COMMENTARIES

Paracas Revisited: Do Shorebirds Compete on Their Wintering Ground?

J. P. MYERS[1] AND B. J. MCCAFFERY[2]

Duffy et al. (1981) conclude that strong competitive interactions do not occur among shorebirds in a tropical wintering site, the Paracas Peninsula and surrounding areas of coastal Peru (13°50'S, 76°20'W). Their results rest mainly on a clever series of comparisons of shorebird-niche attributes, made as the density of different species rose and fell with migration. They also found no decline in shorebird-prey abundance over a 1-month period at the peak of shorebird numbers.

We visited their study area from 6 to 9 March 1982. Our observations of shorebird foraging behavior make us uneasy about accepting their conclusions. We censused the birds and observed whether or not there were aggressive interactions among individuals; we were particularly alert to nonbreeding territoriality. We were in the area for other purposes and thus could not gather intensive, quantitative behavioral data. Based, however, on our previous and extensive experience with a broad range of shorebirds defending nonbreeding territories, including all those that did so on the Paracas Peninsula, we detected this behavior readily (Myers et al. 1979a, 1979b; Myers and Myers 1979; Myers 1980).

In a series of censuses we recorded 17 species of Nearctic migrant shorebirds within the study area of Duffy et al. (Table 1). Our species pool was similar to theirs, as were total numbers counted on the sites for which they provide data. Their paper, however, does not break down censuses into species' totals, so at this level differences between the counts may have prevailed.

Of the 17 shorebird species, 10 had both territorial (intraspecific) and nonterritorial members within their local populations. In four species, intraspecific territoriality was the dominant spacing mode. One species (Least Sandpiper, see Table 1 for scientific names) did not defend territories at Paracas but was regularly territorial at other locations in this coastal sector of Peru, where it occurred more commonly than around Paracas.

Two species also showed clear interspecific territorial behavior. Sanderlings and Black-bellied Plovers consistently defended against Semipalmated Plovers. All three of these species defended territories, and the first two repeatedly supplanted the latter on their defended areas. On two occasions Sanderlings stole invertebrates from Semipalmated Plovers. No interactions involved Sanderlings and Black-bellied Plovers. On one occasion, a territorial Black-bellied Plover supplanted two Lesser Golden Plovers intruding within its territory. We emphasize these interspecific interactions because interspecific territoriality is rare among wintering shorebirds (Myers et al. 1979a, Myers and Myers 1979).

Our fieldwork during this expedition extended northward to Guayaquil, Ecuador (2°12'S, 79°52'W) and southward to Valdivia, Chile (39°49'S, 73°15'W), with stops at several intervening sites along the Peruvian and Chilean coasts. At all sites where we had the opportunity to monitor behavior, we found patterns of aggression and territoriality consistent with our observations at Paracas.

What relevance do these observations have to the thesis of Duffy et al. that shorebirds do not compete for food in this wintering area? Clearly, our observations fall far short of demonstrating competition, but they do indicate that both the mechanism and selective basis for competition exist at Paracas, and they thus make competition far more plausible than Duffy et al. suggest.

The intra- and interspecific territoriality we observed provide the mechanism for interference competition. These interactions are the sorts of dynamic processes on a microscale that result, ultimately, in classic competition. They suggest, moreover, that resources were not superabundant, contradicting one of the major deductions of Duffy et al.

As to the selective basis of these patterns, the rampant presence of feeding territoriality at Paracas indicates a density-dependent effect of shorebird numbers on shorebird feeding efficiency. We made no measurements of this effect, but the weight of the evidence now available suggests that shorebird nonbreeding territories are food-based, i.e. that individuals benefit energetically by preventing others from cropping their food (Myers et al. 1979a, Dugan 1981; see also Gill and Wolf 1980 for nonbreeding territoriality in other taxa).

Duffy et al. note that interyear differences may influence the level of competition in this community. This alone may account for the apparent discrepancies between their results and our observations. Another possible resolution lies in the timing of the two studies: they worked in austral mid-summer, while we worked in late austral summer. Our obser-

[1] The Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103 USA and Department of Biology, The University of Pennsylvania, Philadelphia, Pennsylvania 19104 USA.

[2] Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853 USA.

TABLE 1. Census totals and behaviors of Nearctic migrant shorebirds near Paracas and Pisco, Peru, March 1982.[a]

Species	Bayhead		Sequion		Lagunillas		Pisco Ponds	
	Numbers	Behavior	Numbers	Behavior	Numbers	Behavior	Numbers	Behavior
Lesser Golden Plover *Pluvialis dominica*	0	—	0	—	2	nt	0	0
Black-bellied Plover *Pluvialis squatarola*	130	t + nt(a)	34	t + nt(a)	5	t	0	—
Semipalmated Plover *Charadrius semipalmatus*	280	t + nt(a)	56	t + nt(a)	8	nt	10	nt
Ruddy Turnstone *Arenaria interpres*	10	nt(a)	20	nt(a)	25	nt	0	—
Whimbrel *Numenius phaeopus*	0	—	1	t?	4	t	0	—
Greater Yellowlegs *Tringa melanoleuca*	68	t + nt(a)	3	nt(a)	0	—	1	?
Lesser Yellowlegs *Tringa flavipes*	1	?	0	—	0	—	100+	t + nt(a)
Hudsonian Godwit *Limosa haemastica*	3	nt	0	—	0	—	0	—
Spotted Sandpiper *Actitis macularia*	0	—	0	—	1	t?	3	t
Short-billed Dowitcher *Limnodromus griseus*	75	nt	0	—	0	—	0	—
Pectoral Sandpiper *Calidris melanotos*	2	nt	0	—	0	—	4	t
Baird's Sandpiper *Calidris bairdii*	2	nt	1	nt	0	—	0	—
Semipalmated Sandpiper *Calidris pusilla*	460	nt(a) + t	608	nt(a) + t	10	nt(a)	150	nt(a) + t
Western Sandpiper *Calidris mauri*	1,670	nt(a) + t	815	nt(a) + t	0	—	10	nt(a) + t
Least Sandpiper *Calidris minutilla*	0	—	0	—	0	—	20	nt
Sanderling *Calidris alba*	1,170	nt(a) + t	248	nt(a) + t	73	nt(a) + t	0	—
Stilt Sandpiper *Calidris himantopus*	4	nt	0	—	0	—	0	—

