Feeding Ecology of Western Sandpipers, *Calidris mauri*, and Dunlins, *C. alpina*, during Spring Migration at Hartney Bay, Alaska

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The food habits and feeding ecology of Western Sandpipers (*Calidris mauri*) and Dullins (*C. alpina pacifica*) were compared during two spring migrations at Hartney Bay, Alaska. Their use of the intertidal mud flats overlapped in space and time, but we found important behavioral and dietary differences. Dunlins rested during high tides and fed most heavily during falling tides, usually at the water's edge. Western Sandpipers tended to feed continuously between successive high tides, and were not concentrated at the water's edge. When few or no Dunlins were present, Western Sandpipers shifted their distribution so that a greater proportion fed near the water's edge. Western Sandpiper diets were diverse; Dunlins relied most heavily on a single species of clam, *Macoma balthica*. The number of *Macoma balthica* in the size range taken most frequently by Dunlins decreased over the course of the migration.

Key Words: Dunlin, *Calidris alpina*, Western Sandpiper, *Calidris mauri*, clam, *Macoma balthica*, food habits, feeding ecology, migration, evolution, Alaska.

Natural selection during the non-breeding season may act to regulate shorebird populations and to favor morphological and behavioral differences among species (Recher 1966; Baker and Baker 1973). Competition for food or feeding space during migration may be especially important in these processes (Recher 1966; Holmes and Pitelka 1968; Burger et al. 1977; Duffy et al. 1981; Schneider and Harrington 1981). There have been, nonetheless, few comparisons of the ecology of closely related or morphologically similar species strictly during migration (e.g., Bengtsson and Svensson 1968; Wishart et al. 1981). Some investigators have invoked competition to explain differences in the spatio-temporal segregation of *Calidris* sandpipers (Recher 1966; Recher and Recher 1969; Page et al. 1979), yet behavioral and ecological differences among co-existing species are not, in themselves, evidence that such differences result from competition (Wiens 1977).

The Copper-Bering river delta system in south-central Alaska is a migration stopover point simultaneously important to Western Sandpipers (*Calidris mauri*) and Dunlins (*C. alpina pacifica*) (Senner et al. 1981). This paper compares the food habits and habitat use of these species during spring migration, drawing on data originally gathered to describe the use of the Copper River Delta by shorebirds in relation to oil development and transportation in the northern Gulf of Alaska (Senner 1977, 1979). The results of this study also

bear on the potential importance of migration in the evolution of interspecific differences among shorebirds.

Study Area and Methods

Hartney Bay (60° 30′N, 145° 52′W) is located in Orca Inlet and sheltered by the Heney Mountains at the western fringe of the Copper-Bering river delta (C-BRD) system on the northern Gulf of Alaska coast (Figure 1; also Figure 1 *in* Senner et al. 1981: 273). The physiography, climate, and avian habitats of the region were described by Isleib and Kessel (1973). Tides are semidiurnal, averaging 3.5 m, with a marked inequality between successive low waters. The bay is used most heavily by shorebirds when tidal waters cover the 100s of km² of flats exposed at low and mid-tide stages in the main Copper River Delta to the east. This is especially true when strong winds or storms amplify tides on the outer beaches.

Data presented in this paper were gathered primarily during 27 April — 27 May 1976 and 30 April — 26 May 1977. Some data were gathered during 2-6 May 1975.

