TIMING OF SHOREBIRD MIGRATION IN RELATION TO PREY DEPLETION

DAVID C. SCHNEIDER[1] AND BRIAN A. HARRINGTON

Manomet Bird Observatory, Manomet, Massachusetts 02345 USA

ABSTRACT.—The southward departure of migratory shorebirds (Charadrii) before the collapse of food supplies on the breeding grounds would seem to disprove the hypothesis that migratory timing is a trait actively maintained by selective pressures created by seasonal production of food supplies. In this study we looked at seasonal changes in the food supplies of shorebirds at a migratory stopover to see if dwindling food supplies here might explain early arrival from Arctic breeding grounds. For the three earliest migrants through Plymouth, Massachusetts we found substantial reductions of prey densities (7–90%) during migration (July–September). Reductions in prey density were not substantial before September for a later migrant. Caging experiments showed that the reductions in density of infaunal prey were due to predation. If these reductions are sufficient to cause energetic deficits among late arrivals, then competition may be an important selective agent in shaping migratory patterns. *Received 11 September 1980, accepted 21 April 1981.*

MANY arctic migrants leave their breeding grounds well before the collapse of local food supplies (Thomson 1926:260; Pitelka 1959). Migratory departure before this collapse of local food supplies would appear inconsistent with the hypothesis that migratory patterns are actively maintained by the seasonal production and availability of food resources (see, for example, Van Tyne and Berger 1959). It is possible, however, that early departure from the breeding grounds could result from depletion of food supplies at some subsequent point along the migratory route, such as a staging area. To see if this explanation might be valid, we measured rates of prey depletion at a staging area in Massachusetts during the passage of some of the earliest of all autumn migrants, several species of shorebirds (Charadrii).

METHODS

We carried out our study in Plymouth, Kingston, and Duxbury harbors (42°00′N, 70°40′W), a complex of intertidal flats and marshes lying behind two barrier beaches. The three harbors together have a surface area of 4,070 ha, of which 45.7% is exposed at low tide (Iwanowicz et al. 1974). Tides are semidiurnal, with a range of 2.9 m.

We measured seasonal changes in shorebird abundance by making regular counts at high-tide roosts and at low-tide foraging areas. High-tide counts were made along Plymouth beach from March to November. Low-tide counts were made from mid-July through September at 13 1-ha plots distributed among five intertidal flats (Fig. 1). Plots ranged in composition from hard sand to soft mud. Each plot was 100 m on a side and marked at the corners with lengths of garden hose nailed to stakes driven into the substrate. One or more bird counts were made in each plot in each 2-week period from July through September 1976. Plots were censused for birds at least once each 10-day period from July to September 1977.

We determined the size and identity of shorebird prey by observing foraging behavior, by examining shorebird feces, and by examining gut contents of birds collected for this purpose. Foraging observations were made on a casual basis during visits to the study sites from July through September. Fecal pellets were examined at or near study sites and only if the pellet could be assigned to one bird species. Birds were collected near study plots and then only if seen consuming prey. Collection of birds was limited to

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[1] Present address: Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717 USA.
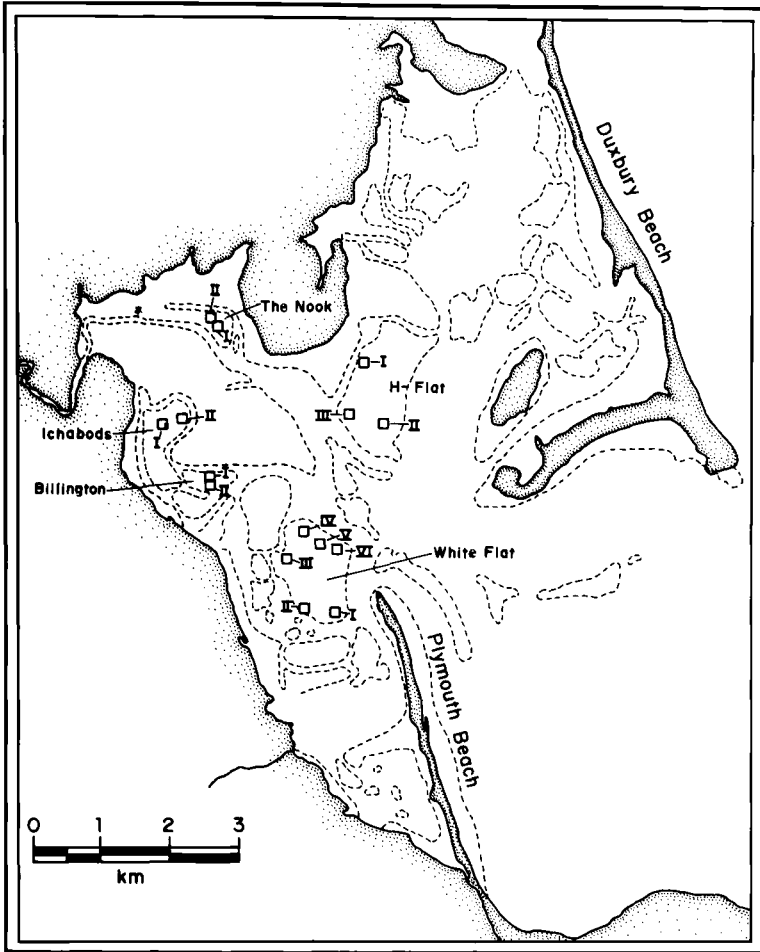
Fig. 1.   Location of intertidal study plots at Plymouth, Massachusetts.

