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OVERVIEW

COLLABORATIVE APPROACHES TO THE EVOLUTION OF MIGRATION AND THE DEVELOPMENT OF SCIENCE-BASED CONSERVATION IN SHOREBIRDS

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Shorebirds are among the most highly migratory creatures on earth. Both the study of their ecology and ongoing efforts to conserve their populations must reflect this central aspect of their biology. Many species of shorebirds use migration and staging sites scattered throughout the hemisphere to complete their annual migrations between breeding areas and nonbreeding habitats (Morrison 1984). The vast distances between habitats they use pose significant challenges for studying their migration ecology. At the same time, the large number of political boundaries shorebirds cross during their epic migrations create parallel challenges for organizations working on their management and conservation.

Nebel et al. (2002) represent a collaborative effort to understand the conservation implications of Western Sandpiper (*Calidris mauri*) migration ecology on a scale worthy of this highly migratory species. The data sets involved in the analysis come from four U.S. states, two Canadian provinces, and a total of five nations. Only by collaborating on this historic scale were the authors able to assemble the information necessary to understand important aspects of the migration ecology of this species, and the implications for conservation of the patterns they discovered.

Collaborative approaches to shorebird migration ecology developed slowly over several decades. The same period also saw the creation of large-scale efforts to monitor and conserve shorebirds. This overview first traces the history of the study of migration ecology of shorebirds during that fertile period, and then describes the monitoring and protection efforts that have been developed in an attempt to address the enormous issues of scale posed by shorebird migration ecology and conservation.

History of Shorebird Migration Ecology Studies

The evolution of bird migrations is a question that has vexed generations of ornithologists. Whereas there have been notable landmark research programs exploring how birds complete their epic journeys, few have focused on the evolutionary roots of migration itself. Larson (1957) stands out for exploring relationships between shorebird migrations and glaciation history. We are not aware of any research programs today focused on an examination of fundamental questions of the evolution of avian migration. Nevertheless, a number of separately managed research programs seem to be touching on some of the evolutionary roots of shorebird migration, and the combined insights from many of those have direct applications in charting worldwide conservation strategies for shorebirds.

There are about 214 species of shorebirds worldwide falling into 11 families. Together, they are an excellent group for studying migration because (1) some species are among the most highly migratory animals on earth, with routine journeys between high northern and southern latitudes; (2) some migrate north to breed, others—especially among Austral species—to the south; (3) among migratory species, some use ''long-hop'' strategies (involving long-distance, nonstop flights), others employ ''short-hop'' strategies; and (4) many kinds have no migrations at all.

Even at family levels there are differing evolutionary trajectories with respect to migration. For example, long-distance migration prevails in a substantial fraction of the sandpiper spe-

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cies, but in fewer of the plovers, and even fewer yet among the remaining families.

In this overview, we focus principally on long-hop migrants. Their spectacular journeys were first highlighted by MacKay (1894), and later by Cooke (1910), who both drew attention to long, transoceanic flights made by shorebirds. They noted the large fat deposits, now known as essential energy stores (Johnston and McFarlane 1967) for successful long-hop migration by shorebirds. But little more attention was given to shorebird migration research until banding studies and winter counts of shorebirds began to grow in the United Kingdom during the 1950s and 1960s (Prater 1979).

Also in the 1960s and 1970s, Raymond McNeil (1970) and students (McNeil and Cadieux 1972a, b; McNeil and Burton 1973) began exploring energetic aspects of long-hop shorebird migration between North and South America. They developed equations modeling fat and energy requirements for successful long-hop flights (McNeil 1969). Their banding and marking programs circumstantially demonstrated that long-hop flights were the rule rather than the exception for many kinds of shorebirds. That was soon bolstered by Richardson's (1976) radar studies of southward migration in eastern Canada. Since then there have been refinements in understanding shorebird migration energetics (e.g. Kersten and Piersma 1987), in tracking of migration using banding (Harrington and Leddy 1982), and using radio telemetry (Warnock and Bishop 1998). Still, research emphasis has focused much more on the ''how'' rather than the ''why'' of long-hop migration.