Transects

Two transects were established perpendicular to the tide for sampling invertebrates, censusing shorebirds, and collecting sandpipers for analyses of their food habits. The transects, measuring 600 x 50 m (I) and 300 x 50 m (II), were located where
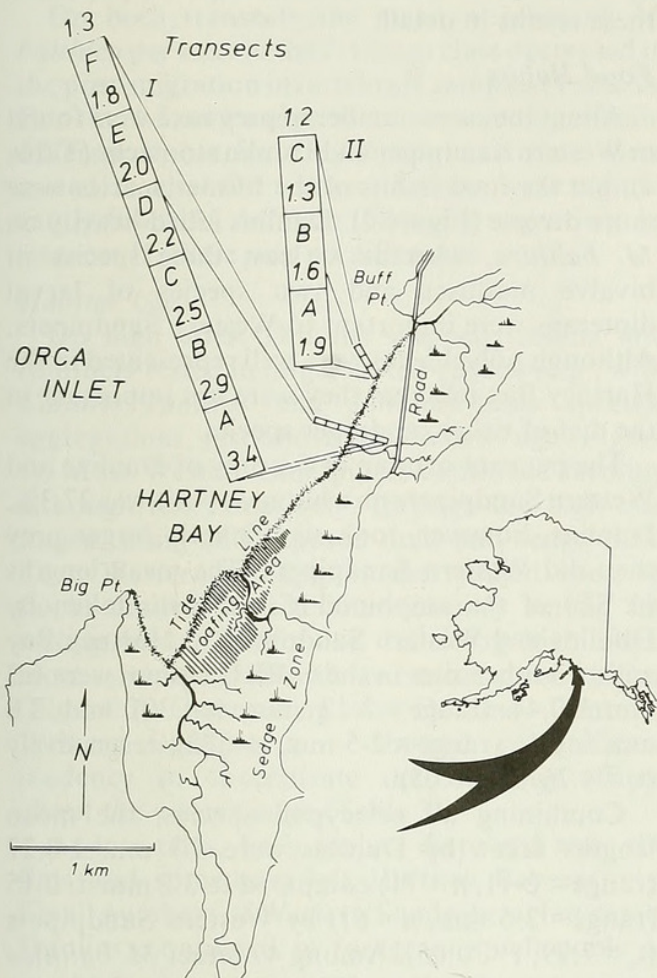
FIGURE 1. Map of the Hartney Bay study site, with an inset showing the location of Hartney Bay in Alaska. The tide line approximates a 3/4 high tide. The enlarged transects show transect numbers, zones, and approximate tidal elevations (m).

feeding shorebirds were concentrated and easily visible from the Hartney Bay road (Figure 1). Because of the distance to it (ca. 1 km) and low-density usage by shorebirds of the lower intertidal zone, the transects did not extend to the mean low water line.

On 1-2 May 1976, prior to the main sandpiper migration, and on 25 May, after the main migration, we sampled the invertebrates on each transect using a stratified random scheme and a 5 x 20 x 3 cm steel frame (*details in* Senner 1977). Faunal samples were washed through a 1 mm screen, and all specimens were sorted, counted, weighed, and identified to the lowest taxonomic level possible. Lengths of all bivalve molluscs were measured to the nearest mm.

Based on the sizes of *Macoma balthica* taken as prey by the sandpipers, we divided the *Macoma* found in the invertebrate samples into three size classes. Within each transect, zone (except A in transect I), and size class, we compared the mean number of *M. balthica* for the pre- and post-migration samples, using a t-test for paired comparisons (Sokal and Rohlf 1981).

In 1976, we censused shorebirds on the two transects 113 times; in 1977, 122 times. Hourly, from high to low or low to high tides, we recorded the number of birds in the exposed zones of each transect. We tallied the respective numbers of Dunlins and Western Sandpipers for each transect and averaged those totals over all of the censuses recorded at each tide time (-5, -4 . . . 0 [= dead low water] . . . + 5, + 6 h). On transect I there were 11-23 censuses for each tide time; on transect II, 3-15 censuses. The averages were then expressed as percentages of the total of the 12 hourly averages for each species. For those censuses in which the tide had not completely exposed the transect, but during which at least two zones were all or partly exposed, we used Wilcoxon's signed-rank test for two groups with paired observations (Sokal and Rohlf 1981) to compare the proportion of sandpipers counted in the zone "containing" the water's edge versus the proportion in the zone or zones above the tide line.

Stomachs

Our analyses of foods taken are based on stomach contents of 87 Dunlins and 61 Western Sandpipers collected at Hartney Bay in the study periods, 1975-1977. For the analysis of food habits — but not weights of stomach contents — we only used stomachs from sandpipers shot while actively feeding. We removed the contents of each stomach (proventriculus and gizzard) within 10 minutes after collection, and preserved them in buffered formalin. In the laboratory we weighed all contents of each stomach, and sorted and counted key parts representing single organisms. We measured the lengths of whole organisms and weighed them separately. Seeds, grit, and vegetable matter were not considered food items (Tuck 1972), but were included in the total weights of stomach contents.