[a] t, territorial; nt, nonterritorial; (a) nonterritorial birds aggressive. When both t and nt birds present within a species, most common behavior given first. Location names follow Duffy et al. 1981.

vations were thus made nearer to the time of northward migration. This could affect prey abundance, and it also could change the condition of the birds. Premigratory birds may have higher energetic demands and thus place greater demands on resources, or premigratory birds may undergo hormonal changes that increase aggression levels. Evidence of the occurrence of nonbreeding territoriality from other studies, however, is inconsistent with this latter interpretation (Myers et al. 1979b).

Independent of our observations, the work of Duffy et al. at best offers a weak test of the competition hypothesis. Their predictions do not incorporate any seasonal changes in resource availability or distribution, nor how those changes might affect shorebird foraging independently of competition. This would seem a critical part of any true null hypothesis. Their data on prey abundance are simply inadequate, particularly for the exclosure: the true sample size of their exclosure experiment is one (one exclosure), obviating any statistical analysis. Moreover, their measurements of prey abundance leave unresolved questions about prey availability (Myers et al. 1980) and a foraging bird's caloric intake rate. Great changes in prey density may have almost no effect on caloric-intake rates, or they may have substantial effects, depending upon prey-handling time, prey size, and prey caloric values as well as the range of prey densities over which the changes occur (Myers et al. MS). Finally, in theory, competition can occur

even between expanding populations with expanding food resources, because it involves changes in the growth rate of populations rather than in population sizes per se. Thus, even if the measurements of prey abundance of Duffy et al. reflect a true maintenance of prey availability during austral mid-summer, one cannot eliminate competition on that basis alone.

In conclusion, we believe the issue of shorebird competition at tropical wintering sites is far from settled. Duffy et al. have done pioneering and creative work on this important matter, but rejecting competition is no less demanding than proving it. The final resolution for this avian community awaits long-term demographic and behavioral work on these wintering populations, research with far greater depth than either we or Duffy et al. have mustered.

Our fieldwork in South America was supported by the World Wildlife Fund-U.S., by ICBP-Panamerican, and by the Committee for Afternoon Projects. Manuel Plenge and Robin Hughes provided much needed advice and encouragement in Peru. Frank Pitelka offered helpful comments on the MS.

Literature Cited

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

Dugan, P. J. 1981. Seasonal movements of shorebirds, in relation to spacing behavior and prey availability. Unpublished Ph.D. dissertation. Durham, U.K., Univ. Durham.

Gill, F. B., & L. L. Wolf. 1980. Nectar loss by Golden-winged Sunbirds to competitors. Auk 96: 448–461.

Myers, J. P. 1980. Territoriality and flocking by Buff-breasted Sandpipers: variations in nonbreeding dispersion. Condor 82: 241–250.

———, & L. P. Myers. 1979. Shorebirds of coastal Buenos Aires Province, Argentina. Ibis 121: 186–200.

———, P. G. Connors, & F. A. Pitelka. 1979a. Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. Auk 96: 551–561.

———, ———, & ———. 1979b. Territoriality in nonbreeding shorebirds. Studies Avian Biol. 2: 231–246.

———, S. L. Williams, & F. A. Pitelka. 1980. An experimental analysis of prey availability for Sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. Can. J. Zool. 58: 1564–1574.

Received 19 August 1982, accepted 5 May 1983.

Paracas Rejoined – Do Shorebirds Compete in the Tropics?

David Cameron Duffy,[1] David C. Schneider,[2] and Natasha Atkins[3]

In our study at Paracas, Peru (Duffy et al. 1981), we predicted that if migratory shorebirds are limited through competition on tropical wintering grounds, then increased shorebird densities during the boreal winter would result in (1) shifts in habitat usage, (2) shifts in foraging behavior, (3) a shift toward feeding over a wider range of the tidal cycle, and (4) reductions in prey abundance. We found no changes in microhabitat usage, no changes in tidal usage, and no overall decrease in prey abundance. We found greater usage of one major habitat by several species during the boreal winter. We listed six factors (including territoriality) that may have led to our results.

During a brief visit to Paracas in March 1982, Myers and McCaffrey (1984) recorded territorial behavior in 10 of 17 species at Paracas, and they recorded nonterritorial aggression in 8 of these 10 species. From this they argue that territoriality and aggression may be limiting mechanisms at Paracas. They further state that our study was, at best, a weak test of the competition hypothesis. We first address their observations, and then we address their comments on our work.

Shorebirds may benefit from territories "by preventing others from cropping their food" (Myers and McCaffrey 1984). Myers and McCaffrey have not shown that birds were defending feeding territories, however. Hamilton (1959) found that during the spring, south of the breeding grounds, only a small proportion of Pectoral Sandpipers (*Calidris melanotus*) established territories, and these were all male birds. This suggests that other factors, such as hormonal levels, may govern territorial behavior in the spring.

[1] Percy FitzPatrick Institute of African Ornithology, The University of Cape Town, Rondebosch 7700, South Africa.

[2] Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717 USA.

[3] Center for Environmental Education, 624 9th Street N.W., Washington, D.C. 20008 USA.