During the 1970s and 1980s, exciting developments grew from expeditions studying Old World shorebirds wintering in west Africa (Dick and Pienkowski 1979). Those programs, and later research based on them, began assessing relationships between metabolic requirements and food resources during nonbreeding periods, and requirements to prepare for northward migration. Although early work suggested food was a limiting factor (e.g. Baker and Baker 1973), the work in west Africa and more recent work (Duffy et al. 1981, Zwarts et al. 1990, Kalejta 1992) suggest that food is not as limiting as once thought. Furthermore, flight efficiency itself is greater than once thought (Kvist et al. 2001).

During the 1970s, the Maritimes Shorebird Survey and the International Shorebird Surveys began surveying shorebird numbers at migration stopover locations. Those and more recent programs have demonstrated that important fractions of the populations of some species were visiting relatively few migration stopover locations, and that those locations appeared essential to sustaining species' populations (Morrison and Harrington 1979, Hicklin 1987, Myers et al. 1987, Harrington et al. 1989).

Surveys of shorebirds in the Western Hemisphere took a quantum leap during the 1980s and early 1990s with the intrepid work of Morrison and Ross (1989), who mapped shorebird numbers during the northern winter on South and Central American coasts; again, large fractions of some species' populations were concentrated on relatively small sections of continental coastlines, as had been found on west African coasts a decade earlier (Dick and Pienkowski 1979), and which became a recurring theme in studies of U.S. Pacific coast shorebirds (Page et al. 1999) and Australasian wintering and migration stopover areas (Wilson and Barter 1998).

Work by Piersma et al. (1995) has demonstrated net metabolic advantages gained by long-distance migrants such as knots and turnstones by moving to warm southern latitudes during the northern winter. One persistent question has been why migratory shorebirds do not simply breed at their wintering latitudes during the austral summer, as done by some of their nonmigratory counterparts. Tropical-breeding shorebirds seem to have smaller clutches than temperate–Arctic breeders, but without integrated information on comparative productivity and survivorship of Arctic- versus tropical-breeding species, the relevance of clutch size is difficult to gauge. Perhaps good insights on survivorship will develop from elaboration of studies such as Nebel et al. (2002). For example, how does within-sex survivorship of male and female Western Sandpipers spending winters at more northerly locations compare to more southerly locations? And if differences are found, are they related to underlying selection of differential migration by males and females? Answering such questions will provide fundamental insights into the evolution of migration, and that, in turn, will help lead to improved conservation planning.

Though never designed for monitoring population trends, data from the previously mentioned migration surveys (Howe et al. 1989, Morrison et al. 1994) suggest that many species of Nearctic-breeding shorebirds are in population decline. Reasons for those declines are unknown. Although there is much debate (e.g. Myers and McCaffery 1984, Duffy et al. 1984), we do not know which limiting factors are most important, or where they occur. Predation may be one important limiting factor (Page and Whitacre 1975). Work by Baker and Baker (1973) and by Recher (1966) suggests that shorebirds face higher competition for food in winter (vs. breeding) habitats. Research in a northern breeding location (Sandercock and Gratto-Trevor 1997) found unsustainably low and declining breeding success of Semipalmated Sandpipers (*Calidris pusilla*), a species thought to be declining rapidly (Morrison et al. 1994). Schneider and Harrington (1981), and later Székely and Bamberger (1992) showed that shorebirds were depleting prey at migration stopover areas, raising questions of whether migration stopover habitat might be limiting to population sizes. Studies of wintering shorebird populations in Europe (Goss-Custard et al. 1995) suggest that reduced amounts of habitat could be causing the carrying capacity of remaining habitat to be exceeded.

