Studies in Avian Biology No. 2:259–261, 1979.

SUMMARIZING REMARKS, PART II

JOHN A. WIENS[1]

It's difficult to know where to begin in summarizing or condensing some essential truths from the preceding papers. Frank Pitelka has presented a global framework for shorebird studies, and the other speakers have added significant contributions. The edifice of knowledge of shorebird biology that emerges is incomplete, of course, but further definition of its design and structure requires new studies and fresh information, not uncertain and premature synthesis.

So saying, I could of course dismiss you all, or I could dwell at length on the spirits of some small but tasteful wineries in the valleys north of here, which I sampled as a way of preparing for this undertaking. Perhaps my hesitancy stems from my naivete about shorebird systems. After all, my own studies have been almost entirely in arid and semi-arid grasslands and deserts, which scarcely qualifies me to comment about coastal wetlands. I don't work with shorebirds. I can identify three, maybe.

It turns out, however, that the kinds of questions that are emerging in shorebird studies, as exemplified by these papers, are the same kinds of things that we have been exploring in deserts and semi-deserts, and others have been investigating in woodlands. I'm coming to the realization, however, that shorebird systems are particularly well suited to obtaining the detailed sorts of observations and conducting the innovative manipulations that are necessary to begin answering some of these questions; more so, in fact, than the sorts of systems I've been meddling with for the last decade. I'd like to draw your attention to several directions or priorities for thinking and research on shorebird systems that may be especially important, in my view.

One of these has to do with the matter of detailed dissections of behavior patterns of individuals, a topic which has received very little attention in this symposium. The paper by Shanewise and Herman on flock structure and flock behavior addressed behavior in such detail, and it indicates some interesting aspects. The size of a flock, for example, may have substantial effects upon the behavioral patterns of individuals in flocks. Regardless of whether flocking represents an adaptation to avoid predation, or to increase feeding efficiency, or both or neither of these, there is no doubt that the formation of flocks, and the foraging of individuals in large aggregations or in small flocks or as solitary birds has differing effects upon prey population dynamics in time and space. These require close attention in studies of shorebird biology.

Other studies not reported in this symposium—investigations like those of Pearson and Parker (1973) in England or Baker (1973) in North America—have used shorebirds as a system to dissect the details of behavioral patterning in time, the sequencing of movements and postures. These also indicate the utility of shorebirds for very detailed dissections of behavioral processes. They suggest that this kind of study may begin to detect something about the perceptual world of a shorebird, to unravel some of the cues that are used, for example, in prey capture, and allow us to resolve some of the facets that enter into studies of

[1] Department of Zoology, Oregon State University, Corvallis, Oregon 97331; present address: Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131.

foraging and prey selection, such as those that Goss-Custard was just describing. We need to know how behavior is structured in time and, perhaps more importantly, what kinds of environmental influences direct the organization of behavioral sequences.

Another area involves the detailed study of foraging behavior itself and its relationship to the density and dispersion and diversity of available prey. Shorebirds are ideally suited, I think, to careful documentation and measurement of individual foraging behavior, and they occupy habitats in which prey availability and patterns can be determined perhaps more readily than in any other kind of system. Such studies ought to be related to the rich and almost exponentially growing body of optimal foraging theory, most of which remains untested. Several papers in this symposium have addressed elements of this, and I think this is an area in which shorebird studies can make fundamental contributions to the advance, or perhaps the re-direction, of a good deal of theoretical ecology. Much of the theory which is being bandied about has to do with what occurs under conditions of equilibrium and assumes that food is limited. We need to know how often this really occurs in shorebird systems. Are the birds that Goss-Custard or Hartwick and Blaylock have been working with always limited by food availability, and does this therefore impose tight constraints on what they can or cannot get away with in their foraging tactics, or may there be considerable variability or slop (what engineers call noise) in the system? Perhaps individuals may vary tremendously in their behavior without paying any real penalties. We don't know this, but I suggest that shorebird systems provide perhaps the most immediate way to begin to unravel this.