reduce the chance of altering usage of study areas. To reduce the number of birds needed, we examined dietary homogeneity of birds of one species using the same foraging technique or the same habitat (sand or mud). This approach is suggested by an observation of Baker and Baker (1973) that shorebird diets could be predicted from a knowledge of species, foraging technique, and prey availability. If diets were homogeneous, then the sample was considered representative. More birds were collected if diets proved to be heterogeneous or if foraging observations suggested that a shift in diet occurred during the study period. Birds were collected in mid- and late August in order to detect major dietary shifts.

We estimated the density of intertidal animals, including shorebird prey, at the onset of migration by collecting 20 core samples at each plot in July 1976. All cores were 10 cm in diameter and 10 cm deep. Each core was washed on a 1-mm sieve. Animals retained were sorted by species and by size class within species. Worms were measured to the nearest centimeter (contracted length); other groups were measured to the nearest millimeter (length or greatest diameter). To see if conditions changed from year to year, we repeated this sampling program in July 1977 at 208 of the 260 sites used in 1976.

Rates of change in the density of invertebrates during shorebird migration were measured by collecting a core in September within 2 m of a July sample. This design was chosen in preference to random sampling because intertidal fauna was patchily distributed, a situation in which paired comparisons are more efficient than an unpaired design in detecting change in faunal numbers. A paired-comparisons analysis (Sokal and Rohlf 1969) was used to test for significant changes in density. We made no attempt in this study to estimate the average density of fauna on intertidal flats. Rather, we deliberately chose

six plots with high bird densities and seven plots with intermediate to low bird densities to give us an idea of the range of conditions experienced by foraging shorebirds at Plymouth.

We set up wire exclosures in 1975, 1976, and 1977 to see whether predators caused decreases in prey density during migration. Each exclosure was 100 cm on a side, 10 cm high, and was constructed of 14-mm mesh hardware cloth folded into shape. Exclosures were set directly on the flat and held in place by wiring cage corners to wooden stakes driven flush with the substrate surface. Each cage was sampled when it was set out in July or August. Cages were sampled again in late September, unless overgrown with algae or undercut by scouring. Each sample consisted of 4 cores taken inside the cage and from 2 to 4 cores taken within 2 m of the cage. Replication was kept to a minimum to reduce disturbance of the substrate. Cages were checked for predators in September to reduce disturbance caused by raising the cage during the experiment.

Data from 1975 exclosures were analyzed by comparing counts inside and outside cages at the end of the experiment. The ratio of cores collected inside and outside was used to compute the expected number of organisms in each of the two categories. This analysis assumes that densities are the same inside and outside the exclosure at the start of the experiment, an assumption that is unlikely because of small-scale patchiness. During 1976 and 1977 this effect was controlled by sampling at the outset of the experiment and then comparing this to the observed difference at the end, using a two-way contingency test. The results of this analysis were checked by a nonparametric test: a Wilcoxon two-sample test (Sokal and Rohlf 1969).

The potential for competition between shorebirds and other predators was determined by noting the activity of animals during invertebrate sampling (July and September) and during shorebird counts (July through September). Movement of predators onto the flats with the flooding tide was checked after invertebrate sampling. Five systematic counts were made at high tide by drifting across the flats in a boat and observing through diving masks and a glass-bottomed box. Four strip counts were made with the box on White flat. The width of each strip was 2 m. The length of each strip was 1 km, based on the direction of drift, point of origin, and known proportions of this flat. Observations were made on White flat (with six study sites) in July and August of 1976 and on three flats with study sites in July, August, and September of 1977. The diet of predators not found in the cages was determined from foraging observations (birds other than shorebirds) or by capturing foraging animals for stomach analysis. Predators were collected in July and August in order to detect any major dietary shifts.

