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.

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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 Unpublished Ph.D. dissertation.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.

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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 non-territorial 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.

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[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.

Myers and McCaffrey do not state how they distinguished territorial interaction from other agonistic behavior. Not all agonistic interactions are attempts to preempt space and the food in it. Large prey that cannot be swallowed immediately are subject to theft by neighbors, unless defended. Agonistic interactions can be expected among visual hunters that spot the same item, especially if prey movement is an important cue (Pienkowski 1983). Dowd (1977) found that aggressive interactions occurred more frequently in sandpipers foraging by visual cues than in birds of the same species foraging by tactile means.

Myers and McCaffrey give no data on the proportion of individuals defending territories. Persistent territoriality is important because it can, if sufficiently widespread, alter the distribution of resources among individuals in a population (Appendix). Persistent territories were demonstrated in a population of Whimbrel (*Numenius phaeopus*) in Panama by Mallory (1981). By making extended observations during repeated visits to one site, Mallory was able to map the shape and location of feeding territories. Territories were presumably occupied by the same bird on successive days, although this could not be confirmed because individual birds could not be marked. Similarly detailed work, based on mapping of territories or on marking of individuals, will be needed to demonstrate whether territoriality is widespread at Paracas or limited to an occasional instance.

We agree that interspecific and intraspecific territoriality can provide a mechanism for competition, but Myers and McCaffrey have not demonstrated that feeding territoriality is "rampant" or that this affects foraging efficiency. We can only conclude that their "selective basis" of interference competition is inferred from northern hemisphere studies cited in their paper. Duffy et al. (1981) argue that competition for limited food at these northern migratory stopovers (which also serve as wintering grounds) may be one of the reasons that prey depletion and shifts in behavior and habitat usage were not observed on the wintering grounds in Paracas.

Myers and McCaffrey state that the true sample size of our exclosure was one. The exclosure was set up in an area of high infaunal density and high shorebird abundance, after an extensive search for such an area. The exclosure was not placed at random and cannot be considered a sample. The experiment could not be repeated at other sites because of wave action, prey mobility, or low bird concentrations. We therefore made repeated collections at several sites, to test for overall trends in abundance. Our conclusion, no overall decrease in prey abundance, was based on the results of repeated collection and the cage experiment. We drew no conclusions from the cage experiment alone.

The lack of change in prey numbers at Paracas is consistent with other studies of shorebirds wintering within 35° of the equator. In South Carolina (32°N) Grant (1981) found no decrease in the density of one prey species during a 57-day period in the fall. At a similar latitude in California, Quammen (1980) found no decrease in benthic prey after January. At a similar latitude in the southern hemisphere, Puttick (1980) reported a maximum prey removal rate of 10% per month. In Panama (8°N) Schneider (MS) found an average decrease of 27% in average density of confirmed prey groups between January and early March and then a slight increase in average density between early March and mid-April.

Myers and McCaffrey (1984) suggest a number of factors that need to be considered in future work on competitive interactions. These factors include seasonal changes in prey populations, prey availability as distinguished from prey density, and caloric requirements of shorebird predators. Prey patchiness needs to be added to this list, as patchiness can affect rates of aggressive interaction (Mallory and Schneider 1979) and as changes in average abundance may not be indicative of prey availability at concentrations above some economic threshold. The list of factors could easily be extended. Rather than extending the list, we wish to make two observations. First, competition may elude even the most complete listing of factors if competition is intermittent, weak, or of historical importance. Second, the work entailed in proceeding through the list might be reduced by developing a working set of hypotheses in order to rank the items on the list.

Further work on the population regulation of shorebirds is urgently needed. We agree with Myers and McCaffrey that long-term research in the tropics must be part of such work. Whatever the relative importance of competitive interactions on tropical wintering grounds, tropical studies are essential for the conservation of migrants that spend the greater part of their lives in tropical and subtropical habitats.

