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IMPORTANCE OF BEACH, MUDFLAT AND MARSH HABITATS TO MIGRANT SHOREBIRDS ON DELAWARE BAY

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Abstract
Shorebirds migrate over long distances from breeding to wintering grounds, stopping at a few bays and estuaries to refuel. Most information on migration of shorebirds concentrates on population dynamics and foraging behavior on intertidal habitats. We studied the behavior of shorebirds on mudflats, beaches and marshes on Delaware Bay to understand how they use different habitats. Dense flocks of shorebirds concentrated on a tidal mudflat, but shorebirds used all the habitats, including several marshes. The overall percent of shorebirds feeding ranged from 34% (open beach), and 59–63% (tidal and non-tidal marshes), to 80% (tidal mudflat). Variations in the percentage of shorebirds engaged in feeding, resting and other behaviors depended on location, date, time, tide and species. A higher percentage of shorebirds fed during the middle of migration, in early to mid-morning, and during low and rising tides than at other times. Some shorebirds fed on the marshes and mudflats during all tidal states, but none fed on beaches at high tide (beaches were too narrow). Within each habitat, the highest percentage of shorebirds engaged in foraging during low tide (marshes) or rising tides (mudflats and beaches). Using the percentage of shorebirds engaged in foraging as an indication of foraging value for each habitat type within the landscape, we concluded that a mosaic of habitat types ranging from mudflats to high marshes is essential to sustain the high populations of shorebirds that use Delaware Bay during spring migration. Copyright © 1996 Published by Elsevier Science Limited

Keywords: shorebirds, habitats, migrants, mudflat, beach, landscape.

INTRODUCTION

Shorebirds, Charadrii are conspicuous members of coastal avifaunas, particularly during spring and fall migration in large estuaries. Most shorebirds are trans-equatorial migrants, and many travel from the high Arctic to the southernmost reaches of Africa and South America (Burger & Olla, 1984; Hockey *et al.*, 1992). While on migration, shorebirds concentrate on extensive coastal wetlands, and migrating or wintering numbers in individual estuaries may reach 100 000–200 000 on any given count (Burger & Olla, 1984). Only four estuarine systems in North America support more than one million shorebirds during migration: Copper River Delta in Alaska; Grays Harbor in Washington; Bay of Fundy between Nova Scotia and New Brunswick; and Delaware Bay between New Jersey and Delaware (Senner & Howe, 1984; Myers *et al.*, 1987). During staging on the Copper River Delta, spring shorebird numbers reach 20 000 000 (Isleib, 1979). In the continental United States, however, Delaware Bay has the highest number of spring migrants, with single counts reaching 270 000 (Clark *et al.*, 1993). Thus it is a critical habitat for the conservation of North American shorebirds.

Studies on migrating shorebirds have concentrated on population censuses and foraging behavior on mudflats and rocky intertidal zones (Goss-Custard, 1980; Burger, 1984, 1986*a*; Aterstam *et al.*, 1992). Although some authors (Burger *et al.*, 1977; Myers *et al.*, 1980; Connors *et al.*, 1981) specifically examined habitat partitioning in shorebirds on beaches and mudflats, habitat use of marshes has been ignored. Most shorebird studies have focused on local scales, and on single mudflats or beaches. Yet studies should encompass a mosaic of habitat patches to determine overall habitat use (Dunning *et al.*, 1992). Wintering habitat use within small estuaries, such as Bodega Bay, California (Connors *et al.*, 1981), Jamaica Bay, New York (Burger & Gochfeld, 1983) and the Wash, England (Goss-Custard, 1977*a*,*b*), has been studied, but few data are available on habitat use within extensive migratory stopover systems such as Delaware Bay. In this study, we examine how shorebirds use marshes, mudflats and beaches on Delaware Bay and adjacent New Jersey. We were interested particularly in documenting whether they fed extensively on marshes, and if these marshes were used only for resting during high tides.

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Most authors note that shorebirds feed on exposed intertidal areas at low tide, and roost in fields, marshes and bays at high tide (Pitelka, 1979). Although almost all studies note the importance of tide in the daily foraging cycle of shorebirds (Connors *et al.*, 1981), few report foraging at high tide when beaches are unavailable. None includes marshes as important foraging sites during any tidal stage.