RESULTS

Timing of migration.—The timing of shorebird migration at Plymouth was about the same for the two earliest arrivals—Short-billed Dowitchers (*Limnodromus griseus*) and Semipalmated Sandpipers (*Calidris pusilla*). The highest counts for these species at both roosting and foraging areas occurred between 10 July and 20 August, with some indication of a reduced number of migrants in 1977 (Fig. 2). The reduced variation in the density of birds at foraging areas in 1977 can be attributed to a higher number of counts rather than to any decrease in variability of numbers across the same sites.

Sanderlings (*Calidris alba*) also began arriving in numbers at Plymouth in July, but peak migration was slightly later than for the two other scolopacids (Fig. 2). Together, the three scolopacids accounted for 90% of the shorebirds counted on the intertidal plots and from 80 to 90% of the birds counted at high tide on Plymouth beach. Black-bellied Plovers (*Pluvialis squatarola*) were also abundant at Plymouth, but the highest counts for this species occurred after 20 August (Fig. 2).

Shorebird diets.—The stomachs of two dowitchers collected from muddy substrates in August 1976 both contained more than half (by volume) of the identifiable remains of bamboo worms (*Clymenella torquata*). Bamboo worms were identified through a telescope while dowitchers pulled them out of the substrate. Dowitchers were seen foraging on bamboo worms from July through August in muddy areas. Less common prey (<10% by volume in either stomach) included 5 individual amphipods (*Acanthohaustorius millsi* and *Trichophoxus epistomus*), 7 individual clams
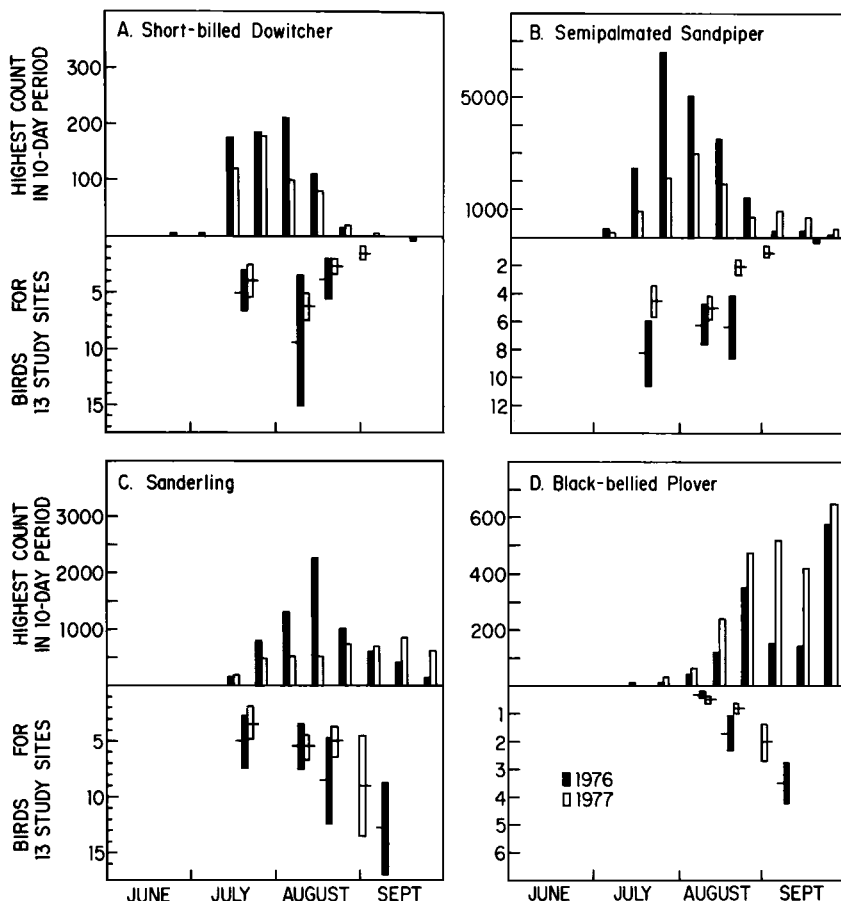
Fig. 2. Seasonal abundance of migratory shorebirds at Plymouth, Massachusetts. Upper scale for each species shows highest count in 10-day periods along Plymouth beach at high tide. Lower scale shows density (birds/ha) in 13 study plots on low-tide flats. Horizontal line indicates mean density. Vertical bar indicates one standard error on either side of the mean.

