

# THE AUK

A QUARTERLY JOURNAL OF  
ORNITHOLOGY

VOL. 98

APRIL 1981

No. 2

## DO SHOREBIRDS COMPETE ON THEIR WINTERING GROUNDS?

DAVID C. DUFFY,<sup>1</sup> NATASHA ATKINS,<sup>2</sup> AND DAVID C. SCHNEIDER<sup>3,4</sup>

<sup>1</sup> Charles Darwin Station, Isla Santa Cruz, Galapagos Islands, Ecuador;

<sup>2</sup> School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut 06511 USA; and

<sup>3</sup> Manomet Bird Observatory, Manomet, Massachusetts 02345 USA

**ABSTRACT.**—If migratory shorebirds (Charadrii) are limited through competition on tropical wintering grounds, then the intensity of competition should increase during the boreal winter, when large numbers of nearctic breeders and their offspring move into their wintering grounds. We tested this hypothesis by making four specific predictions: (1) individual species will increase or decrease their range of habitat and microhabitat use as local densities rise during the boreal winter; (2) species with flexible feeding methods will change them; (3) birds will forage for a greater part of the tidal cycle at higher densities; and (4) food will become scarcer during periods of high density of foraging birds. We carried out our study at Paracas, on the Peruvian coast, by comparing bird numbers and foraging behavior during the boreal summer (May–July 1977) and winter (January and February 1979). Despite the higher density of foraging birds in the winter, we found no systematic change in microhabitat use, nor was there feeding over more of the tidal cycle. We found some suggestion of a shift in the use of major habitat types in the boreal winter, but this was due to greater use of one habitat by a number of species. We found no evidence of any drop in food availability from January to February 1979. Our study was carried out at a major tropical wintering area; the data we collected here do not support the hypothesis that competitive shifts or population limitation necessarily occur on tropical wintering grounds. Received 7 January 1980, accepted 12 September 1980.

THE study of the natural regulation of animal numbers is one of the central concerns of ecology, yet direct data on the subject are scarce because of the difficulties of censusing wild populations or measuring many environmental variables. A potentially profitable approach, at least in stimulating discussion and research, has been the postulating of hypothetical limiting factors and the search for the predicted consequences of such limitations.

Baker and Baker (1973) used this approach to investigate the relative importance of various agents that might limit the numbers of North American shorebirds. Combining a review of the literature with their own field studies (Baker 1973, 1977; Baker and Baker 1973), they concluded that most adult mortality took place away from the breeding grounds and that "shorebird populations are regulated through competitive processes occurring on their wintering habitat."

Their major test involved the prediction that, in the face of greater competition, shorebirds would have narrower feeding niches in order to avoid interspecific competition. The Bakers' field work showed that shorebirds do have narrower feeding niches on their wintering grounds in Florida than on the breeding grounds in Canada. The same narrowing of feeding habits, however, could have also resulted from

---

<sup>4</sup> Present address: Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717 USA.

greater selectivity in response to greater food availability, a mechanism suggested by MacArthur and Pianka (1966) and Krebs (1978). It is also possible that each species of shorebird feeds on only a few types of prey but that prey species on the tundra are widely distributed across a variety of microhabitats, while prey in Florida are more restricted.

Because of these uncertainties, we chose an alternative test. If shorebirds are limited through competition on tropical wintering grounds, then the intensity of competition should vary with the density of shorebirds, resulting in changes in feeding behavior, habitat use, or the availability or rate of supply of food. As in other niche studies, we assumed that optimal foraging styles or habitats would differ among bird species under conditions of resource limitation. Interspecific differences in optimal foraging styles or location are at least possible for shorebirds feeding in the intertidal zone, which exhibits variation in substrate composition, water content, and the depth, distribution, and size of marine invertebrates. We also assumed that, under conditions of food limitation, a measurable change in feeding would occur due either to behavioral plasticity of individuals or to differential mortality. Behavioral plasticity has been reported frequently in shorebirds (Goss-Custard 1970, 1977; Baker 1974; Hartwick and Blaylock 1979; Myers et al. 1979b; Strauch and Abele 1979). Differential mortality related to differences in feeding mode has not been reported in shorebirds. If it occurs, it should be rapid, due to the demands of homeothermy.

If competition for food limits shorebirds, we make the following predictions:

1. A species will change its use of habitat and microhabitat as densities change, using relatively few habitats if competition comes from other species and using habitats more equally if competition comes from conspecifics (MacArthur and Pianka 1966; MacArthur 1972).

2. Shorebird species with flexible methods will change them as the densities of shorebirds change. If intraspecific competition is responsible, species should show a more equal use of foraging methods in the winter than in the summer. A more unequal use of foraging method should result from greater competitive pressure from other species.

3. Shorebirds will forage over a greater range of the tidal cycle at higher densities if food is more difficult to obtain (Evans 1976).

4. Food will be scarce and become scarcer with time. It will be possible to measure the effect of shorebirds on the abundance or rate of supply of food.

To test these predictions we visited the same wintering ground twice: once during the boreal summer when shorebird densities were low and then again during the boreal winter when more shorebirds were present.

#### METHODS

We carried out our study at a major wintering ground of shorebirds, the Reserva Nacional de Paracas and the wetlands around the town of Pisco, Departamento de Ica, Peru, 13°40'S, 76°08'W. We visited the area from 21 May to 13 July 1977, and from 15 January to 5 February and 14–16 February 1979. The coastline runs south to north but is broken south of Pisco by the Paracas peninsula, a head-shaped promontory that creates a northward-facing bay, the Bay of Paracas. A strong upwelling occurs offshore, and the winds in the Pisco area show a strong landward set from May to July and from August to September (Gunther 1936). The tides are semidiurnal, with a range of about 1 m. We studied 11 sites, which represented the major habitats of the area (Fig. 1).

1. La Mina: Four rock ledges on the southeast side of the Paracas Peninsula, with an intertidal area of about 0.1 ha. These ledges are exposed to a strong swell. About a quarter of the area, near the low tide mark, is covered by barnacle and mussel beds.