Most of these studies report numbers of shorebirds present by habitat, but there are few data on the percent of birds engaged in different activities as a function of habitat. We undertook this study to determine whether shorebirds used marshes extensively for foraging. If so, then they may be essential foraging habitats and not just convenient, safe roosting areas. Moreover, the marshes may be critical habitats that are necessary for conservation of migrant shorebirds in Delaware Bay, and without them shorebirds may be unable to obtain enough food.

Delaware Bay is a critical staging area for many species of shorebirds that concentrate in the spring to feed on the eggs of horseshoe crabs *Limulus polyphemus* (Senner & Howe, 1984; Castro *et al.*, 1989). The importance of Delaware Bay was discovered in the early 1980s and extensive work there has concentrated on documenting maximum numbers along the beaches, on foraging behavior and on conservation issues (Dunne *et al.*, 1982; Burger, 1986*b*; Myers, 1986, 1989). The adjacent marshes were considered only as roosting areas for shorebirds during high tides or at night, but in this paper we document their importance as an integral part of shorebird foraging strategy, particularly for some declining species such as sanderling *Calidris alba* and semipalmated sandpipers *C. pusilla*. Moreover, a significant proportion of the population of red knots *C. canutus* moves through Delaware Bay (Howe *et al.*, 1989; Clark *et al.*, 1993). The relative importance of marshes suggests the need to preserve and protect them for the conservation of migrant shorebirds that move through Delaware Bay. Moreover, since land acquisition decisions are forthcoming, it is imperative to understand which habitats serve an important role in shorebird foraging ecology.

STUDY AREA AND METHODS

Our overall research plan was to survey five specific Delaware Bay and Atlantic marsh and beach habitats to examine habitat use and behavior of shorebirds during the spring migration. These marshes were selected to be typical of the overall habitat in the region, based on aerial surveys of the entire region over an 8-year period (Clark *et al.*, 1993). Factors that were used to determine that these sites were representative included the species and percent cover of vegetation, elevation, percent and distribution of open water and shorebird use. In our 8 years' of experience, shorebirds using the marshes were almost always spread out over the whole marsh complex. As these factors make sampling difficult, they have accounted for the failure of shorebird biologists to study these habitats. None the less, in total, they are extremely important. The results reported in this study are part of a New Jersey state program to understand shorebird population dynamics, behavior and habitat use on Delaware Bay and adjacent Cape May peninsula and to develop an overall conservation program for shorebirds. As part of the program, regular aerial surveys of beaches and mudflats were conducted, and these flights documented the movement of shorebirds among our study sites (Clark *et al.*, 1993). Whereas Clark *et al.* (1993) document the abundance of shorebirds on different beaches and the movement of birds between beaches and marshes, they do not examine foraging behavior in the different habitat types.

The shorebird migration through Delaware Bay is synchronous, and occurs from mid-May to the first week in June each year (Clark *et al.*, 1993). During the peak period of spring migration (22 May–4 June) in 1991 and 1992, we studied shorebird behavior at two marshes on the Atlantic Ocean side, a marsh on the Delaware Bay side, and at a beach and mudflat site on Delaware Bay (Table 1; Fig. 1). Although the study sites differed in size, we observed birds only in an area 200×200 m. The maximum distance among sites was between Stone Harbor and Moore's Beach (22 km). The beach site received direct tidal surf, while the mudflats and some of the marshes received tidal waters daily. Atlantic Marsh and Dennis Creek were largely non-tidal in that the ponds in this high marsh were flooded only during excessively high tides occurring once or twice a month.

In 1991, observers were situated in three habitat types: Delaware Bay mudflat (West Creek); Delaware Bay beach (Moore's Beach); and at a coastal marsh (Atlantic Marsh at Stone Harbor) for periods of from 2–5 h per day. In 1992, observers surveyed two habitats: Delaware Bay marsh (Dennis Creek); and Stone Harbor marsh. Data were taken in 2–3 h sample periods (1 or 2 per day per marsh) during different tidal states.

All shorebirds were counted and their behavior noted in scan samples every 20 min. The information collected on different days in the same habitat is independent because the species composition and number of birds present varied markedly from day to day and hour to hour, indicating that the same birds were not returning to the same marshes on successive days.