(*Tellina agilis*), and a nereid polychaete. Dowitchers at Plymouth also fed by shallow probing in sandier substrates. The stomachs of two birds collected from sandy substrates both contained more than half (by volume) of amphipods (*Acanthohaustorius millsi* and *Trichophoxus epistomus*). Less common prey included 1 amphipod (*Protohaustorius deichmannae*), 4 clams (*T. agilis*), a nereid polychaete, and 2 snails (*Mitrella lunata* and *Nassarius trivittatus*). Small clams (*Gemma gemma*) were found in all 4 stomachs, but in only 1 stomach were any of the clams crushed, and in this case only 3 out of the 30 clams were crushed. Undigested *Gemma* were found in the intestines of these birds, so *Gemma* were not considered a nutritively important part of the diet. *Gemma* are likely to be ingested while the bird is taking other prey, because these clams, like sand grains, adhere to anything wet.

The diet of Sanderlings at Plymouth proved to be homogeneous for all birds sampled. The stomachs of four birds collected from three different areas in August of 1976 contained more than 90% by volume of shrimp (*Crangon septemspinosa*). Shrimp fragments came from individuals that were between 0.5 and 2 cm in length.

TABLE 1. Tidal flat predators at Plymouth, Massachusetts. Diets are listed for those predators not found in wire cages (14-mm mesh) set on the flats. Prey listed are those that accounted for more than 10% (by volume) of the material in any one stomach or that were found in more than one stomach. Nc = number of stomachs collected (August 1976). Np = number of stomachs in which particular prey were found. V = visual confirmation of a prey species taken in field. H = present on flats at high tide. L = present at low tide.

Predators (Nc)	In cage	Tide	Prey (dimensions are lengths in centimeters)
Carcinus maenas	Yes	H, L	
Polinices duplicata	Yes	H, L	
Crangon septemspinosa	Yes	H, L	
Limulus polyphemus (7)	No	H, L	*Nereis* sp., 2 (Np = 3); *Gemma gemma*, 0.2 (Np = 2)
Pseudopleuronectes americanus			
<15 cm length	No	H	Unknown. Fishing attempts on flats unsuccessful at high tide.
20–40 cm long (11)	No	Absent[a]	Caprellids, 0.5–1 (Np = 8); Capitellids, 0.5–2 (Np = 5); *Gammarus*, 0.2–0.6 (Np = 5)
Limnodromus griseus (4)	No	L	*Clymenella*, >2 (V) (Np = 2); *A. millsi*, >0.2 (Np = 3); *T. epistomus*, >0.2 (Np = 4); *T. agilis*, >0.3 (Np = 4)
Calidris pusilla (4)	No	L	*Crangon*, 0.5–2 (V) (Np = 3); *A. millsi*, >0.2 (Np = 1); *P. deichmannae*, >0.2 (Np = 1); unidentified polychaetes (not nereids), >2 (Np = 1)
Calidris alba (6)	No	L	*Crangon*, 0.5–2.5 (V) (Np = 4)
Pluvialis squatarola (2)	No	L	*Crangon*, 1–3 (V) (Np = 2); *Nereis virens*, >2 (V) (Np = 2); *Gemma*, 0.3 (V) (Np = 2); *Scoloplos robustus*, >2 (V) (Np = 1); *Cerebratulus lacteus*, >2 (V) (Np = 1)

[a] Collected from subtidal area near study flat.

One nearly intact shrimp measured slightly over 2 cm. Less common prey included one amphipod (*Gammarus mucronatus*), an ostracod, a crab (*Carcinus maenas*), a nereid polychaete, and a beetle. An attempt was made in 1977 to find Sanderlings that were not feeding on *Crangon*. Two birds were eventually collected, and both were found to have eaten primarily *Crangon*. *Gemma* were present in the stomachs, but 6 of the 8 clams were intact and undigested.

The diet of Semipalmated Sandpipers was homogeneous with respect to common prey, but not with respect to less common prey. Stomachs were collected from three birds that had been feeding by probe-multiple-steady behavior (Baker and Baker 1973). All three contained more than 50% by volume of *Crangon*; all *Crangon* pieces were from shrimp between 0.5 and 2 cm in total length. Less common prey included haustoriid amphipods (1 stomach) and an unidentified polychaete (1 stomach). Semipalmated Sandpipers at Plymouth also employed probe-multiple-halting behavior (Baker and Baker 1973). Haustoriid amphipods (*A. millsi* and *P. deichmannae*) and a polychaete (probably a spionid) were found in the stomach of a bird that had been feeding by probing. *Crangon* and spionids were confirmed as prey by visual observations from July and August 1977. Another amphipod (*G. mucronatus*) was added to the list of prey in 1977, based on observations of birds foraging in wracks of green algae found on the flats that year. *Gemma* were found in all four stomachs collected in 1976, but out of 55 clams 43 were intact and undigested.