So, why are shorebirds undertaking their amazing migrations? Though there are many questions, the developing picture suggests the migrations have evolved to take advantage of seasonally predictable ''blooms'' of invertebrate animal production at widely separated points of the world. Butler et al. (2001) showed that shorebird densities are higher in areas of high coastal productivity, and suggested that the pattern of relatively rich areas has influenced long distance shorebird migrations. For example, greatly increased biological production occurs in north temperate wetlands and Arctic biomes each spring. A month or two later, peak invertebrate biomass occurs in marine intertidal habitats at temperate latitudes; and those pulses are in opposite calendar synchrony at north and south latitudes. In some instances, the blooms are at very specific times and places, for example the breeding of horseshoe crabs (*Limulus polyphemus*) on Delaware Bay (Tsipoura and Burger 1999) or of *Corophium* amphipods on the Bay of Fundy (Hicklin and Smith 1984), whereas others appear to be more generalized seasonal pulses of biological production involving many different taxa, as for example the Arctic flush of berries, spiders, and insects occurring every year (Syroechkovski and Lappo 1994). Although the migrations necessary to move between these blooms would seem to be risky, it appears that they may not be; adult annual survivorship of some of the longest distance migrants such as knots (Harrington et al. 1988) or turnstones (Metcalfe and Furness 1985) is on the order of 80%. What does appear to be at risk are the ''stepping stone'' resources fundamental to the long-hop migration strategies, because many are rapidly being modified or lost because of human influence. For example, the disappearance of the Rocky Mountain locust (*Caloptenus spretus*), which was responsible for plagues in the central United States in the late 1800s, may be one factor that contributed to the demise of the Eskimo Curlew (*Numineus borealis*), an extreme long-distance migrant (see Gill et al. 1998).

In summary, many shorebirds that migrate long distances appear to depend on a few highly productive but widely scattered locations during both migration and wintering periods. Evidence is beginning to grow that the availability of food at those sites is limiting both in winter and during migration, and that the number and quality of sites is declining due to habitat conversion and degradation. It is thus not surprising that many shorebird species appear to be declining. These hypotheses, however, all need much more careful evaluation, and the necessary research will probably only be possible with collaboration on the scale pioneered by Nebel et al. (2002). Better information is particularly needed on the importance of specific sites, limiting factors at those sites (e.g. food vs. disturbance), and on which species and populations are declining.

Conservation Programs and Their Potential Contributions to Shorebird Research

A great deal of ongoing avian research targets specific problems or theoretical issues by examining individual species in particular locations, or specific habitats and their biodiversity. The evolutionary approach exemplified by Nebel et al. (2002), which involves coordination of independent research on a single species in multiple countries, bridges the gap between basic science and applied conservation concerns. The complex migratory patterns of shorebirds require a broad scope for basic avian research to contribute meaningfully not only to evolutionary questions, but also to conservation concerns for the future preservation of species. On one hand, conservation agencies and organizations need scientific research to justify and support funding for their management goals. On the other hand, research programs should be based on thinking at a migratory scale about the diverse habitat needs of shorebirds throughout their life-cycles. Conservation and research efforts at this time are uniquely poised to provide mutual benefits to each of those goals.

During the past five years, various conservation programs have contributed to providing much needed information on types of habitats and specific sites that are important for shorebirds at various times in their migrations, as well as estimating population sizes and documenting declines in some species. However, bird conservation initiatives need specific research on the factors that limit populations, because of the threats to populations if any one segment of their migratory cycle is impaired or eliminated though anthropogenic effects. Several shorebird conservation programs have provided models for that kind of broad collaboration at national, international, and hemispheric scales. Those efforts are beginning to provide some large-scale data, as well as collaborations that can contribute meaningfully to ongoing research, while also beginning to identify the places where future targeted research would most meaningfully contribute to better conservation.