Several contributions to this symposium have alluded to energetics as an organizing framework; this is apparent, for example, in the work of Goss-Custard, of Johnson, and of Myers, Connors and Pitelka. It indicates, I think, that we need to give much closer attention to integrating energetics into large-scale ecological investigations, both in terms of energy flow in the system and in terms of the energetic options or costs/benefits that are faced by individuals or populations in pursuing particular tactics and strategies. What, for example, are the energetic consequences of the various exploitation systems documented for Arctic shorebirds by Pitelka, Holmes, and MacLean (1974)? It's apparent, however, that there may be severe difficulties in applying the rather simple energetic models that are now available to real-world situations: Johnson's demonstration of the failure of Pennycuick's (1975) model to produce reasonable estimates of flight energetics is an example—we simply can't have birds falling into the ocean this frequently. We need fresh approaches to model development that incorporate insights from biology rather than systems engineering.

Shorebird studies over the past decade or two (or three) have undergone a development which has led from an initial emphasis solely on breeding studies (perhaps as a result of the suggestions by David Lack and others that the real action must occur then, because that's when the offspring are produced) to increasing concern with what is happening on the wintering grounds. Now some are beginning to wonder what is happening to link breeding ground dynamics and wintering ground dynamics together. What happens during migration? What are the constants and the variables involved? There are some really nifty things that shorebirds can do in these wide-ranging areas that they occupy—the fixed staging areas or fixed wintering ground locations or breeding grounds. We need to explore

the extent to which the so-called conservative or opportunistic adaptive strategies noted for breeding sandpipers by Pitelka and his students (1974) apply to non-breeding dynamics. Are there parallel or perhaps additional social exploitation systems that are practiced in wintering areas, or in transit along the way? What is the stability of these? What is the role or the composition of the non-breeding element of populations that occurs in some areas during the boreal breeding season?

Finally, I think we need to pay close attention to the overall stability and predictability of the systems in which these relationships occur. How variable are the environmental conditions faced by shorebirds through time and space? What role does interspecific competition play in the determination of the various population attributes that we see? How do shorebirds respond to environmental certainty or uncertainty? We have some leads in this—studies having to do with the structuring of social systems such as those of Schamel and Tracy or of Myers et al., or investigations of feeding relationships such as that of Strauch and Abele, reported on here—but this whole matter deserves intensified effort.

Obviously what's needed in order to resolve questions about the environmental relations of shorebirds and all these areas that I've only just touched upon are long-term, detailed, on-site studies that are operated within fairly well-defined theoretical frameworks, that ask questions rather than simply gather data. It is necessary to evaluate the natural patterns and magnitudes of variation in shorebird densities, distributions, behavior patterns, territorialism, non-territorialism, food habits, energetics, and so on, in order to get a fix on how these things vary under natural conditions. You can't determine how these features vary naturally by going to one area for one week and making a few observations with nothing particular in mind. It's just not that simple. What happens one year in one location may be different the next year in the same location, or the same year in a slightly different location. I think it's critical to our understanding and management of shorebird and coastal wetland systems that we undertake these long-term studies. Somehow, some way, someone has to convince the granting agencies that operating on a short-term funding frame will simply not produce the kind of science we need. It's absolutely essential that we understand the patterns and magnitudes of natural variation in these sytems if we are ever to develop a realistic approach to management. Otherwise, if we go in and disturb the system in some way, we have no idea whether the deviations from what we saw before are directly due to the disturbance that's been perpetrated on the system, or whether these simply represent natural variations tied to a variety of natural causes, which in all likelihood would have occurred anyway. The contributions to this symposium give encouraging evidence that achieving the necessary understanding is not as remote as it once seemed.

LITERATURE CITED

BAKER, M. C. 1973. Stochastic properties of the foraging behavior of six species of migratory shorebirds. Behaviour 45:242–270.

PEARSON, R. G. AND G. A. PARKER. 1973. Sequential activities in the feeding behavior of some Charadriiformes. J. Nat. Hist. 7:573–589.

PENNYCUICK, D. J. 1975. Mechanics of Flight. Pp. 1–75 *in* D. S. Farner and J. R. King (eds.), Avian Biology, Vol. 5. Academic Press, New York.

PITELKA, F. A., R. T. HOLMES AND S. F. MACLEAN, JR. 1974. Ecology and evolution of social organization in arctic sandpipers. Amer. Zool. 14:185–204.