TABLE 2. Initial density and rates of loss of prey species of migratory shorebirds at Plymouth, Massachusetts in 1976 and 1977. H and L indicate high and low density sites in July. Percentage change is for mid-July to mid-September. All percentage values differ significantly from zero at $P < 0.05$ for a paired-comparisons analysis.

Major prey of each bird		Animals/m² (1976)[a]	Percentage change (1976)[b]	Animals/m² (1977)[c]	Percentage change (1977)[d]
Short-billed Dowitchers					
Clymenella torquata	>3 cm	207 (H)	−80%	261 (H)	−21%
		11 (L)	−50%	0 (L)	+
Trichophoxus epistomus	>2 mm	117 (H)	−80%	175 (H)	−64%
		36 (L)	−83%	8 (L)	−100%
Tellina agilis	>3 mm	1,178 (H)	−90%	185 (H)	−64%
		78 (L)	−67%	38 (L)	+480%
Semipalmated Sandpipers					
Acanthohaustorius millsi	>2 mm	453 (H)	−81%	1,540 (H)	−42%
		187 (L)	−47%	115 (L)	−67%
Protohaustorius deichmannae	>2 mm	131 (All)	−7%	223	−86%
Gammarus mucronatus	>2 mm	9 (All)	−50%	2	+220%
Crangon septemspinosa	<2 cm	20 (All)	−33%	12	+400%
Sanderling					
C. septemspinosa	<2.5 cm	21 (All)	−32%	15	+306%
Black-bellied Plover					
C. septemspinosa	>1 cm	2 (All)	−33%	7	+160%
Worms[e]	>3 cm	16 (All)	−45%	22	−25%
Gemma gemma	>3 mm	no count		no count	

[a] Density estimates for each species based on 260 core samples collected at 13 sites in July.
[b] Based on 260 samples at the same 13 sites in September.
[c] Based on 208 samples at the same 13 sites in July.
[d] Based on 208 samples in September.
[e] *Nereis virens, Scoloplos robustus,* and *Cerebratulus lacteus.*

Black-bellied Plovers were relatively late arrivals, so it was of interest to see if the diet of this species differed from that of the early migrants. The greatest volume of prey, based on foraging observations and on examination of the stomachs of two birds, was accounted for by two annelids (*Nereis virens, Scoloplos robustus*) and a nemertean (*Cerebratulus lacteus*). All worms exceeded 2 cm in length, based on examination of undigested remains in the proventriculus and anterior end of the gizzard. *Crangon* were the next most important item, based on stomach contents. Stomachs also contained crushed bivalves—*Gemma* (3–4 mm in diameter), *Mytilus edulis* (3–10 mm in length), and *Mya arenaria* (3–10 mm in length). These prey species were confirmed as important diet items by observing foraging birds.

The value of fecal pellets in determining diets was limited, because only a limited number of prey species could be identified down to species. Mussels (*M. edulis*) were found in the fecal pellets of all common sandpipers in 1977, but were found only in the fecal pellets of Knots (*Calidris canutus*) in 1976. This was considered an unusual dietary item for sandpipers other than Knots, because small mussels were found in the fecal pellets of other sandpipers during 1977 only. A large number of small mussels (less than 1 cm long) were present on the flats in 1977, but not in 1975, 1976, 1978, or 1979.

The results of the stomach analyses were then summarized (Table 1). Subsequent analysis was focused on those prey items that accounted for more than 10% (by volume) of the contents of any one stomach or that occurred in more than one stomach, even if the prey item never reached 10% of any one stomach. No attempt

TABLE 3. Results of cage experiments at Plymonth, Massachusetts. I = density of organisms inside cage (per 10 cm diameter core). O = density outside cage. N = number of cores taken inside cage. M = number of cores taken outside cage. *P*-values are based on one-tailed tests.

| | Start | | | End | | | |
Prey	N/M	I/O		I/O	N/M	G-statistic	P
1975 (1 cage: 31 July to 17 September; 2 cages: 10 August to 18 September)							
C. torquata				7.1/5.4	18/24	4.72[a]	0.015
Haustoriid amphipods				2.4/1.2	18/24	8.97[a]	0.002
T. epistomus				2.6/0.6	18/24	27.83[a]	0.001
1976 (1 cage: 12 August to 27 September; 1 cage: 24 August to 24 September)							
C. torquata	5/7	1.2/1.6	<	2.3/0.9	8/11	5.57[b]	0.009
A. millsi	5/7	0/0.14	<	0.25/0	8/11	3.46[b]	0.030
1977 (1 cage: 23 June to 30 September)							
C. torquata	2/7	5.0/12.4	<	9.5/3.4	2/5	9.25[b]	0.002
Spionids	2/7	5.0/7.14	<	3.5/1.4	2/5	2.84[b]	0.045
Amphipods	2/7	2.0/3.0	<	1.0/1.0	2/5	0[b]	not significant

[a] H_0: I = O; H_A: I > O.