We estimated the biomass of food items ingested by individual sandpipers by multiplying the number of organisms in each taxon by appropriate mean dry weights determined from representative specimens from the faunal or stomach samples (Holmes 1966; Senner 1977). Female Dunlins take larger *M. balthica* than do male Dunlins (Senner 1977), so we adjusted the estimate of the biomass (soft parts only) of this prey by the proportions of small ($\leq$ 5 mm) and large ($>$ 5 mm) intact individuals in the stomachs of the respective sexes.

Frequency of occurrence of food items was calculated after Hartley (1948); per cent composition of the total food items was calculated on a biomass basis (Holmes 1966). We compared overlap in diets by summing the per cent values

shared for any and all prey classes of the two sandpiper species (Holmes and Pitelka 1968). We used the Tukey-Kramer method to compare the mean wet weights of the stomach contents, by species and tide stage (Sokal and Rohlf 1981).

Results

Invertebrate Prey Base

Considering the pre-migration samples for the two transects together, 5 species of bivalve molluscs (Pelecypoda) accounted for 89.2% of the biomass (mg dry weight); 12 species of polychaete worms (Polychaeta) accounted for 10.4% of the biomass. One bivalve, *M. balthica*, comprised 88.4% of the total biomass. The next most important species was a polychaete, *Nephtys ciliata*, which accounted for 6.2% of the total biomass. Two amphipods (Amphipoda), *Anisogammarus* species and *Corophium salmonis*, made

TABLE 1. Frequency of occurrence (%) of prey taxa represented in the stomachs of Western Sandpiper (N = 61) and Dunlin (N = 87) collected at Hartney Bay.

Prey Taxon	Western Sandpiper	Dunlin
Polychaeta		
Abarenicola sp.	-	2
Arachnida		
Acararina, unidentified	2	-
Crustacea		
Crustacea, unidentified	3	2
Harpacticoida, unidentified	5	-
Campylaspis sp.	3	-
Amphipoda, unidentified	3	10
Gammaridae, unidentified	-	2
Anisogammarus sp.	-	2
Corophium salmonis	20	18
Insecta		
Insecta, unidentified adult	-	3
Diptera, unidentified adult	2	-
Chironomidae, unidentified larva	33	8
Dolichopodidae, unidentified larva	30	15
Gastropoda		
Gastropoda, unidentified	5	2
Littorina sp.	3	2
Pelecypoda		
Pelecypoda, unidentified	11	2
Mytilus edulis	56	18
Clinocardium sp.	23	13
Astarte sp.	2	-
Macoma balthica	52	91
Mya sp.	39	36
Veneridae, probably *Transenella tantilla*	8	7
Animal Fragments, unidentified	7	7

up < 1% of the biomass. Senner (1977) presented these results in detail.

Food Habits

About the same number of prey taxa were found in Western Sandpiper and Dunlin stomachs (Table 1), but the food habits of the former species were more diverse (Figure 2). Dunlins relied heavily on *M. balthica*, whereas at least three species of bivalve molluscs and two species of larval dipterans were important to Western Sandpipers. Although polychaetes were well represented in the Hartney Bay infauna, they were not important in the diet of either sandpiper species.

The per cent overlap in the prey of Dunlins and Western Sandpipers on a biomass basis was 27.3%. Dunlins, however, took significantly larger prey than did Western Sandpipers. The mean lengths ($\pm$ SE) of the amphipod *C. salmonis* taken by Dunlins and Western Sandpipers at Hartney Bay and two other sites in the C-BRD system were 6.3 mm $\pm$ 0.44 (range = 2-12 mm, n = 30) and 3.8 mm $\pm$ 0.16 (range = 2-5 mm, n = 22), respectively (t_s = 4.76, $P < 0.05$).