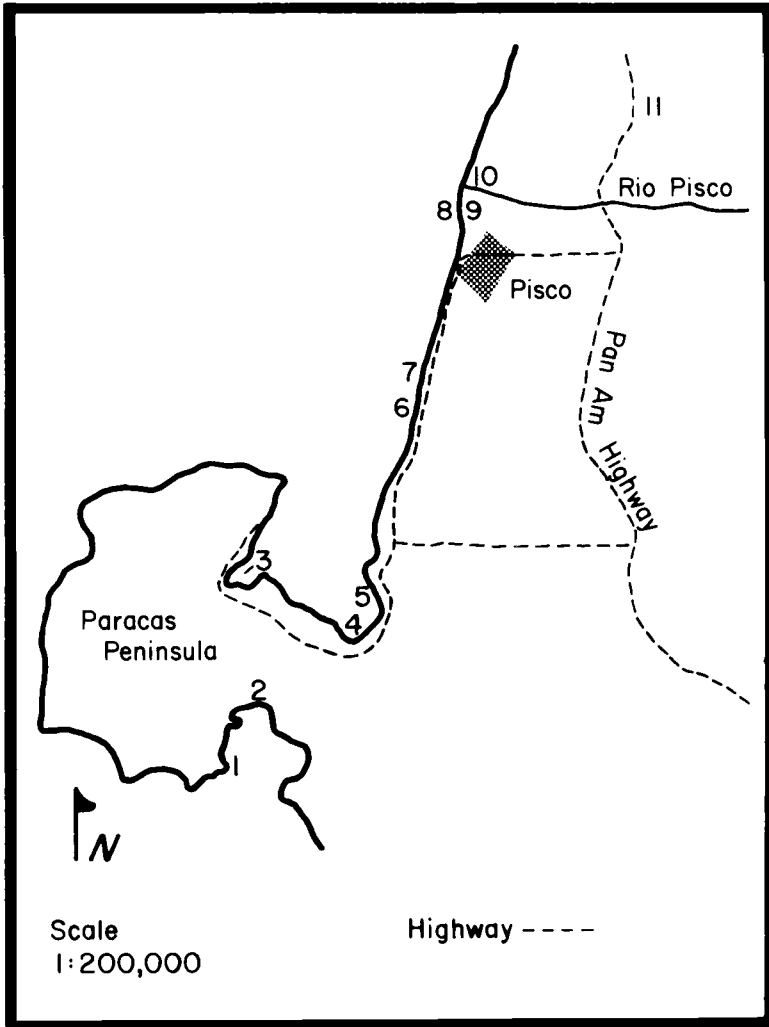


Fig. 1. Study sites at Paracas and Pisco, Peru. Numbers refer to study sites described in the text.

2. Lagunillas: Two rock ledges adjacent to the headquarters of the Reserva, with an intertidal area of about 0.2 ha. These ledges are exposed to strong swell and are inhabited by barnacles, snails, limpets, mussels, and a few urchins. The outer perimeter of the ledges, roughly 15% of the total area, was covered in January 1979 by a mat of green algae, which harbored large numbers of amphipods.

3. Sequion: A protected beach with no wave action, located at the head of a narrow cove on the southwest side of the Bay of Paracas. Intertidal area is estimated at around 0.9 ha along about 900 m of shoreline. A sandflat at the head of the cove accounts for almost one-quarter of the intertidal area, the rest of the cove being fringed by a narrow beach with clay banks. Few marine invertebrates inhabit the intertidal zone. Flies are numerous over about 20% of the area, near the mid-tide mark.

4. Bayhead: A series of small inlets along the southeast side of the Bay of Paracas. The intertidal area is approximately 2 ha, with a shoreline of about 2 km at high tide and 3 km at low tide. The beach is exposed to little or no wave action and consists of poorly sorted sand, evidently blown into the bay from the south by the prevailing winds. The lower beach is inhabited by polychaetes and small crustaceans; there are flies and a few other insects in the upper intertidal where algae is deposited by extreme tides.

5. Dunes: A sandy beach along the eastern shore of the Bay of Paracas. The intertidal area is roughly

1 ha with a shoreline of 1.5 km. The beach is 5–10 m in width, with a few muddy flats at low tide along the southern end. High tide reaches the foot of the low dunes to the east, which are covered with *Portulaca* sp. Most of the invertebrate life on this beach is carried ashore in the algal wrack that is blown ashore by the afternoon wind and is stranded at falling tide. A few crabs inhabit the piles of dead shells, principally mussels, that are heaped along the shore.

6. Kilometers 22–23, Pisco-Paracas Highway: A steep cobble beach exposed to strong swell. The intertidal area is less than 0.1 ha, with a shoreline of exactly 1 km. The substrate consists of banks of dead shells washed up or deposited by fishermen.

7. Kilometers 23–24, Pisco-Paracas Highway: The intertidal area is much broader than at the preceding site, extending 50–100 m out from the beach. An offshore bar reduces the intensity of swell, allowing a heavy growth of algae on the pebble-cobble substrate. Amphipods inhabit the algae. The site is down current from a fish meal plant and is periodically covered by fish oil. Recovery seems to take less than 1 month.

8. Pisco Playa: A steep sandy beach just north of the town of Pisco. The beach is exposed to strong surf and is overwashed during the monthly highest tides. The intertidal is roughly 0.5 ha along 1 km of shore. The macrofauna are limited to a few donacid clams.

9. Pisco Ponds: This site (20 ha) is located behind the Pisco Playa barrier beach. It is intersected by a causeway. A pond to the south of this is approximately 1.8 ha, of which about one-half is shallow enough for shorebirds to use. The small pond to the north of the causeway is estimated to be 0.8 ha, almost all of it usable by shorebirds. A very large pond farther north was not measured. The ponds and surrounding grass are flooded during spring tides, then slowly drain and evaporate. Cattle and goats keep the grass short. Large quantities of oily fish residue had been dumped in the ponds from a fish meal plant at the causeway. Fish, fly larvae, and corixid beetles inhabit the shallow pools. Amphipods and beetles inhabit the wet grass around pond margins. The amount of damp ground and shallow water fluctuates during the month. Pools and damp ground accounted for more than half of the area during a run of neap tides in late January.