[b] Proportionately fewer organisms were expected outside the cage after the experiment: H_0: Start (I/O) = End (I/O); H_A: Start (I/O) < End (I/O).

was made to analyze changes in the density of less common prey items, because the size limits for these prey species could not be set without a massive and potentially disruptive collection of birds.

Change in the density of major prey.—For all three of the early migrants at Plymouth, prey density decreased between mid-July and mid-September 1976 (Table 2). Loss rates were greater for prey of dowitchers and Semipalmated Sandpipers than for prey of Sanderlings and Black-bellied Plovers. Prey losses occurred again in 1977 for infaunal prey, but at lower rates than in 1976. Epifaunal prey (*Crangon* and *Gammarus*) did increase in density in 1977.

Cause of losses.—It was of interest to know whether the losses we observed were due to physical factors, creating "hard" selective pressures (Wallace 1968) toward early migration, or to predators competing for the same food, creating "soft" selective pressures on migratory timing. Cage experiments showed that losses from sedentary infaunal populations did not occur inside the cages in 3 successive years (Table 3). Observed densities inside the cage exceeded densities outside the cage at the end of the experiment in 7 out of 8 instances (Table 3, ratio I/O at end of experiment). The probability of obtaining this or a more extreme proportion (0 out of 8) is $(1 + 8)/2^8$, or less than 4%. A Wilcoxon two-sample test (Sokal and Rohlf 1969) was performed for each of the three cages (1976 and 1977) where initial and final samples were collected. The null hypothesis, that cores taken outside the cage after the experiment would rank as high in number of organisms as cores taken inside the cage and cores taken at the start, was rejected at the 5% level for each cage. This statistically significant result cannot be attributed to a chance placement of cages in a patchy environment; the measured density inside the exclosures at the start of the experiment did not exceed the measured density outside at the start in 5 out of 5 cases where density was measured (Table 3). For epifaunal prey (*Crangon* and *Gammarus*), we could not determine the cause of loss because these species moved on and off the flat at each tide.

Because predators were the primary source of losses among infaunal invertebrates, we visited the flats at both high and low tides to see if other predators were com-

TABLE 4. Rate of loss of shorebird prey at sites heavily gouged by horseshoe crabs compared to rates of loss at sites with little or no gouging. Average loss = organisms/m² in July minus organisms/m² in September 1976. Significance levels are based on single-way analyses of variation in loss. Percentages are the among group sum of squares (2 groups) divided by the total sum of squares.

Shorebird prey	Average loss/m²		Variation in loss explained by presence of gouges
	Heavily gouged	Little or no gouging	
Clymenella torquata	35.0	26.2	2%
Acanthohaustorius millsi	40.1	223.2	negative relation
Protohaustorius deichmannae	12.6	29.3	negative relation
Trichophoxus epistomus	8.5	5.1	6% $P < 0.50$
Spionid polychaetes	9.3	9.6	negative relation

peting with shorebirds for their prey. Three species of gulls foraged on the flats at low tide—Great Black-backed (*Larus marinus*), Herring (*L. argentatus*), and Ring-billed gulls (*L. delawarensis*). The two former species broke open large snails, clams, and crabs, rather than taking smaller items and swallowing them whole, as did shorebirds. Ring-billed Gulls did take *Crangon* in shallow water at the edge of the flats and thus could be taking some of the same prey as shorebirds. Snowy Egrets (*Egretta thula*) also took shrimp in shallow water. Both Ring-billed and Herring gulls ate large worms stolen from Black-bellied Plovers. Herring Gulls were never observed catching worms on their own; Ring-billed Gulls occasionally caught large polychaetes.

Naticid snails (*Polinices duplicata* and *P. heros*) also foraged on the flats at low tide throughout the summer. Naticids were observed feeding on clams (*Gemma gemma, Ensis directus, Mytilus edulis, Tellina agilis*) and on snails (*Nassarius trivittata*).

Four predators were observed during high-tide searches—naticids, green crabs (*Carcinus maenas*), horseshoe crabs (*Limulus polyphemus*), and small (<10 cm long) flatfish (*Pseudopleuronectes americanus*). Twelve small flatfish were observed in the four strip counts on White flat, giving an observed density of 15 fish/ha. Larger flatfish were never observed on the flats.