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LITERATURE CITED

DOWD, T. 1977. The foraging behavior and ecology of Semipalmated Sandpipers at a migration stopover in Plymouth, Massachusetts. Unpublished MS thesis. Boston, Massachusetts, Boston Univ.

DUFFY, D. C., N. ATKINS, & D. C. SCHNEIDER. 1981. Do shorebirds compete on their wintering grounds? Auk 98: 215–229.

GRANT, J. 1981. A bioenergetic model of shorebird predation on infaunal amphipods. Oikos 37: 53–62.

HAMILTON, W. J. 1959. Aggressive behavior in migrant Pectoral Sandpipers. Condor 61: 161–179.

MALLORY, E. P. 1981. Ecological, behavioral and morphological adaptations of a migratory shorebird, the Whimbrel (*Numenius phaeopus*), in its different environments. Unpublished Ph.D. dissertation. Hanover, New Hampshire, Dartmouth College.

———, & D. C. SCHNEIDER. 1979. Agonistic behavior in Dowitchers feeding on a patchy resource. Wilson Bull. 91: 271-278.

MYERS, J. P., & B. L. MCCAFFREY. 1984. Paracas revisited: Do shorebirds compete on their wintering grounds? Auk 101: 197-199.

PIENKOWSKI, M. W. 1983. Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators. Marine Ecol. Prog. Ser. 11: 141-150.

PUTTICK, G. M. 1980. Energy budgets of Curlew Sandpiper at Langebaan Lagoon, South Africa. Estuar. Coast. Mar. Sci. 11: 207-215.

QUAMMEN, M. L. 1980. The impact of predation by shorebirds, benthic feeding fish, and the crab, *Pachygrapsus crassipes*, Randell 1839 on shallow living invertebrates in intertidal mudflats of two southern California lagoons. Unpublished Ph.D. dissertation. Irvine, California, Univ. California.

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MATHEMATICAL APPENDIX (D. Schneider)

If U_i is prey consumption (KJ/day) of individual i then average intake of the population is $1/N\sum^{N} U_i = \bar{U}$.

In the case of complete territorial preemption a proportion (p) of the individuals will obtain a full ration and $N(1 - p)$ individuals will obtain no ration.

The mean intake ($\bar{U}_t$) will equal p and the variation in intake ($\tilde{U}^2$) will be $(p)(1 - p) = p - p^2$.

$$\tilde{U}^2 = p - p^2.$$

Differentiation with respect to p gives:

$$\delta\tilde{U}^2/\delta p = 1 - 2p.$$

That is, the variance in intake within the population will increase as p, the proportion of individuals preempting all feeding habitat, decreases from 1 to 0.5. A decrease in p might occur if the predator population expands, or if individuals expand territories in response to a declining food abundance.

If territoriality breaks down at high density, then redistribution of resources can occur. In the extreme case all individuals will obtain the same number of prey, and the variance in intake under nonterritorial conditions ($\tilde{V}^2$) will be zero.

Then $\tilde{U}^2 \geq \tilde{V}^2 \geq 0$.

If H is the number of hours spent foraging by the entire populations in one day, then let q be the proportion of hours spent foraging at high density sites, and $(1 - q)$ be the proportion at low density sites. Total variance in consumption ($\tilde{T}^2$) is the weighted sum:

$$\tilde{T}^2 = (1 - q)\tilde{U}^2 + (q)\tilde{V}^2 = \tilde{U}^2 + q(\tilde{V}^2 - \tilde{U}^2).$$

Then

$$\delta\tilde{T}^2/\delta q = \tilde{V}^2 - \tilde{U}^2.$$

Because $\tilde{U}^2 \geq \tilde{V}^2$, the variance in intake will decrease as more time is spent at high densities. The decrease in the variance will be large if $p < 1$ and if redistribution is complete ($\tilde{V}^2 = 0$). A smaller decrease will occur if $\tilde{V}^2 > 0$. The analysis can be extended to other sources of variation in food intake.