10. Rio Fields: A field no longer in cultivation, roughly 5 ha in area, just north of main channel of Pisco River.

11. Agua Santa: A series of salt sloughs, short-grass fields, and reed beds lying in a depression in the desert north of Pisco. The water in this depression comes out of the mountains from the east, flows under the old Pan-American highway through culverts, and then westward through a series of channels. Overflow spreads out into large shallow ponds with salt deposits that are white or tinted green and pink. The salt grasses are kept short by grazing goats, and the shallow pools are inhabited by fly larvae, snails, fish, and corixid beetles. Two ponds were regularly surveyed. The largest pond west of the old highway has an area of roughly 3 ha, of which about one-third is usable by shorebirds. The largest pond just east of the old highway is roughly 10 ha in area, with half of this being shallow enough to be usable by shorebirds.

*Census counts.*—During our May–July visit, we censused each site at least four times during each of four tidal stages; during January, we visited each site two different times during a tidal stage.

We divided the tidal cycle into four stages. High and Low occurred from 1 h before to 1 h after the times of dead high and dead low tides according to Peruvian naval tables (Anon. 1978, 1979). Rising and Falling tides were the remaining, intervening periods.

Censuses were made by identifying and counting all birds at a study site. In addition, the feeding microhabitat and method were recorded for each active bird (see below), except for one study site (Bayhead) where we selected two study plots for the collection of feeding data in 1979. We never censused a site on consecutive tides and rarely censused a site more than once a day.

The only species identification problems were with Semipalmated and Western sandpipers (*Calidris pusilla* and *C. mauri*). We realized that there is considerable overlap in bill length (Phillips 1975, Stevenson 1975), but we called birds with long and slightly drooping mandibles Western Sandpipers and those with shorter bills Semipalmated Sandpipers. For intermediate cases or when we could not distinguish the bill, we called them “peep.” Our identification methods were consistent with previous studies in the area, for we found the same characteristics noted by Ashmole (1970): a tendency for Western Sandpipers to feed by probing and to feed in deeper water.

*Microhabitats.*—We divided the substrates into 10 microhabitats: grass; dry mud; wet mud; dry sand; wet sand; wrack; rock and its epifauna; ankle-deep water; knee-deep water; and belly-deep water. Not all microhabitats were represented at each site. All feeding birds were assigned to one or more of the microhabitat categories. If an individual fed in two habitats, that bird was given a value of 0.5 in each.

*Feeding method.*—Baker and Baker (1973) distinguished several components of foraging behavior in

shorebirds: pecking versus probing, single and multiple probing, locomotion between attempts, etc. We measured pecking versus probing because of our previous experience with the lability of this component in individual Semipalmated Sandpipers at Plymouth, Massachusetts. Individual birds were assigned to one or the other category during a count, depending on the behavior that it displayed when counted. If a bird used both behaviors during a count, it was assigned a value of 0.5 in both categories.

*Food availability.*—We collected and analyzed fecal pellets at each of the major sites in order to determine the major prey of shorebirds. Polychaetes were identified to family by setae and jaws. Hinges were used to identify clams, legs were used to identify arthropods, bones indicated the presence of fish, and echinoderms could be identified by their distinctive skeletal remains. Nemertean worms were the only potential prey without hard parts. These worms are often visible between capture and ingestion by shorebirds.

We tested for change in prey availability during the boreal winter by making counts in January relative to some unit of effort, as described below, then repeating that method at the same site a month later. On exposed intertidal flats the unit of effort was a 10-cm diameter core taken to a depth of 10 cm. Ten centimeters exceeds the bill length of any shorebird commonly found at Paracas. For algae washing ashore at one site, Dunes, we counted the number of animals in a clump of algae, then divided by the area covered by that clump. In the short grass at Pisco Ponds we counted the number of insects and amphipods visible along 1-m by 2-cm transects created by parting the grass.

We set up an enclosure to see if shorebirds had any impact on prey numbers at Bayhead, a site with some of the greatest density of feeding shorebirds. We nailed a square cage (1 m by 1 m) made of chicken wire to the top of four stakes driven into the sand. The sides of the cage extended down the stakes to about 20 cm above the sand, a design that allows high-tide predators, such as fish, to enter. We observed the feeding movements of birds around the canopy to make sure that this design discouraged entry by birds. We collected two core samples under the canopy and three within 1 m of the canopy on 24 January 1979. After 25 days we took four samples inside and four samples within 2 m of the canopy. All cores were 10 cm in diameter, 10 cm deep, washed on a 1-mm sieve, and counted while the animals were still alive.

*Data analysis.*—Because of the number of bird counts and the difficulty of ensuring that data were normally distributed, we employed nonparametric statistical tests. We analyzed change in habitat usage and feeding method by using a convenient measure of dispersion, the coefficient of variation (CV); (Sokal and Rohlf 1969). The CV was computed from the mean and variance in counts of birds per species at each site, birds per microhabitat at each site, and frequency of each feeding method for each species at a site. A CV was computed for each species and each of four tidal periods to control for changes in foraging method or habitat usage due to tidal stage. A decrease in CV from the boreal summer to the boreal winter indicated that birds had used habitats, microhabitats, or feeding methods in a more equitable manner. An increase in this statistic meant that birds were using fewer habitats, microhabitats, or feeding methods. The number of categories remained the same in summer and winter analyses. We applied the McNemar test for significance of changes, with the Binomial Test (Siegel 1956) to see whether increases or decreases in CV prevailed to any significant degree in any one comparison.

## RESULTS

*Changes in density.*—Before testing for shifts in feeding or site use, we had to determine whether or not more birds were, in fact, using the Paracas region during the boreal winter than during the summer.