We focus on the seven most abundant species: semipalmated sandpiper; sanderling; red knot; dunlin *Calidris alpina*; semi-palmated plover *Charadrius semipalmatus*; ruddy turnstone *Arenaria interpres*; and dowitcher *Limnodromus griseus*. The following data were recorded before each scan sample: location; date; time of day; habitat; tide state (high, falling, low, rising); species; and number of birds present. Then, in successive scan samples, we recorded the percentage of

Table 1. Description of shorebird study sites on Cape May peninsula, New Jersey

Location	System	Year of study	Habitat	Tidal conditions	Number of samples	Mean number of shorebirds feeding	Percentage of shorebirds feeding	Mean number of all shorebirds	Overall percentage of shorebirds present
Moore's Beach	Delaware Bay	1991	Beach	Direct surf	399	21 ± 55	45	47 ± 168	9
West Creek	Delaware Bay	1991	Mudflat	Tidal	399	232 ± 1214	65	357 ± 1414	69
Stone Harbor	Atlantic Ocean	1992	Marsh	Tidal	224	20 ± 46	59	34 ± 65	6
Dennis Creek	Delaware Bay	1992	Marsh	Tidal to non-tidal	301	30 ± 77	62	48 ± 100	9
Atlantic Marsh	Atlantic Ocean	1991	Marsh	Non-tidal[a]	119	23 ± 85	63	36 ± 99	7

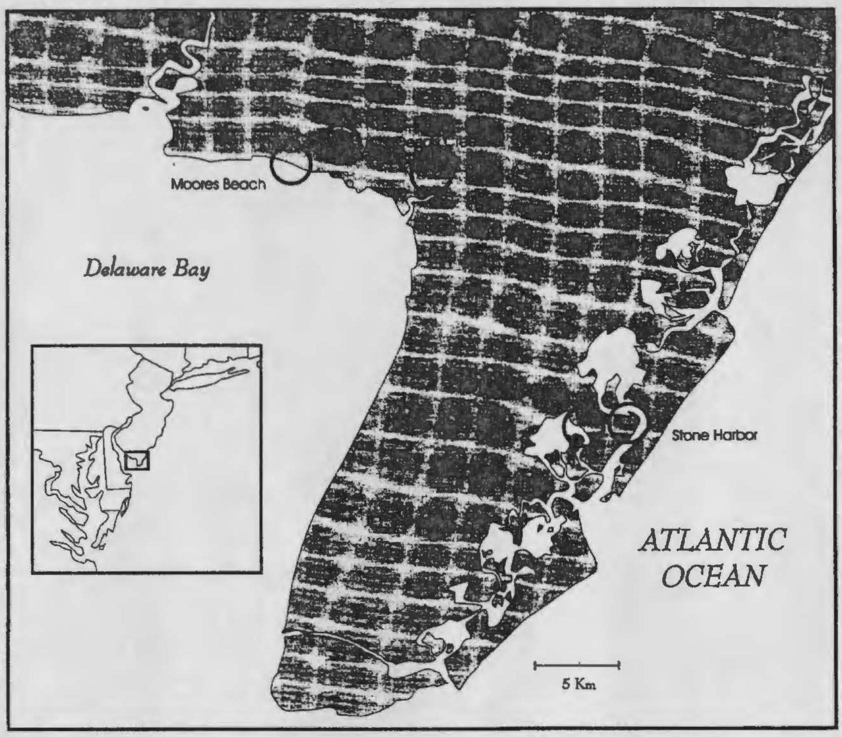

Fig. 1. Map of study sites.

shorebirds that were feeding, alert and resting. To determine the total number of shorebirds present, we summed the total of each species present during any given scan sample period. In both years, tidal state was determined both in the field and from tide charts.

In this paper, we examine both site and habitat effects on use and behavior because the degree of tidal flooding in marshes varied from nearly daily inundation to inundation only during the most extreme storm tides (Atlantic Marsh). Although we use models to examine how the factors interact, we also use a univariate presentation of data to allow for an understanding of shorebird response to specific factors.

We used multiple linear regression procedures on ARC-SINE transformed data (PROC GLM; SAS, 1985) to examine the effects of the independent variables (location, date, tide, time) on the behavior of shorebirds. In all cases, models were constructed using the raw data (rather than percentages). Then we used regression procedures to examine the effects of the independent variables on the most abundant species.