Combining all pelecypod species, the mean lengths taken by Dunlins were 5.7 mm $\pm$ 0.27 (range = 2-11, n = 71) compared to 3.2 mm $\pm$ 0.15 (range = 2-6 mm, n = 61) by Western Sandpipers (t_s = 7.79, $P < 0.05$). Among 49 intact *M. balthica* ingested by Dunlins, 57% were in the 7-12 mm class; 33%, 4-6 mm; and 10%, 1-3 mm. For Western Sandpipers, 3 of 4 intact *M. balthica* were in the 4-6 mm range and 1 was in the 1-3 mm range.
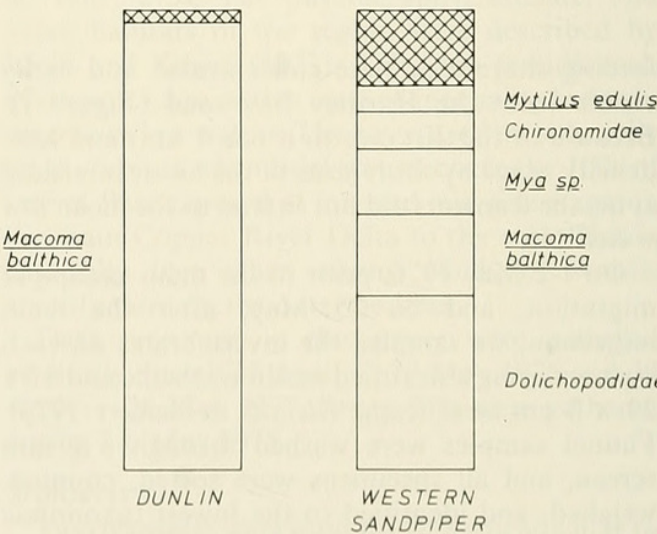

FIGURE 2. Stomach contents of Western Sandpipers and Dunlins collected at Hartney Bay, expressed as per cent composition of total estimated prey biomass. Hatched bars show the sum of food items which, individually, comprised less than 5% of total food items.

Prey Depletion

On both transects the mean number of *M. balthica* per zone in the 7-12 mm class decreased in the post-migration invertebrate samples (Table 2). For the 1-3 mm range there were no significant differences, but for the 4-6 mm class there were mixed results. On transect I there were significantly fewer *M. balthica* following migration; on transect II, there was no difference.

Habitat Use

On high tides, Dunlins stopped feeding and routinely rested in large, mixed-species (e.g., with *Calidris canutus* and *Limnodromus* species) aggregations, just above the water's edge (Figure 1). Most Western Sandpipers continued feeding, although less intensively, through the high tide stages, using still-exposed mud and sedge flats. Even Western Sandpipers that joined roosting flocks tended to feed intermittently among the resting birds. Within 1 h following high tides, most sandpipers of both species resumed feeding (Figure 3). On receding tides Dunlins — but not Western Sandpipers — showed a significant tendency to concentrate their feeding efforts about the water's edge (Table 3).

At low tides, both species dispersed over the flats and sometimes left Hartney Bay entirely. Small numbers of Western Sandpipers, but rarely Dunlins, continued to forage at small pools of water in the mid- and upper-intertidal zone (Figure 3), probably taking amphipods and insect larvae. On 24 of 26 censuses when transect I was entirely exposed, feeding Western Sandpipers chose zones C and D, the zones in transect I having the greatest invertebrate biomasses (1976 data only; Senner 1977).

As rising tides decreased the exposed tide flats, some birds left Hartney Bay and Orca Inlet, presumably to resume their migration to the northwest or to seek alternative roosting or feeding sites elsewhere in the C-BRD system. These departures were often balanced by new arrivals. Sandpipers in the bay, often numbering in the tens of thousands (Senner et al. 1981), became progressively concentrated above rising tide lines. Dunlins still showed a significant association with the water's edge, although less strong than on falling tides (Table 3). As on falling tides, Western Sandpipers showed no significant affinity to the water's edge on rising tides.

We conducted 14 censuses on rising and falling tides in which Western Sandpipers were present and Dunlins were largely absent ($< 15\%$ of the combined total) from the transect. In nine censuses a higher proportion of Western Sandpipers was found in the zone with the tide line (Table 3). The intra-habitat distribution of Dunlins did not change in the absence of Western Sandpipers.