We analyzed data from the four major sites: Bayhead, Dunes, Sequion, and Pisco Ponds, because these were the most densely populated sites during summer and winter visits. At each site the mean number of birds per count was compared for the two seasons. In 15 of the 16 cases, there were more birds present during the northern winter (Wilcoxon signed ranks test, one-tailed,  $P < 0.005$ ; Fig. 2). Most of the increase came from the more common species such as Sanderling (*Calidris alba*) and Semipalmated and Western sandpipers. Black-bellied Plover (*Pluvialis squatarola*), Semipalmated Plover (*Charadrius semipalmatus*), and Greater Yellowlegs (*Tringa melanoleuca*) increased to a lesser degree, while some of the less common species [Short-billed Dowitcher (*Limnodromus griseus*), Ruddy Turnstone (*Arenaria*

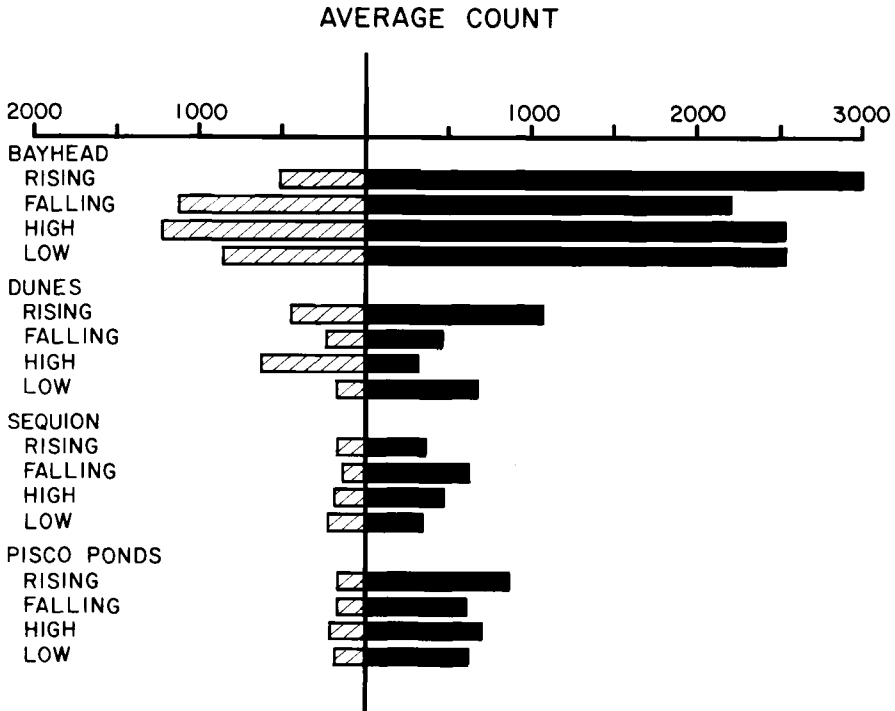


Fig. 2. Shorebird counts at Paracas, Peru during the boreal summer (May–July 1977; diagonal bars) and the boreal winter (January–February 1979; solid bars).

*interpres*), and Knot (*Calidris canutus*)] actually became less frequent during the boreal winter.

1. Site use. For each of the eight most common species, we compared the proportional use of sites at high (boreal winter) and low (boreal summer) shorebird densities. One site, Agua Santa, was excluded because major changes in water level attracted birds to areas that were difficult to observe. We analyzed the coefficients of variation (Fig. 3) for each species during both seasons, predicting (1) clumping of each species into a narrower and unique habitat range (a higher CV) as a response to interspecific competition, or (2) spreading out across habitats (a lower CV) in response to intraspecific competition. Two species showed a decreased CV. The remaining six species had increased CV values, suggesting an increased specialization in response to increased interspecific competition. These six, however, all showed identical shifts in habitat use: a decrease in use of the Dunes and an increase in use of Bayhead and Pisco Ponds. The disproportionate use of these two sites during the boreal winter can be seen in Fig. 2. This lack of separation of species into unique habitats points to changes in the environment rather than increased specialization by each species.

2. Microhabitat use. We examined microhabitat use at the four major sites for the most common species. We analyzed the coefficients of variation for each species by tidal stage (combining sites), making predictions similar to those described above for site use. For the eight species analyzed, 41 of the records showed an increase in CV and 43 a decrease. There was no consistent response to the higher shorebird densities during the boreal winter.

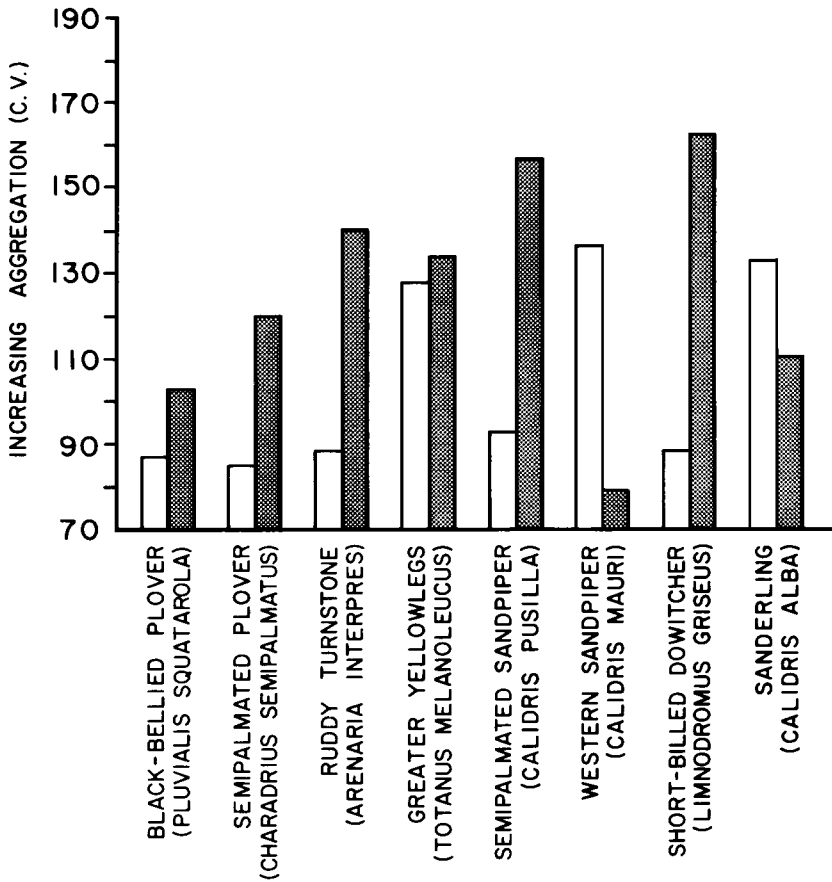


Fig. 3. Change in the distribution of common shorebird species over 10 study sites, representing the range of habitats used by shorebirds at Paracas Bay, Peru. Low values indicate even distribution; high values indicate aggregation of species at a few sites. Light bars represent birds during boreal summer (May-July 1977), and shaded bars represent boreal winter birds (January-February 1979).