The models procedure determines the contribution of the first variable, and then determines the contribution of the second and subsequent variables on the r^2 (SAS, 1985). Thus, if two independent variables are highly correlated, only the variable giving the highest r^2 is entered in the model. The model selection procedure gives the r^2, F-value, and levels of significance for the model, and F-values and levels of significance for each significant variable. In these analyses, we used each scan sample as an independent sample. We found that there is rapid turnover in the numbers and species composition over a 20-min period. Although most birds may be feeding during one scan sample, during the next 20 min, they may mostly be resting due to changing available foraging habitat.

We also use Kruskal–Wallis χ^2 tests to determine whether variables differ significantly among habitats, localities, or tide states. This univariate approach was used only after regression procedures indicated a significant effect of that independent variable. Unless otherwise noted, we present means ± 1SD in the text and tables.

RESULTS

All shorebirds

Nearly 68% of all shorebirds studied were at West Creek (the tidal mudflat), and the rest were fairly evenly divided among the other sites (Table 1). Within each location, the overall percent of shorebirds that were feeding ranged from 45 (Moore's Creek beach) to 65% (West Creek mudflat).

The models for all shorebird species combined explained 36–49% of the variation in the percent of shorebirds feeding, alert, or resting (Table 2). For feeding and resting, all six independent variables were significant in explaining variations. Tide did not contribute to explaining variations in alert behavior (Table 2). Shorebirds engaged in more feeding in the middle of the migration period (26–29 May, 64%) compared to earlier (52%) or later (59%). The percentage of shorebirds feeding at different times of the day for all sites usually varied from 38 (16:00 h) to 86% (09:00 h, Table 3). Most shorebirds were flying around from 07:00 to 08:00 h, and no more than 30% of the shorebirds were resting at any time of day (Table 3).

Location influenced shorebird behavior (Table 2). The percentage of birds engaged in foraging was lowest on Moore's Beach (45%), and varied from 59–65% for the other sites (Fig. 2). The percentage of shorebirds resting increased along the tidal gradient. A significantly higher percentage of shorebirds fed on mudflats (65%) than on beaches (45%) or marshes (61%, $\chi^2 = 15{\cdot}9$, $d.f. = 1$, $p < 0{\cdot}001$).

Table 2. Models explaining variations in the percentage of shorebirds feeding, alert and resting

	Feeding	Alert	Resting
Model			
F	8·56	7·96	11·46
p	0·0001	0·0001	0·0001
r^2	0·42	0·36	0·49
d.f.	6,552	6,552	6,552
Independent variables entering the model (*F*, *p*)			
Location	10·15 (0·0001)	30·9 (0·0001)	39·1 (0·0001)
Date	11·50 (0·0001)	2·3 (0·007)	14·5 (0·0001)
Tide	20·03 (0·0001)	NS	14·0 (0·0001)
Time	2·7 (0·0008)	11·1 (0·0001)	5·1 (0·0001)
Species	7·13 (0·0001)	2·2 (0·03)	7·5 (0·0001)
Location × tide	8·1 (0·0001)	NS	5·5 (0·0001)

NS, not significant.

Shorebird activity also varied by habitat and tide stage (Table 4). In general, a higher percentage of the birds that were present fed at low tide in marshes, rising and falling tides on mudflats, and on rising tides on beaches. The pattern is clearer in examining resting behavior; shorebirds seldom rested on the beach, and they rested at low tide on mudflats and at high tide on marshes.

When tide is examined for all sites, it is clear that shorebirds feed mainly at falling, low and rising tides, and rest at high tide (Fig. 3). Although the total number of shorebirds foraging during rising tides ($\bar{X} = 1812$) was considerably higher than at other tidal states ($\bar{X}$ for high tide = 83), it must be remembered that the shorebirds are concentrated on a rising tide at the very few available mudflats, but can spread out during high tide over vast areas of marsh. Very few shorebirds were alert during this study (< 8% during all tides). Many, however, were engaged in running or flying, particularly during high and falling tides.

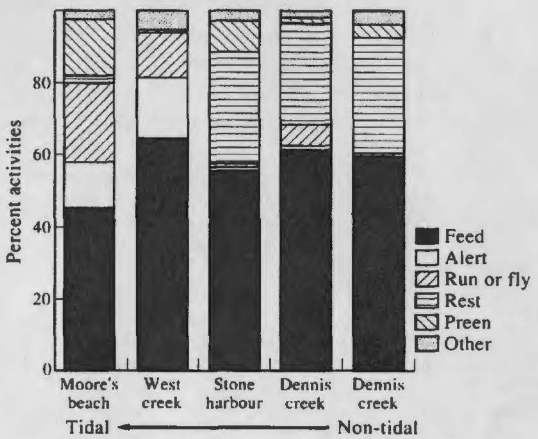

Fig. 2. Percentage of shorebirds engaged in a variety of activities at the study sites.