TABLE 2. Mean numbers of *Macoma balthica* per sample, by size class, before and after the spring shorebird migration on two transects at Hartney Bay. Values shown are x̄ ± 1 SE. Following each group, t_s for a t-test for paired comparisons is shown. For each zone $n = 6$, except in I-B, where $n = 4$. An asterisk (*) indicates a significant difference, $P < 0.05$, between pre- and post-migration means.

| Size Class (mm) | Transect I | | | Transect II | | |
| | Zone | Sample Period | | Zone | Sample Period | |
		Pre	Post		Pre	Post
1-3	B	0.8 ± 0.8	0.8 ± 0.8	A	2.2 ± 0.5	5.5 ± 2.2
	C	1.8 ± 0.7	2.8 ± 0.7	B	2.7 ± 1.3	7.7 ± 1.6
	D	3.0 ± 1.0	1.2 ± 0.6	C	2.0 ± 0.9	3.2 ± 0.4
	E	3.2 ± 1.0	5.8 ± 1.2		$t_s = 2.88$, df = 2	
	F	2.3 ± 0.4	7.2 ± 4.6			
		$t_s = 1.35$, df ± 4				
4-6	B	1.5 ± 1.2	0.5 ± 0.3	A	3.3 ± 0.8	0.7 ± 0.3
	C	5.2 ± 1.1	4.5 ± 1.0	B	2.2 ± 0.9	2.7 ± 0.8
	D	3.3 ± 0.8	2.3 ± 0.4	C	1.0 ± 0.6	0.8 ± 0.2
	E	1.3 ± 0.5	0.7 ± 0.4		$t_s = 0.827$, df = 2	
	F	1.0 ± 0.4	1.5 ± 0.6			
		$t_s = 2.47^*$, df ± 4				
7-12	B	3.8 ± 3.8	2.0 ± 2.0	A	6.3 ± 1.7	1.8 ± 0.5
	C	16.3 ± 1.8	12.3 ± 2.4	B	3.3 ± 0.6	0.7 ± 0.5
	D	7.7 ± 1.6	1.3 ± 0.6	C	1.8 ± 0.6	0.3 ± 0.2
	E	1.3 ± 0.6	0.8 ± 0.3		$t_s = 3.27^*$, df = 2	
	F	2.7 ± 1.5	0.5 ± 0.2			
		$t_s = 3.21^*$, df ± 4				
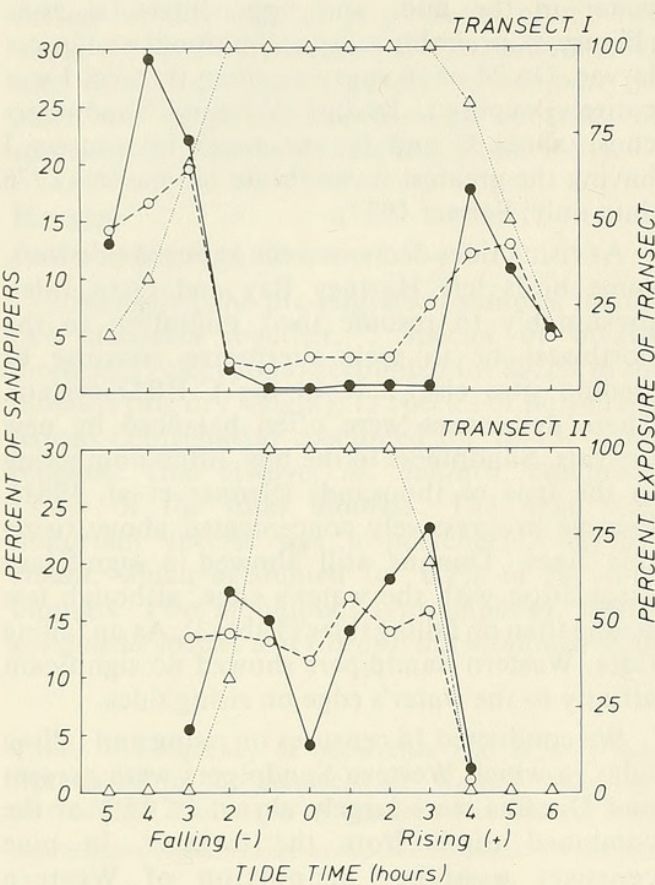
FIGURE 3. Proportions (%) of the average numbers of Western Sandpipers (open circles) and Dunlins (closed circles) using two Hartney Bay transects in relation to tide time and per cent exposure (triangles) of the transects.