3. Shifts in feeding method. Not all species of shorebird used both pecking and probing, so we confined our analysis to those species that were present in both summer and winter and that used both methods in at least one period. We expected to see an increase in CV if birds responded to competition by restricting themselves to one feeding method and a decrease if birds responded by diversifying their feeding mode.

We found that the CV increased for one species and decreased for four other species at the higher densities prevailing in the boreal winter. Because we were looking at variation between categories, this result points to a more equitable use of pecking and probing at high bird densities.

4. Foraging intensity. We predicted that competition for food at the high densities prevailing in the boreal winter would result in a less restricted use of certain parts of the tide cycle, as birds increased their time spent looking for food. Goss-Custard et al. (1977) note that overwintering shorebirds in Britain spend more time foraging at high tide, apparently in response to the difficulty in obtaining food. The time that birds spent foraging could not be measured without banding large numbers of birds,

TABLE 1. Instances of an increased or decreased proportion of birds feeding during the boreal winter, as compared to the boreal summer, for major species, major sites, and for each tidal period.

	Increases	Decreases	Significance ( <i>P</i> )
Species			
Black-bellied Plover	3	12	0.018
Semipalmated Plover	5	7	0.387
Ruddy Turnstone	5	8	0.151
Greater Yellowleg	4	4	0.637
Semipalmated Sandpiper	6	6	0.613
Western Sandpiper	6	6	0.613
Sanderling	1	12	0.003
Site			
Bayhead	10	17	0.125
Sequion	4	16	0.006
Dunes	8	8	0.598
Pisco Ponds	8	14	0.143
Tidal stage			
Low	8	13	0.19
Rising	7	17	0.03
High	8	12	0.25
Falling	7	13	0.13

so we chose an alternative measure, the proportion of birds feeding at any one time. We tested our prediction by looking, within each of the seven most common species, at the proportion of birds actively feeding within each of four tidal periods. This design gave us 112 potential comparisons (4 locations  $\times$  4 tides  $\times$  7 species) of the percent of birds feeding in summer with birds of the same species, same tide period, and same location in the boreal winter. Of these comparisons, we found 30 cases of an increased proportion of birds feeding, 55 cases of a decreased proportion, and 27 cases that proved to be unscorable because of a lack of birds upon which to compute a proportion. We broke these totals down by species, location, and site (Table 1) and found that Sanderlings and Black-bellied Plovers showed a significantly greater number of instances of a decreased proportion of birds feeding in the winter, at high densities, than in the summer, at lower densities. Despite the presence of more birds in the boreal winter, we found that birds did not feed during a wider range of the tidal cycle.

*Food availability.*—Our final prediction was that increased pressure on food supplies would reduce the density of prey. We determined the major types of prey by looking at fecal pellets and by watching foraging at sites where we knew which types of invertebrates were present. Table 2 shows which animals were available as prey at each of the four major sites and which were found in fecal pellets. We focused our attention on the three species of *Calidris*, because by virtue of similar size and large numbers these were the most likely to interact competitively.

The type of prey taken depended on site. At Dunes a gammaridean amphipod made up the bulk of the fecal pellets and was the most common invertebrate in the macrophytic algae washing ashore. At Bayhead fecal pellets collected contained ostracod remains, the setae and jaws of nereid polychaetes, and setae from other polychaetes. Spionid and capitellid polychaetes were the most common invertebrates in the intertidal mud at Bayhead. Flies at Sequion far outnumbered the few marine invertebrates found in the intertidal mud. Fly larvae and pupae were the only visible animals found in the mud banks used for foraging by sandpipers. Fecal pellets from





TABLE 3. Results of bird exclosure experiment at Paracas, Peru in 1979. Numbers are animals present in each 10-cm diameter core. Each column represents one core sample. The null hypothesis of no change was tested against the alternative hypothesis of proportionately more organisms beneath the canopy after the experiment.

		24 January					18 February						
		Inside		Outside			Inside			Outside			
Spionids	<0.5 cm	103	110	178	49	71	0	20	0	0	0	0	0
	0.5-1 cm	8	34	11	2	10	30	90	50	99	13	19	22
	>1 cm	0	0	0	0	0	16	36	55	36	16	21	14
Capitellids	<1 cm	1	9	4	1	5	61	47	55	66	60	71	61
	1-2 cm	1	0	4	0	0	0	74	34	26	0	2	0
	>2 cm	0	0	0	0	0	0	1	1	1	1	0	0
Tanaids		0	1	1	0	0	7	4	3	2	3	0	2
Total in each core		113	154	194	52	86	114	272	198	230	93	113	99

		Inside/Outside		$H_0: A(I/O) = B(I/O)$ $H^1: A(I/O) > B(I/O)$
		Before	After	
Spionids	<0.5 cm	0.57	20/0	$\chi^2 = 35.1 H^1$ accepted $P < 0.001$ $\chi^2 = 4.67 H^1$ accepted $P < 0.05$ $\chi^2 = 16.54 H^1$ accepted $P < 0.001$
	0.5-1 cm	2.74	3.64	
	>1 cm	$I = 0$	1.74	
Capitellids	<1 cm	1.5	0.98	$H^1$ rejected: $A(I/O) < B(I/O)$ $\chi^2 = 184.5 H^1$ accepted $P < 0.001$ sample too small to test at 5% level
	1-2 cm	0.38	4.19	
	>2 cm	$I = 0$	3.0	
Tanaids		$I = 0$	2.29	$\chi^2 = 4.49 H^1$ accepted $P < 0.05$

these birds consisted of small flecks, possibly the remains of immature flies. At Pisco Ponds fecal pellets of sandpipers contained the easily recognized remains of beetles, one of the most common invertebrates living in the higher parts of the marsh. Fecal pellets from Agua Santa consisted largely of the wings and legs of corixids, one of the few forms of life found in this habitat (Table 2).