Table 3. Effect of time of day on shorebird behavior (means ± SD)

Time of day	Number of samples	Mean number of birds	Percent feeding	Percent resting	Percent flying
06:00	42	0·2 ± 0·8	0	0	0
07:00	84	0·6 ± 3·7	56	8	17
08:00	56	0·1 ± 0·7	50	0	50
09:00	63	5 ± 20	86	0	10
10:00	77	39 ± 96	74	10	5
11:00	126	33 ± 75	60	20	3
12:00	133	43 ± 89	63	20	5
13:00	77	47 ± 94	69	19	7
14:00	105	76 ± 194	53	26	10
15:00	154	63 ± 188	50	19	8
16:00	133	54 ± 156	38	20	5
17:00	161	224 ± 821	54	14	8
18:00	168	355 ± 1362	61	23	2
19:00	63	792 ± 2413	57	29	7

Table 4. Percentage of shorebirds engaged in feeding and resting by habitat and tide state

Habitat	Fall	Low	Rise	High	$\chi^2(p)$
Marsh					
Feed	60	88	72	19	36·1 (0·0001)
Rest	29	7	28	62	30·3 (0·0001)
Mudflat					
Feed	68	53	79	54	9·3 (0·05)
Rest	9	18	8	0	2·7 (NS)
Beach					
Feed	37[a]	48	79	—[b]	7·2 (0·007)
Rest	3	5	1	—	NS

[a]Another 21% are running or flying.
[b]None present.
NS, not significant

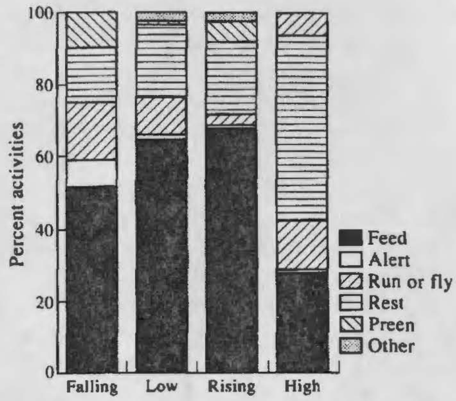

Fig. 3. Percent of shorebirds engaged in a variety of activities as a function of tide state. Relative numbers of shorebirds feeding as a function of tide state are shown in Table 7.

Individual species

We constructed models for foraging of the most abundant species (Table 5). Between 53 and 84% of the variation in the percent of individuals engaged in feeding was due to location, date, tide and time of day. For all models (except for dunlin and dowitcher), location was the most significant variable (i.e. had the highest F-value), and location × tide entered five of the seven species models as a significant variable.

The percentage of each species using individual study sites varied (Kruskal–Wallis $\chi^2 = 4000$, $p < 0{\cdot}0001$), and differed from the overall percent for all shorebirds combined (Table 6). The differences were greatest for dunlin, dowitchers and sanderlings. A higher than expected percentage of sanderlings used West Creek, but a lower percentage of dunlin and dowitchers did (both used Dennis Creek extensively). Stone Harbor also was used more extensively by semi-palmated plover and dunlin, and Atlantic Marsh was used by turnstones and knots more than expected on the basis of the overall pattern.

Table 5. Models explaining variation in percentage of each species engaged in feeding

	Semi-palmated sandpiper	Semi-palmated plover	Sanderling	Dunlin	Ruddy turnstone	Red knot	Dowitcher
Model							
F	7·56	4·66	2·50	2·96	4·35	2·79	7·03
p	0·0001	0·0001	0·02	0·0001	0·0001	0·0006	0·0001
r^2	0·70	0·68	0·68	0·53	0·68	0·60	0·84
d.f.	33,135	17,37	17,24	26,88	20,54	23,58	23,38
Independent variables entering model (F, p)							
Location	19·1 (0·0001)	14·5 (0·0001)	3·4 (0·05)	NS	14·6 (0·0001)	5·7 (0·0006)	4·9 (0·003)
Date	8·3 (0·0001)	4·2 (0·0001)	NS	6·0 (0·0001)	NS	4·3 (0·001)	21·0 (0·0001)
Tide	16·7 (0·0001)	3·9 (0·02)	2·5 (0·06)	NS	NS	NS	5·9 (0·001)
Time	2·3 (0·0008)	2·7 (0·02)	3·1 (0·01)	NS	3·2 (0·004)	NS	2·5 (0·01)
Location × tide	3·2 (0·003)	NS	NS	3·3 (0·009)	2·6 (0·05)	2·6 (0·03)	2·5 (0·07)

NS, not significant.