The shorebird conservation plans recently completed for the United States (Brown et al. 2001) and Canada (Donaldson et al. 2000) both identify the need for adequate monitoring programs to determine the actual population trends of North American shorebirds. Those plans spurred efforts to develop international programs for both monitoring and research. One program that exemplifies the collaborative approach to shorebird monitoring is the new international program called the ''Program for Regional and International Shorebird Monitoring'' (PRISM; Bart et al. 2003a). PRISM is a comprehensive effort to estimate shorebird population sizes and trends, to identify causes of declines, and to assist in developing conservation programs for populations at risk. Most long-distance migrants breed in the far north where comprehensive, annual surveys during the breeding season are probably not feasible. The approach to population size monitoring under PRISM involves occasional comprehensive surveys on the breeding grounds to obtain essentially unbiased estimates of population size; frequent (though not always annual) surveys at a few accessible locations in northern regions; and annual surveys of migrating shorebirds in temperate regions. If disturbing trends are suggested by the surveys at accessible locations in northern regions, or by the annual migration surveys, then the comprehensive, breeding-grounds surveys will be repeated to obtain updated population sizes and thus estimates of change in population size. The comprehensive surveys are expected to take ~5 years to complete and will be repeated at 15–20 year intervals even if the other surveys do not indicate declines. That approach avoids the high cost of annual surveys in remote northern areas but also avoids complete reliance on trend estimates from surveys that could have substantial bias due to nonrandom selection of sites (northern surveys) or to trends in movement behavior and detection rates (migration surveys).

The comprehensive surveys of northern areas use a well-defined sampling plan to select plots and double-sampling to produce essentially unbiased estimates of density and thus population size (Bart and Earnst 2002). Plots are selected using stratified sampling with coarse habitat information used to delineate two or three strata. More detailed habitat information is then used to construct habitat-based models. The models may also include additional independent variables such as distance to the coast or elevation. Those models are then used to estimate density and, from that population size, throughout the study area. Statistical analysis includes uncertainty about detection rates, which are estimated from the subsample of intensively searched plots, as well as unexplained plot-to-plot variation in numbers recorded on the rapid surveys. This survey will increase our knowledge of distribution, regional abundance, and habitat relationships as well as provide baseline information on population size. Limited information is also being collected on productivity. Methods are well-developed for Arctic regions (Bart et al. 2003b), and design of the boreal surveys has just begun.

The migration surveys are being designed to estimate the mean number of birds present, throughout southern Canada and the conterminous United States, during a well-defined study period. To design the survey, temperate areas of Canada and the United States have been partitioned into 143 ''bird monitoring regions'' based on the boundaries of bird conservation regions (United States North American Bird Conservation Initiative Committee 2000) and provinces or states. A separate regional assessment is being prepared for each bird monitoring region. The assessment summarizes information that will be useful in designing the shorebird surveys including (1) information on species that use the region, their abundance, and timing of use; (2) a detailed description of areas used by shorebirds during the study period; (3) suggestions for survey methods and estimates of detection rates; and (4) a discussion of potential bias in trend estimates for the region due to access problems or low, and possibly variable, detection rates. The regional assessment also identifies information gaps and describes pilot studies to provide the needed information. In the past, regional assessments have been restricted to shorebirds, but assessments are now being prepared that include consideration of all aquatic species. Upon completion of the assessment, a meeting will be held with groups that may have an interest in the surveys, where the pilot studies will be prioritized, and an action plan will be developed for carrying out the highest-priority studies. That process is expected to take several years but should produce, for the first time, a comprehensive plan for conducting migration surveys that identify a useful parameter (i.e. the mean number of birds of each species in the study area, during the study period), outlines a well-defined sampling plan to collect the data, and provides realistic estimates of potential bias. Estimates of power and allocation of effort investigations will also be possible based on the regional assessments and pilot studies.

PRISM organizers hope to extend that approach into the Neotropics, but that must be done in concert with the host countries. The first step will be for representatives from those countries and from PRISM to work together to develop an approach that meets the goals of all participants. The biggest weakness of the temperate surveys will probably be that they would be compromised by a long-term change in the speed with which migrants pass through the temperate region. This source of potential bias would be completely removed by extending the study area to include the Neotropics because then the study area would cover all locations where the birds might be during the study period (except for species that winter outside the western hemisphere). Extending PRISM to the Neotropics should thus be a high priority during the coming decade.