Weights of Stomach Contents

The mean weights of stomach contents may provide an indication of feeding activities in relation to tides or other factors (e.g., Couch 1966). Mean weights of stomach contents for both species were lowest among individuals collected on high tides, indicating reduced food intake at this tidal stage (Table 4). The mean weights of Dunlin stomach contents increased sharply on the falling tide, but showed no significant change between falling and rising tides. This pattern suggests that the rate of intake diminishes after the tide has receded. The mean weights of Western Sandpiper stomach contents did not increase significantly between high and falling tides, but did between falling and rising tides (Table 4). This pattern indicates that Western Sandpipers continued to feed actively through the low and rising tide stages, before slowing — but not necessarily stopping — their feeding during high tides.

Discussion

From late April to mid-May, millions of migrating Dunlins and Western Sandpipers stop to feed and rest in the C-BRD system (Isleib and Kessel 1973; Isleib 1979; Senner et al. 1981). In most years the persistence of snow and ice on higher wetlands restricts feeding by Dunlins and Western Sandpipers to intertidal habitats (Senner et al. 1981). Tens of thousands to one million or more sandpipers of both species may simultane-

TABLE 3. Number of censuses, by species and tide stage, in which the proportion of sandpipers in the transect zone "containing" the water's edge exceeded the proportion of sandpipers in the zone or zones above the water's edge. Values shown are the number of censuses, the total number of censuses (n), and t_s for Wilcoxon's signed-rank test. An asterisk (*) indicates statistical significance, $P < 0.05$.

Species	Rising	Falling	Rising & Falling
Western Sandpiper vs. Western Sandpiper	10 (26)	13 (28)	-
	156.5	186.5 -	
Dunlin vs. Dunlin	14 (21)	23 (27)	-
	65.0*	17.0*	
Dunlin vs. Western Sandpiper[a]	9 (18)	20 (23)	-
	30.0*	0.0*	
Western Sandpiper vs. Western Sandpiper			
(absent Dunlin)[b]	-	-	9 (14)
			20.6*
Dunlin vs. Dunlin			
(absent Western Sandpiper)	-	-	7 (10)
			15.0*

[a]Comparison of number of censuses in which the proportion of Dunlins in the zone containing the water's edge exceeded the proportion of Western Sandpipers in that same zone.
[b]The species in parentheses comprised < 15% of the combined total of Western Sandpipers and Dunlins on the entire transect for each census.

TABLE 4. The mean wet weights (mg) of stomach contents, by tide stage, from Western Sandpipers (N = 49) and Dunlins (80) collected at Hartney Bay. Values shown are $\bar{x} \pm 1$ SE, (n). An asterisk (*) indicates that adjacent pairs of means differ significantly, $P < 0.05$.

Species	High[a]		Falling		Rising
Western Sandpiper	107 ± 10.3		136 ± 11.6	*	204 ± 21.3
	(15)		(22)		(12)
Dunlin	190 ± 17.8	*	358 ± 26.4	*	397 ± 22.9
	(27)		(31)		(22)

[a]High tide = the period 1 h before through to 1 h after actual high tide.

ously use the intertidal zone of the C-BRD system (Isleib 1979). Beyond their large numbers in, and overlapping use of, the C-BRD system, Dunlins and Western Sandpipers are broadly sympatric and extensively synchronous during spring and fall migrations and on their breeding grounds (Senner 1979; A.O.U. 1983).

The mean body mass of Western Sandpipers is about 44% of the Dunlin mean; culmen length is about 64% of the Dunlin mean (calculated from Table 1 in Senner et al. 1981: 276). Based on Recher (1966), Baker and Baker (1973), and Baker (1977), it is predictable that Western Sandpipers take smaller and more diverse prey than Dunlins. The larger Dunlin is more stenophagic, takes larger prey than Western Sandpipers, and feeds less continuously than Western Sandpipers (cf. Burger et al. 1977: 756).