Table 6. Percentage of shorebirds at the different study sites — overall the distribution of shorebirds varied among species

	Moore's Beach	West Creek	Dennis Creek	Stone Harbor	Atlantic Marsh	Kruskal–Wallis $\chi^2(p)$ comparing each species to all shorebirds[a]
All shorebirds	10	68	9	6	7	—
Semi-palmated sandpiper *Calidris pusilla*	15	74	4	4	3	0·0001
Semi-palmated plover *Charadrius semipalmatus*	0	73	7	20	0	0·0001
Sanderling *Calidris alba*	2	98	0	0	0	0·0001
Dunlin *Calidris alpina*	2	32	51	15	0	0·0001
Ruddy turnstone *Arenaria interpres*	11	80	1	1	7	0·0001
Red knot *Calidris canutus*	8	85	1	1	5	0·0001
Dowitcher *Limnodromus griseus*	0	51	47	1	1	0·0001

[a]All Kruskall–Wallis χ^2 above 9000.

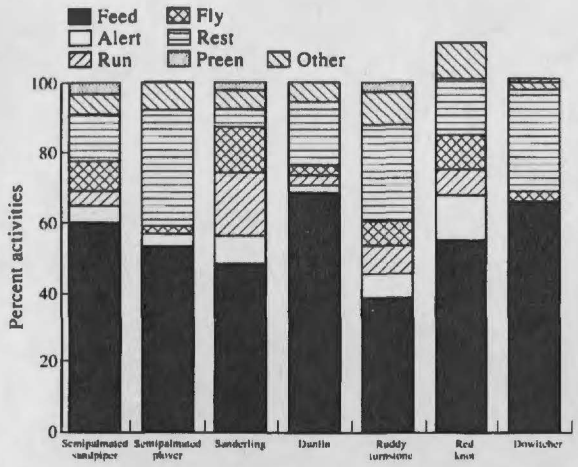

Fig. 4. Percentage engaged in various activities by species. Species are arranged in increasing size, with semi-palmated sandpiper being the smallest.

The percentage of individuals engaged in different activities varied by species (Fig. 4). Generally, the smallest and the largest species had the highest percentage of individuals engaged in feeding, and the fewest individuals engaged in preening. The percentage of shorebirds resting and preening, i.e. clearly not engaged in feeding or the pursuit of prey, was much higher for semi-palmated plover (41%) and ruddy turnstones (37%) than the other species (all less than 30%, Fig. 4). Both of these species are predominantly visual foragers that often probe for larger prey items than the other species.

Overall, the mean number of birds engaged in feeding varied by tidal stage (Table 7). Highest numbers of all species except semi-palmated plover, dunlin and dowitchers fed on rising tides compared to other tides. Almost no turnstones and knots fed at low tide, and no sanderlings fed at high tide (Tables 7 and 8).

The percentage of shorebirds resting also varied as a function of tide state (Table 9). Most species rested at

Table 7. Mean (±SD) number of birds engaged in feeding as a function of tide for all study sites

	Falling tide	Low tide	Rising tide	High tide	Kruskal–Wallis $\chi^2(p)$
Semi-palmated sandpiper	77±135	84±139	1210±2452	24±26	24·5 (0·0001)
Semi-palmated plover	3±11	86±356	6±13	6±13	13·1 (0·01)
Sanderling	6±31	2±10	357±1666	0±0	5·9 (NS)
Dunlin	38±78	40±125	33±62	16±23	3·1 (NS)
Ruddy turnstone	13±30	0±0	82±261	7±25	15·1 (0·004)
Red knot	7±22	0±1	80±242	10±38	21·3 (0·0003)
Dowitcher	13±54	28±82	22±104	4±7	6·5 (NS)

NS, not significant.