Two of these predators, naticids and green crabs, can be eliminated as significant sources of depletion of shorebird foods because both were found inside cages. Horseshoe crabs and flatfish were not found in the exclosures and hence might have contributed to prey losses. Horseshoe crabs occurred on the flats for a few days each month, during periods of spawning activity. The stomachs of horseshoe crabs found on the flats in July and August did not contain the nutritively important prey of the three early arriving sandpiper species at Plymouth (Table 1). The diet of small flatfish could not be evaluated directly, for they could not be caught by fishing over the flats at high tide. Adult flatfish, twice the size of those found on the flats, could be caught in deeper water. These fish were found to have eaten prey of about the same size taken by shorebirds, roughly 3–30 mm in greatest dimension (Table 1). Overlap in diet between shorebirds and small flatfish is unlikely, unless flatfish continue to feed on the same size prey when 20–40 cm long as when 10 cm long. A shift to larger prey with increasing size has been reported for *P. americanus* from Long Island Sound (Richards and Riley 1963).

Horseshoe crabs gouged the flats in some areas at Plymouth at low tide, and the gouging, rather than the feeding, might have contributed to infaunal losses outside

wire exclosures. To test this possibility, we compared loss rates at heavily gouged sites to loss rates at sites with little or no gouging. Single-way analyses of variance showed that gouging did not account for a significant proportion of the variation in the loss of any major infaunal prey species (Table 4).

We concluded that predators caused the decrease in density of infaunal prey observed between July and September at Plymouth. Competition between shorebirds and other predators is unlikely, unless juvenile flatfish (<10 cm) at Plymouth consume the same size prey as the adults (20–40 cm).

DISCUSSION

Explanations of bird migration have been offered since the time of Aristotle; admirable summaries of these ideas are given by Clarke (1912) and Dorst (1956). Migration was first attributed to the action of selective forces by Wallace (1874), but subsequent treatments have dealt more with the origin of the phenomenon than with the selective forces maintaining it (see, for example, Thomson 1926, Wetmore 1926, Phillips 1951). Bird migration has been discussed in terms of current ecological forces by Williamson (1953) and Richardson (1978), who suggested that weather conditions favor migration at certain times, and by Lack (1960), who suggested that weather acts as a proximate cue while the seasonal production of food supplies ultimately maintains migratory patterns.

The logic of this trophic explanation is impeccable. Birds need an almost continuous caloric supply due to the demands of homeothermy (Dorst 1974), but food supplies are normally seasonal at any one location, even in the tropics (Sinclair 1978, Wolda 1978). To solve this problem, individuals must be able either to hibernate or to utilize a sequence of foods. For birds, storage of sufficient fat to survive several months without food is precluded by the mechanical limitations of flight. Only large and flightless birds, such as penguins (Spheniscidae), are known to exist for long periods of time off fat reserves. For a highly mobile group such as birds, organized migration is a simple way to obtain an almost continuous food supply when seasonal pulses of productivity follow predictable sequences from latitude to latitude. Seasonally predictable but nonsynchronous pulses of prey productivity at different locations would favor those individuals that inherit the behavioral and physiological equipment to migrate to appropriate locations at appropriate times of the year.

Early departure from the breeding ground is important for patterns of social organization in breeding shorebirds (Myers in press) as well as for the issue of what factors influence migration. Our finding of seasonal depletion at a staging area along the migratory route is consistent with a trophic explanation of this departure. If these reductions are sufficient to cause energetic deficits among late arrivals, then competition may be an important selective agent in shaping migratory patterns.

Depletion such as we report here is not unusual for the area. July decreases in the density of invertebrate animal populations have been documented at other locations in Massachusetts (Whitlatch 1977). The role of birds in causing declines at other migratory stopovers has yet to be determined by experimental manipulations.

Our caging study did not permit us to conclude that shorebirds were solely responsible for the observed losses. It would be surprising if prey consumption by juvenile flatfish were to equal prey consumption by shorebirds during July and August. Food consumption by small *P. americanus* has been estimated at 2–3.4% of body weight/day (Pearcy 1962). Food consumption by small birds is thought to

be an order of magnitude greater (e.g., Dorst 1974). Mayaud (1950) reported that food consumption by a captive Sanderling approached its own body weight/day. Small flatfish weigh the same or less than shorebirds. A 10-cm flatfish weighs 20 g and a 15-cm flatfish weighs 60 g, based on a regression for this species by Pearcy (1962). The three early migrants at Plymouth fall into the 25–125-g range. Thus, fish densities would have to exceed bird densities by an order of magnitude in order to have the same impact on prey as shorebirds. Fish would have to attain remarkable densities to match food consumption by birds at some of the well-used sites on White flat. During August 1976 the average count of the three common scolopacids per 1-ha study site ranged from 9 birds at the least-used site to 60 birds at the best-used site.