We predicted that the availability of prey would drop in response to feeding pressures of the large numbers of birds at well-used sites. To test this, we collected samples at one or more sites within each habitat in January, then repeated a sample at the same site in mid-February. Samples were relocated to within 5 m of the original site, to reduce the effects of patchy invertebrate distribution on estimates of change in availability of prey and potential prey. We found nine cases of more invertebrates at a location on the second visit and six cases of fewer invertebrates (Table 2). This did not differ significantly from the distribution of cases under the hypothesis of no change (equal number of decreases and increases). The sample size was sufficient to detect a decrease of 50% or more at the 5% confidence level. Thus we could not accept the hypothesis that invertebrate numbers decreased at foraging sites.

As a second test for change in prey availability, we carried out a more intensive study at one of the more heavily used sites, Bayhead. On 25 January we took five cores at 20-m intervals in one foraging transect. We took two replicate cores at three sites distributed through the other foraging transect. We took replicate cores at all eight sites on 18 and 19 February. At only one of the eight sites did we find fewer invertebrates. Because shorebirds tend to take larger prey items (for summary of studies see Griffiths 1975), we also looked at changes within size categories. For animals less than 1 cm in length, we found nine cases of increased numbers and one case of decreased numbers. For animals greater than 1 cm in length, we found five

cases of increased numbers and three cases of decreased numbers. We had a total of 18 cases, rather than 8, because we made comparisons for several groups at one site: capitellids, spionids, etc. The chances of obtaining 14 increases and 4 decreases in a situation where increases actually equal decreases is about 1 in 10. The chances of obtaining this in a situation where decreases are twice as numerous as increases is less than 1 in 100.

As a third test we set up a caging experiment to see if birds had any impact on prey numbers. We set the canopy up at a site used by large numbers of foraging shorebirds in order to increase our chances of finding a decrease in prey numbers. The canopy reduced usage by foraging shorebirds, based on the observation that *Calidris* sandpipers walked around rather than under the canopy. The results of the experiment (Table 3) show that the density of invertebrates outside of the canopy did not change significantly ( $P < 0.05$ ) during the course of the experiment. The density of animals beneath the wire canopy rose to a significant degree during the experiment (Table 3). Shorebirds did not reduce prey density at one of the heavily used sites in our study. We tried to increase our chances of finding a drop in the number of invertebrates by visiting all foraging sites, choosing patches of high prey density for repeated sampling, and choosing a site with high bird density to carry out the caging experiment. Despite our best efforts in three different tests, we could not accept the hypothesis that invertebrate numbers decreased.

#### DISCUSSION

If the wintering grounds are the place of greatest stress for shorebirds, leading to population regulation (Baker and Baker 1973), then we might expect to see reduction of food resources and shifts in foraging behavior on the wintering grounds. The best evidence for food limitation of shorebirds on wintering grounds comes from Europe, at a temperate latitude, where birds deplete food supplies (Goss-Custard et al. 1977, O'Connor and Brown 1977, Evans et al. 1979) and some bird species have substantial mortalities (Heppleston 1971).

In contrast, we found no evidence of a narrowing of habitat use or feeding method such as one might expect to result from interspecific competition at tropical latitudes, nor did we find reductions in prey density comparable to those reported from higher latitudes. We found some expansions in usage, such as one might expect from intraspecific pressures. Birds did not spend a greater proportion of their time foraging in the winter than in the summer, however, and thus did not seem to be facing any greater stress than at lower summer densities. Our data do not support the hypothesis that population limitation in shorebirds always occurs on the wintering grounds.

Results similar to ours have been reported from wintering grounds other than Europe. Strauch and Abele (1979) concluded that three species of plover do not actively compete during the winter in Panamá. Schneider, working in the same area (MS), found no evidence of reduction in prey density during the last third of the wintering season. Hartwick and Blaylock (1979) concluded that food was neither limiting Black Oystercatchers (*Haematopus bachmani*) in California nor being depleted by them.

It might be objected that these studies, like ours, are in some way atypical, because they were carried out in areas of coastal upwelling and high productivity. It should be noted, however, that all of the large concentrations of shorebirds re-

ported for the neotropics (Murphy 1936, Spaans 1978) coincide with the upwellings reported by Schott (1931a,b).

Our study, like any other niche study, rests on a number of premises. The major premises of this study were: (1) increase in bird numbers results in increased pressure on critical resources, especially food supplies, and increased pressure on food supplies in turn reduces these below some level that becomes critical for individual birds; and (2) reduction of food supplies to a critical level results in an observable shift in foraging behavior, due either to behavioral plasticity of individuals (habitat selection, foraging style, etc.) or differential survivorship of individuals with differing behaviors. A failure to observe a shift under conditions of food limitation could result from several mechanisms: lack of behavioral plasticity, delayed mortality, or the exact balancing of intraspecific (diversifying) and interspecific (convergent) competitive forces. Balancing forces or a lack of plasticity seem unlikely in our study, because we did observe a shift toward disproportionate use of the same habitat by several species. Delayed mortality is effective only if birds are unable to remedy a deficient fat reserve en route northward. It is possible that competitive interaction leading to changes in foraging behavior occurs intermittently in the tropics rather than every year (Wiens 1977). A test of this must await a long-term study.

We suggest that other factors may be reducing the importance of competition for food on tropical wintering grounds.

