similar zonation of feeding in two other calidridines, *Calidris ferruginea*, which feeds below the water's edge, and *C. ruficollis*, which feeds above it.

The least partitioning of habitat occurred on the inner beach, which also had the highest densities of feeding birds. Wave action on the inner beach was not pronounced and most birds fed near the edge of the gently receding water. Here for example, Sanderlings and Knots had no opportunities to segregate with respect to wave action as on the outer beach. Associated with high bird densities were high levels of aggression, suggesting that competition for food or feeding space was more intense on the inner beach than in the other habitats.

Although the shorebirds in this study were not individually marked, there appeared to be much movement of individuals among the major habitats. The apparent need to exploit several different habitats supports Baker and Baker's (1973) suggestion that many shorebirds encounter less abundant exploitable food resources at lower latitudes than on their arctic or subarctic breeding grounds. In terms of feeding strategies, search time and effort may become a more important factor in the energy budgets of migrant shorebirds (see Schoener 1971).

Shorebirds in our study area were feeding somewhere during all daylight hours except for the hour before high tide (Fig. 11). Any individual bird could optimize its feeding opportunities by moving from one habitat to another at strategic times, but in each habitat it would encounter different feeding conditions with respect to substrate, wave action, wetness, prey species, and other factors. Its feeding efficiency would probably vary among these habitats. Hence one might expect many shorebird species that use tidal feeding sites to evolve flexible foraging strategies and diversified feeding techniques, permitting generally efficient exploitation of most of the food resources. This should be especially true for small species with high metabolic rates and a need to feed more frequently.

Temporal segregation.—We found feeding activity to be a function of tide time rather than time of day (during daylight hours). No nocturnal data were collected. Shorebirds fed on the mudflat for the 6 hour period around low tide (the entire time it was exposed), on the inner beach for the 3 hours following high tide, and on the outer beach after both high and low tides (Fig. 11). Highest concentrations of birds occurred shortly after low tide on both the mudflat and the outer beach and after high tide on the inner beach.

On the inner beach all species fed only during the first 3 hours after high tide. Their sudden disappearance during the 3rd hour may have been related to the exposure of mudflats in the *Spartina* marshes rather than to a sudden reduction in food availability, but it also coincided with a reduced rate of exposure of intertidal space that resulted from a steepening beach slope. Because substantial new areas no longer were being exposed, prey availability may have decreased.

On the outer beach Sanderlings reached peak densities after low and after high tide. Ehlert (1964) found a similar buildup of feeding Sanderlings on Helgoland in the North Sea 2–3 hours after high tide, but he was unable to determine where and to what extent they fed at or near low tide.

On the mudflat Oystercatchers, Dowitchers, and Black-bellied Plovers showed patterns similar to that of Sanderlings on the outer beach. Although the mudflat was exposed only for a 6-hour period around low tide, these species showed bimodal patterns of abundance, with the higher peaks after low tide (Fig. 6). Semipalmated Plovers showed only one peak, which coincided with the highest peak of the other three species. Only Knots reached peak levels before low tide. Interestingly, Knots and Semipalmated Plovers were the only species that fed commonly in all three habitats. The differences between the time-abundance curves of these two species and those of the other three might be a result of preferences for other habitats during certain stages of mudflat exposure. Despite these differences, four of the five species on the mudflat reached peak abundance between 1.5 and 2.5 hours after low tide. Ehlert's (1964) data for Dunlins on extensive tidal flats showed peaks for feeding birds at 1 hour before and 1 hour after low tide. Fewest numbers were recorded about 1 hour after high tide. By analyzing stomach contents he documented the same pattern for quantity of prey items taken. Couch (1966) obtained similar results for stomach contents of several species on intertidal flats in Washington. Stomachs of Sanderlings, Dunlins, Western Sandpipers, and Least Sandpipers (*Calidris minutilla*) contained greatest volumes of food during the first 3 hours after low tide, with somewhat lesser amounts before low tide.

In all these studies, the high densities of birds after low tide suggest that the availability of food is greatest during this period. Recher (1966) proposed that shorebirds should exhibit greatest segregation when food items remain constant or decrease. In our study we found that spatial segregation of species in terms of microhabitat use on the mudflat was somewhat less marked around low tide than at higher water levels. If densities of feeding birds reflect food availability, our data support Recher's suggestion. However, part of the temporal variability we found in microhabitat selectivity can be explained by the physical inability of short-legged species to forage successfully in the wetter microhabitats at high water levels.

In summary, several lines of evidence from our data suggest that niche specialization is occurring in mixed-species aggregates of migrating shorebirds in New Jersey with respect to habitats, microhabitats and temporal response to tidal fluctuations. These factors, together with interspecific variation in body size, feeding methods, and preferred prey items presumably reduce competition within these groups. But to what extent niche differences among these species have evolved in direct response to interspecific feeding competition remains unresolved. The possibility that such differences are competition-induced is suggested by the fact that most shorebirds spend most of the year in mixed-species flocks, and certain species tend to associate consistently. Interactions among shorebirds during the nonbreeding season may be of paramount importance in the evolution of differences among species.

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