Our finding of food depletion at a migratory stopover is consistent with the hypothesis that migratory timing is a trait that is actively maintained by selective forces created by seasonal production of food supplies. Direct confirmation of this hypothesis requires some demonstration that the timing and direction of migration has a heritable component and that tardy arrivals have a lower survivorship or reproductive success than birds that arrive when prey supplies are at seasonal maxima.

LITERATURE CITED

BAKER, M. C., & A. E. M. BAKER. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. Ecol. Monogr. 43: 193–212.

CLARKE, W. E. 1912. Studies in bird migration. London, Gurney and Jackson.

DORST, J. 1956. Les migrations des oiseaux. Paris, Payot.

——. 1974. The life of birds. New York, Columbia Univ. Press.

IWANOWICZ, H. R., R. D. ANDERSON, & B. A. KETSCHKE. 1974. A study of the marine resources of Plymouth, Kingston, and Duxbury bays. Massachusetts Dept. Nat. Res. Monogr. 17: 1–37.

LACK, D. 1960. The influence of weather on passerine migration. A review. Auk 77: 171–209.

MAYAUD, N. 1950. Alimentation. Pp. 654–688 in Traite de Zoologie, vol. 15 (P.-P. Grasse, Ed.). Paris, Masson et cie.

MYERS, J. P. In press. On cross-seasonal interactions in the evolution of sandpiper social systems. Behav. Ecol. Sociobiol.

PEARCY, W. G. 1962. Ecology of an estuarine population of winter flounder, Pseudopleuronectes americanus (Walbaum). IV. Food habits of larvae and juveniles. Bull. Bingham Oceanogr. Coll. 18: 65–78.

PHILLIPS, A. R. 1951. Complexities of migration: a review with original data from Arizona. Wilson Bull. 63: 129–136.

PITELKA, F. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. Condor 61: 233–264.

RICHARDS, S. W., & G. A. RILEY. 1967. The benthic epifauna of Long Island Sound. Bull. Bingham Oceanogr. Coll. 19: 89–135.

RICHARDSON, W. J. 1978. Timing and amount of bird migration in relation to weather. A review. Oikos 30: 224–272.

SINCLAIR, A. R. E. 1978. Factors affecting the food supply and breeding season of resident birds and movement of Palaearctic migrants in a tropical African savannah. Ibis 120 :480–497.

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman.

THOMSON, A. L. 1926. Problems of bird migration. London, G. Witherby Ltd.

VAN TYNE, J., & A. J. BERGER. 1959. Fundamentals of ornithology. New York, John Wiley.

WALLACE, A. R. 1874. Migration of birds. Nature 10: 455.

WALLACE, B. 1968. Topics in population genetics. New York, Norton.

WETMORE, A. 1926. The migration of birds. Cambridge, Massachusetts, Harvard Univ. Press.

WHITLATCH, R. B. 1977. Seasonal changes in the community structure of the macrobenthos inhabiting the intertidal sandflats of Barnstable Harbor, Massachusetts. Biol. Bull. 152: 275–294.

WILLIAMSON, K. 1953. Migration into Britain from the north-west, autumn, 1952. Scottish Natur. 65: 65–94.

WOLDA, H. 1978. Fluctuations in abundance of tropical insects. Amer. Natur. 112: 1017–1045.

THE WILSON ORNITHOLOGICAL SOCIETY ANNOUNCES LOUIS AGASSIZ FUERTES, MARGARET MORSE NICE, AND PAUL A. STEWART AWARDS

Fuertes Awards are available to all ornithologists, although graduate students and young professionals are preferred. Nice Awards are intended for independent researchers without access to funds and facilities available at colleges and universities, and thus are restricted to amateurs, including high school students. Any type of research may be funded by both Fuertes and Nice Awards. Stewart Awards are available to any applicant for ornithological research, especially for studies of bird movements based on banding and analysis of recoveries and returns and investigations in economic ornithology.

One Fuertes Award of at least $100, one Nice Award of $100 and one or more Stewart Awards of $200 each will be made. Interested applicants should write to **Carl D. Marti, Department of Zoology, Weber State College, Ogden, Utah 84408.** Completed applications must be received by **1 March 1982.** Decisions will be announced at the 1982 Annual Meeting of the Wilson Ornithological Society, to be held 6–9 May 1982.