Western Sandpipers feed either on the surface or by probing (Ashmole 1970), and exploit a wider range of intertidal habitats than do Dunlins. Because of its longer beak and legs, the Dunlin is better able to exploit the flooded area immediately below the tide line. Preference for the water's edge as it moves across a tidal flat suggests that it is a prime place for capturing such prey as *M. balthica* (Vader 1964; Recher 1966; Prater 1972).

The behavioral and dietary differences we documented for these congeners at Hartney Bay are consistent with other comparisons during the non-breeding season (Couch 1966; Recher 1966; Recher and Recher 1969; Holmberg 1975; Gerstenberg 1979). Our results also parallel comparisons of other *Calidris* species "pairs" in which the larger species made greater use of the area about the water's edge and had a more selective diet (Bengtsson and Svensson 1968; Ashmole 1970; Thomas and Dartnall 1971). Thomas and Dartnall (1971: 24) also noted a "small change" in the intrahabitat distribution of the smaller Red-necked Sandpipers (*C. ruficollis*) in the absence of the larger Curlew Sandpipers (*C. ferruginea*).

The Dunlin is a less aggressive species than the Western Sandpiper (Recher and Recher 1969), and we saw little interspecific aggression. Yet the mere presence of substantial numbers of Dunlins may have excluded Western Sandpipers from the space near the tide line (cf. Goss-Custard 1980). Wishart et al. (1981) noted that in mixed flocks of feeding shorebirds (three species), dominance was related directly to body size.

An altered pattern of resource usage in the presence or absence of other species is not necessarily evidence of competition (MacNally 1983). Yet the shift in the Western Sandpipers' feeding microhabitat in the absence of Dunlins and the likelihood of a decreasing supply of *M. balthica* during the migration (Table 2) indicate conditions in which competition may occur.

To the extent that interspecific competition for feeding space and prey occurs, it does so within the context of a highly variable environment [Burger (1984) described abiotic factors influencing shorebird migration]. In some years migrant shorebirds may encounter severe limitations in food availability or quality at one or more of their traditional stopping points. Weather and extraordinary tides affect the availability of feeding habitats (Gerstenberg 1979; Page et al. 1979) as well as the behavior and availability of invertebrate prey (e.g., Evans 1976). Weather and such other factors as salinity also affect the recruitment and survival of intertidal invertebrates potentially available as prey (e.g., Crisp 1964).

Limitations in food supply may decrease foraging success so that some shorebirds will arrive on their breeding grounds with depleted reserves of depot lipids or other body constituents. Such reserves may be important to reproductive success at high latitudes (e.g., Irving 1960; Raveling 1979), where severe weather may delay reproductive activities and reduce food availability. Behavioral and morphological characteristics that enable individual migrants to forage more successfully — and arrive with greater fat reserves — than their conspecifics can be translated into adaptations at the population level. The few days spent at one or a few critical stopping areas along a migration route are spatio-temporal "bottlenecks" (Myers et al. 1987) in which variable environmental conditions — supplemented or reinforced by competitive

interactions — may exert a strong selective influence on shorebird populations.

Acknowledgments

Literature Cited

American Ornithologists' Union. 1983. Check-list of North American birds. Sixth edition. American Ornithologists' Union, Lawrence, Kansas.

Ashmole, M. J. 1970. Feeding of Western and Semi-palmated Sandpipers in Peruvian winter quarters. Auk 87: 131–135.

Baker, M. C. 1977. Shorebird food habits in the eastern Canadian Arctic. Condor 79: 56–62.

Baker, M. C., and A. E. M. Baker. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. Ecological Monographs 43: 193–212.

Bengtsson, S. A., and B. Svensson. 1968. Feeding habits of *Calidris alpina* L. and *C. minuta* Leisl. (Aves) in relation to the distribution of marine shore invertebrates. Oikos 19: 152–157.

Burger, J. 1984. Abiotic factors affecting migrant shorebirds. Behavior of Marine Animals 6: 1–72.

Burger, J., M. A. Howe, D. C. Hahn, and J. Chase. 1977. Effects of the tide cycles on habitat selection and habitat partitioning by migrating shorebirds. Auk 94: 743–758.

Couch, A. B. 1966. Feeding ecology of four species of sandpipers in western Washington. M.Sc. thesis. University of Washington, Seattle.