Table 8. Percentage of shorebirds feeding on different tidal states

	Falling tide	Low tide	Rising tide	High tide	χ^2 value (p)
Semi-palmated sandpiper	49	76	83	23	19·8 (0·0001)
Semi-palmated plover	53	74	52	15	9·4 (0·02)
Sanderling	38	63	58	[a]	8·2 (0·02)
Dunlin	71	61	70	44	NS
Ruddy turnstone	37	2	48	22	3·4 (0·01)
Red knot	53	20	59	48	NS
Dowitcher	60	75	79	28	NS

[a]Too small a sample for analysis.
Given are Kruskal–Wallis χ^2 values on raw data; NS, not significant.

Table 9. Percentage of shorebirds resting on different tidal states

	Falling tide	Low tide	Rising tide	High tide	Kruskal–Wallis $\chi^2(p)$
Semi-palmated sandpiper	12	7	7	52	26·3 (0·0001)
Semi-palmated plover	29	19	34	67	9·7 (0·02)
Sanderling	2	4	20	[a]	13·8 (0·0001)
Dunlin	12	23	19	47	16·7 (0·002)
Ruddy turnstone	18	87	36	65	10·7 (0·002)
Red knot	10	57	25	15	6·1 (NS)
Dowitcher	37	15	21	55	NS

[a]Too small a sample for analysis.
NS, not significant.

Table 10. Percentage feeding as a function of habitat and tide for several species

	Falling tide	Low tide	Rising tide	High tide	$\chi^2(p)$
Semi-palmated sandpiper					
Mudflat	82	45	81	43	8·5(0·05)
Beach	38		79		8·1(0·006)
Marsh	57	92	84	19	45·1(0·0001)
Dunlin					
Mudflat	96	31	71	—	8·8(0·03)
Beach	64		100		NS
Marsh	73	92	67	44	14·1(0·002)
Ruddy turnstone					
Mudflat	58	86	66	31	NS
Beach	39		60		NS
Marsh	7	2	0	19	NS
Sanderling					
Mudflat	66	42	85	0	6·0(0·05)
Beach	34		79		NS
Marsh		78	10		5·9(0·07)

NS, not significant.

high tide, except for red knot that rested at low tide. Clearly, shorebirds present in mixed species groups behave differently.

For three of the four most abundant species, the percentage of individuals feeding by tide state and habitat varied significantly (Table 10). Ruddy turnstones did not show significant differences in the percentage feeding as a function of tide for any habitat. The differences in percentage feeding were most pronounced for marshes and mudflats, rather than beaches.

DISCUSSION

Factors affecting habitat use

Time of day

Shorebirds whose activities are closely linked to tides are affected by time of day. Both the duration of feeding (Ehlert, 1964) and shorebird numbers (Burger, 1984) vary by time of day, although McLachlan *et al.* (1980) found that sandplover *Charadrius marginatus* numbers did not vary by time of day, but sanderling numbers did. These studies censused shorebird numbers and did not record behavior. Even when no daily differences in numbers were reported, differences in behavior might exist. That is, shorebirds may show differences in the ratio of number feeding to number resting at different times of day. We found that time of day, season, tide, location and habitat contributed significantly to explaining the percentage of shorebirds engaged in feeding, resting and being alert. We suggest that it is essential to examine the behavior of shorebirds on all habitats before a meaningful conservation or land-acquisition plan can be developed.

Habitat and location

Night foraging is one viable option for increasing foraging time (Evans, 1979; Hartwick & Blaylock, 1979; Dugan, 1981; Pienkowski, 1982; Robert & McNeil, 1989; Robert *et al.*, 1989); and using alternate habitats when beaches and mudflats become unavailable during high tide is another. Although most shorebird studies focus on mudflats and beaches (Burger, 1984), our study clearly documents the importance of marshes for foraging in several species. In this study, we examined shorebird behavior in three habitats: beach, mudflats, and marshes. Our data indicate that all three habitat patch types are important, albeit at different tidal states. Although the relative importance for feeding and resting varies among species, most species used all habitats during some tidal states. Overall shorebird behavior and total numbers present did not vary markedly among the three marshes we studied, but particular species used these marshes differently. Dowitchers and dunlin used Dennis Creek nearly one-half of the time, and turnstones and knots used Atlantic Marsh more frequently than the other species. These differences depend only on the relationship of habitat use within each species, and thus correct for relative abundance among species. The differences in use between Stone Harbor marsh and Atlantic Marsh suggests that there may be a yearly difference (these sites were studied in different years), or that a more fine-scale habitat and behavioral analysis is required.