1. Number and spacing of staging areas. A number of studies have identified "staging grounds" that may be critical for the successful completion of migration (Bradstreet et al. 1977, Ferns et al. 1979, Hughes 1979, Isleib 1979, Senner 1979). The number and spacing of these areas may be especially critical for smaller species, in which power to weight relations dictate intermediate stopovers (Odum et al. 1961). The reduction of estuarine areas in North America (e.g. Speth 1979) could represent a new pressure for some migrants.

2. Food at migration stopovers. The resources available at staging areas, rather than the cost of moving between distant areas, may be limiting if food is depleted at staging areas (e.g. Schneider 1978) and birds require maximum fat reserves to complete migration, as suggested by McNeil (1969). Berthold (1975) cites longer estimated flight ranges for shorebirds than does McNeil; thus it would be of interest to know whether shorebirds with less than maximum fat reserves show reduced survivorship or arrive in South America in poor condition.

3. Territoriality. Territoriality may limit some populations of birds (Kluyver and Tinbergen 1953), and wintering shorebirds may defend feeding territories, presumably to protect food or access to food (Myers et al. 1979a). If territoriality is important in regulating shorebirds in winter, however, one would expect far less of the variability characteristic of this behavior (Myers et al. 1979a). Further work may show that for certain species [e.g. plovers (*Pluvialis* spp. and *Charadrius* spp.)] and certain habitats (e.g. "short grass pampas and seasonal wetlands of coastal Argentina": Myers et al. 1979a) territoriality limits the resident population. For others, such as Sanderlings, territoriality breaks down at high densities, suggesting that it is ineffectual in regulating numbers in an area for at least this species (Myers et al. 1979b).

4. Predation on the wintering ground. Goss-Custard (1979) and Prater (1979) regard winter predation by raptors as negligible in Britain, but at lower latitudes Page and Whitacre (1975) found that raptors could take a significant proportion of wintering shorebirds in California. We have no data on this for Peru, but we did

observe two or three Peregrine Falcons (*Falco peregrinus*) hunting shorebirds in our study areas. T. Luscombe (pers. comm.) has found coastal marshes to be an important winter habitat for this falcon in Peru. In Panamá, one of us (DCS) observed these falcons hunting shorebirds at two sites on the Bay of Panamá, Farfan, and Agua Dulce. Peregrine Falcons and other raptors are currently reduced in numbers because of environmental contaminants (Hickey 1969). Thus predation by raptors may have been more important for shorebirds in the past.

5. Storms and bad weather. Evans (1976) and Heppleston (1971) suggest that inclement weather may restrict feeding and increase heat loss so that conditions become critical for survival over short periods of time. Major mortality may follow extended periods of bad weather (Dobinson and Richards 1964). Storms are not restricted to temperate latitudes. Sand storms at Paracas can bury intertidal organisms under several centimeters of sand and dust (Craig and Psuty 1968: 77, cf. Plate 4-3c), reducing the rate of food supply to shorebirds.

6. Parasitism and disease. There are no studies of the relation between disease and parasitism in the ecology of shorebirds. Studies of the importance of parasite levels, fat storage, and breeding condition in shorebirds may prove to be interesting, because we have found parasites in the intestines of more than half of the 16 birds collected at Plymouth, Massachusetts (42°N, 70°40'W).

#### CONCLUSIONS

Our study resulted in no evidence that nearctic shorebirds face strong competitive pressures on a tropical wintering ground. Thus factors other than competition must be considered in further studies of this group in the tropics. A complete enumeration of major wintering areas and an explanation of why each attracts large numbers of these arctic migrants represent the necessary first steps in planning for the survival of these species.

#### ACKNOWLEDGMENTS

We thank The Organization of American States, The International Union for the Conservation of Nature, The International Council for Bird Preservation, the National Science Foundation, and Princeton University for their support of this work. Thanks go to the Ministerio de Agricultura for permission to work in the Reserva Nacional de Paracas and to Felipe Benavides, who made the facilities at the Paracas Institute freely available. We owe a debt to the following people, who helped us each in his own way: Dr. A. Brack, W. Brown, Dr. M. Dourojeanni, R. Feeney, C. Gamba, C. Hays, Dr. H. Horn, Dr. J. P. Myers, E. Ortiz, M. Plenge, Dr. C. Ponce, B. Torres, and P. Yengle. The two junior authors appreciate the poor marksmanship of a nameless Peruvian soldier while firing at their Land Rover.

#### LITERATURE CITED

- ANONYMOUS. 1978, 1979. Tabla de mareas. Dirección de hidrografía y navegación de la marina. Ministerio de marine, Republica Peruana. Callao.
- ASHMOLE, M. J. 1970. Feeding of Western and Semipalmated sandpipers in Peruvian winter quarters. *Auk* 87: 131-135.
- BAKER, M. C. 1973. Stochastic properties of the foraging behavior of species of migratory shorebird. *Behavior* 45: 242-270.
- . 1974. Foraging behavior of Black-bellied Plover. *Ecology* 55: 162-167.
- . 1977. Shorebird feeding behavior in the eastern Canadian Arctic. *Condor* 79: 56-62.
- , & A. E. M. BAKER. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. *Ecol. Monogr.* 43: 193-212.
- BERTHOLD, P. 1975. Migration: Control and metabolic physiology. Pp. 77-128 in *Avian biology*, Vol. 5 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