Crisp, D. J., *Editor*. 1964. The effects of the severe winter of 1962-63 on marine life in Britain. Journal of Animal Ecology 33: 165–210.

Duffy, D. C., N. Atkins, and D. C. Schneider. 1981. Do shorebirds compete on their wintering grounds? Auk 98: 215–229.

Evans, P. R. 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. Ardea 64: 117–139.

Gerstenberg, R. H. 1979. Habitat utilization by wintering and migrating shorebirds on Humboldt Bay, California. Studies in Avian Biology 2: 33–40.

Goss-Custard, J. D. 1980. Competition for food and interference among waders. Ardea 68: 31–52.

Hartley, P. H. T. 1948. The assessment of the food of birds. Ibis 90: 361–381.

Holmberg, N. D. 1975. The ecology of seven species of shorebirds (Charadrii) in north Humboldt Bay, California — 1970 to 1971. M.Sc. thesis, Humboldt State University, Arcata, California.

Holmes, R. T. 1966. Feeding ecology of the Red-backed Sandpiper (*Calidris alpina*) in Arctic Alaska. Ecology 47: 32–45.

Holmes, R. T., and F. A. Pitelka. 1968. Food overlap among coexisting sandpipers on northern Alaska tundra. Systematic Zoology 17: 305–318.

Irving, L. 1960. Nutritional condition of Water Pipits on Arctic nesting grounds. Condor 62: 469–472.

Isleib, M. E. 1979. Migratory shorebird populations on the Copper River Delta and eastern Prince William Sound, Alaska. Studies in Avian Biology 2: 125–129.

Isleib, M. E., and B. Kessel. 1973. Birds of the north gulf coast-Prince William Sound region, Alaska. Biological Papers of the University of Alaska Number 14.

MacNally, R. C. 1983. On assessing the significance of interspecific competition to guild structure. Ecology 64: 1646–1652.

Myers, J. P., R. I. G. Morrison, P. Z. Antas, B. A. Harrington, T. E. Lovejoy, M. Sallaberry, S. E. Senner, and A. Tarak. 1987. Conservation strategy for migratory species. American Scientist 75: 18–26.

Page, G., L. E. Stenzel, and C. M. Wolfe. 1979. Aspects of the occurrence of shorebirds on a central California estuary. Studies in Avian Biology 2: 15–32.

Prater, A. J. 1972. The ecology of Morecambe Bay. III. The food and feeding habits of Knot (*Calidris canutus* L.) in Morecambe Bay. Journal of Applied Ecology 9: 179–194.

Raveling, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. Auk 96: 234–252.

Recher, J. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47: 393–407.

Recher, J. F., and J. A. Recher. 1969. Some aspects of the ecology of shorebirds. II. Aggression. Wilson Bulletin 81: 140–154.

Schneider, D. C., and B. A. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. Auk 98: 801–811.

Senner, S. E. 1977. The ecology of Western Sandpipers and Dunlins during spring migration through the Copper-Bering river delta system, Alaska. M.Sc. thesis, University of Alaska, Fairbanks.

Senner, S. E. 1979. An evaluation of the Copper River Delta as a critical habitat for migrating shorebirds. Studies in Avian Biology 2: 131–145.

Senner, S. E., G. C. West, and D. W. Norton. 1981. The spring migration of Western Sandpipers and Dunlins in southcentral Alaska: numbers, timing, and sex ratios. Journal of Field Ornithology 52: 271–284.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co., New York.

Thomas, D. G., and A. J. Dartnall. 1971. Ecological aspects of the feeding behavior of two Calidridine sandpipers wintering in south-eastern Tasmania. Emu 71: 20–26.

Tuck, L. M. 1972. The snipes: a study of the genus *Capella*. Canadian Wildlife Service Monograph Number 5.

Vader, W. J. M. 1964. A preliminary investigation into the reactions of the infauna of the tidal flats to tidal fluctuations in water level. Netherlands Journal of Sea Research 2: 189–222.

Wiens, J. A. 1977. On competition and variable environments. American Scientist 65: 590–597.

Wishart, R. A., P. J. Caldwell, and S. G. Sealy. 1981. Feeding and social behavior of some migrant shorebirds in southern Manitoba. Canadian Field–Naturalist 95: 183–185.