At first glance, the total number of shorebirds using mudflats was greater than any of the three marshes. However, the total amount of mudflats on Delaware Bay is small (limited to around creeks), concentrating the shorebirds in these few areas. By contrast, there are extensive salt marshes all along the narrow beaches. Since the shorebirds leave the mudflats and beaches entirely at high tides, we hypothesize that they are spreading out over the marshes. We feel our estimate that 50–63% of the shorebirds present on marshes are feeding may be indicative of shorebird behavior over the extensive, unsampled marshes; the marshes are serving an important conservation function.

Habitat and tide

Tide is the major factor influencing the distribution, abundance and behavior of shorebirds (Evans, 1979; Burger, 1984, 1986*a*; Brennan *et al.*, 1985). Tide affects both the amount of foraging space and the availability of prey (Recher, 1966; Evans, 1979; Puttick, 1980). In this study, shorebirds fed in all habitats, at all tidal states, except when mudflats were covered with water at high tide. The percentage of shorebirds feeding during the different tidal states ranged from 37 to 79% on the beach, from 53 to 79% on the mudflat, and from 19 to 88% on the marsh, suggesting that each habitat was important for foraging during nearly all tidal stages.

The relatively low percentage of birds feeding on the beach bears examination since beaches are often preferred habitats for shorebirds (Burger *et al.*, 1977). Our data indicate a higher percentage of shorebirds running or flying on the beach and mudflat than on the other habitats, which could reflect that birds run or fly to avoid people or predators, or to search for prey or suitable foraging sites. We defined feeding as those shorebirds actually engaged in searching for prey or pecking. Some of the time shorebirds ran and flew was undoubtedly part of finding more suitable feeding sites. Alternatively, the shorebirds could spend more time running and flying at Moore's Beach and West Creek because they were disturbed by people or predators (Burger, 1986*b*; Myers, 1989).

The species that we studied use Delaware Bay as a stopover on their way to Arctic breeding grounds in Canada. The high shorebird numbers on Delaware Bay in the spring occur over only a 3-week period (Clark *et al.*, 1993), and marked individuals may remain for up to 9 days (Niles & Clark, unpublished data). No other extensive stopover area is known between their wintering and their breeding grounds (Myers *et al.*, 1987). The primary attraction, horseshoe crab eggs, are available only in late May and early June (Myers, 1986), and the shorebird migration coincides with this peak in prey availability. The shorebirds must arrive on their northern breeding grounds in sufficient time to breed in the short Arctic summer. Selection pressures are high to arrive with some fat reserves to allow for rapid egg production. Thus, shorebirds stopping on Delaware Bay in late May and early June must obtain as much energy reserves as possible in as little time as possible (Myers, 1989). Any strategy that allows them to feed nearly all day, regardless of tide state, would be adaptive. We suggest that the shorebirds in Delaware Bay in spring migration feed nearly all the time, and rest only minimally, even during high tide.

Landscape considerations

The importance of different patches for ecological systems has resulted in the development of landscape ecology (Bormann & Likens, 1979; Forman & Godron, 1981, 1986; Addicott *et al.*, 1987; Turner, 1989; Wiens, 1989; Dunning *et al.*, 1992). We believe landscape-scale processes are important for shorebird use of Delaware Bay where there is a mosaic of beaches, tidal creeks and marshes adjacent to the Bay and the Atlantic Ocean, which are separated by houses and human development. These habitats form patches that provide the resources for one of the largest concentrations of migrant shorebirds in the world (Myers, 1986; Clark *et al.*, 1993).

In addition to the massive resource provided by spawning horseshoe crabs, we hypothesize that the mosaic of habitat patches on Cape May peninsula is essential to maintain the large migrant shorebird population. Although the horseshoe crabs are not limited as a resource, access to this resource is limited by tide state, human disturbance and the sheer numbers of feeding shorebirds. During high tides, no eggs are available because only dry sand is exposed, and around high tide there is limited vertical space. Given the distribution of patches (beach, mudflats, creeks, marshes) along Delaware Bay and on the Cape May peninsula, and their relative suitability for feeding and resting, it appears that shorebirds must move between patches with changes in tidal cycle.

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