- BRADSTREET, M. S. W., G. W. PAGE, & W. G. JOHNSTON. 1977. Shorebirds at Long Point, Lake Erie, 1966–1971: seasonal occurrence, habitat preference, and variation in abundance. *Can. Field-Natur.* 91: 225–236.
- CRAIG, A. R., & N. P. PSUTY. 1968. The Paracas papers. Studies in marine desert ecology. OCC Publ. #1. Boca Raton, Florida, Dept. Geog., Florida Atlantic Univ.
- DOBINSON, H. M., & A. J. RICHARDS. 1964. The effects of the severe winter of 1962/63 on birds in Britain. *Brit. Birds* 57: 373–435.
- EVANS, P. R. 1976. Energy budget and optimal foraging strategies in shorebirds: some implications for their distribution and movement in the nonbreeding season. *Ardea* 64: 117–139.
- , D. M. HERDSON, P. J. KNIGHT, & M. W. PIENKOWSKI. 1979. Short-term effects of reclamation of part of seal sands, Teesmouth on wintering waders and Shelduck. I. Shorebird diets, invertebrate densities, and the impact of predation on the invertebrates. *Oecologia* 41: 183–206.
- FERNS, P. M., A. H. GREEN & P. D. ROUND. 1979. Significance of the Somerset and Gwent lands in Britain as feed areas for migrant Whimbrel, *Numenius phaeopus*. *Biol. Conserv.* 16: 7–22.
- GOSS-CUSTARD, J. D. 1970. The responses of Redshank [*Tringa totanus* (L.)] to spatial variations in the density of their prey. *J. Anim. Ecol.* 39: 91–113.
- . 1977. The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *J. Appl. Ecol.* 14: 721–739.
- . 1979. Effect of habitat loss on the numbers of over-wintering shorebirds. *Studies in Avian Biol.* 2: 167–177.
- , R. A. JENYON, R. E. JONES, P. E. NEWBERRY, & R. LE B. WILLIAMS. 1977. The ecology of the Wash. II. Seasonal variation in the feeding conditions of wading birds (Charadrii). *J. Appl. Ecol.* 14: 701–719.
- GRIFFITHS, D. 1975. Prey availability and the food of predators. *Ecology* 56: 1209–1214.
- GUNTHER, E. R. 1936. A report on the oceanographical investigations in the Peru coastal current. *Discovery Rep.* 13: 109–276.
- HARTWICK, E. B., & W. BLAYLOCK. 1979. Winter ecology of a Black Oystercatcher population. *Studies in Avian Biol.* 2: 207–215.
- HEPPELSTON, P. B. 1971. The feeding ecology of Oystercatcher (*Haematopus ostralegus*) in winter in northern Scotland. *J. Anim. Ecol.* 40: 651–672.
- HICKEY, J. J. 1969. Peregrine Falcon populations, their biology and decline. Madison, Wisconsin, Univ. Wisconsin Press.
- HUGHES, R. A. 1979. Notes on Charadriiformes of the south coast of Peru. *Studies in Avian Biol.* 2: 49–53.
- ISLEIB, M. E. 1979. Migratory shorebird populations on the Copper River delta and eastern Prince William Sound, Alaska. *Studies in Avian Biol.* 2: 125–129.
- KLUYVER, H. N., & L. TINBERGEN. 1953. Territory and the regulation of density in titmice. *Arch. Neerl. Zool.* 10: 265–289.
- KREBS, J. R. 1978. Optimal foraging: decision rules for predators. Pp. 23–63 *in*: Behavioural ecology (J. R. Krebs and N. B. Davies, Eds.). Oxford, Blackwell.
- MACARTHUR, R. A. 1972. Geographical ecology. New York, Harper & Row.
- , & E. PIANKA. 1966. On the optimal use of a patchy environment. *Amer. Natur.* 100: 603–607.
- MCNEIL, R. 1969. La Détermination du contenu lipidique et la capacité de vol chez quelques espèces d'oiseaux de rivage (Charadriidae et Scolopacidae). *Can. J. Zool.* 45: 525–536.
- MURPHY, R. C. 1936. Oceanic birds of South America. New York, Amer. Mus. Nat. Hist.
- MYERS, J. P., P. C. CONNORS, & F. A. PITELKA. 1979a. Territoriality in nonbreeding shorebirds. *Studies in Avian Biol.* 2: 231–246.
- , ———, & ———. 1979b. Territory size in wintering sanderlings. The effects of prey abundance and intruder density. *Auk* 96: 551–561.
- O'CONNOR, R. J., & R. A. BROWN. 1977. Prey depletion and foraging strategy in the Oystercatcher *Haematopus ostralegus*. *Oecologia* 27: 75–92.
- ODUM, E. P., C. E. CONNELL, & H. L. STODDARD. 1961. Flight energy and estimated flight ranges of some migratory birds. *Auk* 78: 518–527.
- PAGE, G. & D. F. WHITACRE. 1975. Raptor predation on wintering shorebirds. *Condor* 77: 73–83.
- PHILLIPS, A. R. 1975. Semipalmated Sandpiper identification, migrations, summer and winter ranges. *Amer. Birds* 29: 799–806.
- PRATER, A. J. 1979. Shorebird census studies in Britain. *Studies in Avian Biol.* 2: 157–166.
- SCHNEIDER, D. 1978. Equalisation of prey numbers by migratory shorebirds. *Nature* 271: 353–354.

- SCHOTT, G. 1931a. Kaltes Wasser vor der Kuste von Venezuela und Kolumbian. *Ann. Hydr. Mar. Met.* 59: 224-226.
- . 1931b. Der Peru-Strom und seine nordliche Nachbargebiete in normaler und anormaler Ausbildung. *Ann. Hydr. Mar. Met.* 59: 161-169, 200-213, 240-252.
- SENNER, S. E. 1979. An evaluation of the Copper River delta as critical habitat for migrating shorebirds. *Studies in Avian Biol.* 2: 131-145.
- SIEGEL, S. 1956. *Nonparametric statistics for the behavioral sciences.* New York, McGraw-Hill.
- SOKAL, R. R., & F. J. ROHLF. 1969. *Biometry.* San Francisco, W. H. Freeman.
- SPAANS, A. L. 1978. Status and numerical fluctuations of some North American waders along the Surinam Coast. *Wilson Bull.* 90: 60-83.
- SPETH, J. 1979. Conservation and management of coastal wetlands in California. *Studies in Avian Biol.* 2: 151-155.
- STEVENSON, H. M. 1975. Identification of difficult birds. III. Semipalmated and Western sandpipers. *Florida Field Natur.* 3: 39-44.
- STRAUCH, J. L., JR., & L. G. ABELE. 1979. Feeding ecology of three species of plovers wintering on the Bay of Panama, Central America. *Studies in Avian Biol.* 2: 217-230.
- WIENS, J. A. 1977. On competition and variable environments. *Amer. Sci.* 65: 590-597.