The development of PRISM will have important implications for both studies of migration ecology in shorebirds, and efforts to conserve their habitats. As additional data become available, large-scale analysis similar to Nebel et al. (2002) should become possible for other species that have been less well studied. Monitoring data will also guide efforts to determine the species most at-risk and the most critical habitats. But ultimately, the most important step to ensure the future of shorebirds will be the strength of the programs designed to protect their habitats on the hemispheric scale at which they live their lives.

Internationally coordinated research in the context of the broader issues affecting birds across their migratory habitats necessitates knowledge of important sites throughout the hemisphere. The Western Hemisphere Shorebird Reserve Network (WSHRN) was founded in 1986 to facilitate the protection and management of migratory shorebirds through conservation of their key habitats using sound science, international collaboration, and strong local partnerships. Today, WHSRN is a voluntary international coalition of organizations and communities dedicated to the conservation of shorebirds across the Americas. One benefit of the network's efforts is that shorebirds have been recognized as a new priority of many major conservation programs. WHSRN currently includes 55 designated sites and over 250 partner organizations responsible for over 8 million hectares of the most critical shorebird habitat (and productive wetlands) across the Americas and many additional sites meeting the criteria for inclusion in the network have been identified (Harrington and Perry 1995).

The strength of WHSRN's program originates with motivated landowners and stakeholders responsible for the most important shorebird habitats in the hemisphere. The network provides scientific support, resources for training and public awareness, and international leadership to link wetlands, shorebirds, and communities into an effective coalition with common goals and complimentary resources. The mission of WHSRN is the conservation of shorebirds and their habitats across the Americas. The primary goal of WHSRN is to restore shorebird populations to the levels of the mid-1970s (the earliest reliable counts). Working with a network involving all of the major sites used by shorebirds has become an effective model for the simple idea ''think globally and work locally.''

Four specific programs of WHSRN and their rationale are as follows.

Uniting key shorebird sites and partners into the network.—Participation in WHSRN as a designated reserve provides sites and community partners with international recognition that enhances their program funding opportunities, collaboration with network partners, and access to network support services.

Organizational strengthening and project development with local and regional conservation groups.—The ultimate success of our efforts will be determined, in large part, by dedicated and capable local organizations empowered to sustain effective conservation.

Educational and public awareness campaigns with conservation partners.—Public understanding and support is essential for local and international conservation efforts to succeed. Environmental education by teachers and public outreach specialists is an important tool in motivating the general public to understand, support, and participate in conservation.

Scientific information exchange and training for biologists, land managers, and community leaders.-Conservation and land management decisions require the best scientific knowledge to be effective. The purpose of our information and training program is to provide wildlife biologists, land managers, researchers, and community leaders with optimal methods, updated data, and coordinated priorities for shorebird habitat enhancement and management across the hemisphere.

WHSRN criteria recognize three levels of sites based on the ''sum of all maximum counts'' to quantify the actual and potential shorebird use of any area. Additional criteria for dispersed areas in breeding and staging sites are under development and will be based on recommendations provided by PRISM and further analysis of data from the International Shorebird Survey and other programs. The development of the network attempts to reflect the enormous scale of shorebird migration, and provide a practical approach to addressing the complex international conservation issues that result from their long-distance migrations.

But despite the remarkable advances in understanding the migration ecology of shorebirds that have occurred in the last two decades, and the parallel advances in collaborative approaches to conservation, much remains to be done. There are many hypotheses about the causes of population declines, and many clear risks to shorebirds, particularly given expected changes in sea level and their effects on shorebird habitats. Understanding the evolution of the complex migrations of shorebirds, and resolving the many different hypotheses about reasons for their ongoing declines, will require future research and conservation efforts involving collaborations on the scale exemplified by Nebel et al. (2002) and her coauthors. Broad collaborative partnerships like PRISM and WHSRN will be critical in understanding the migration ecology of shorebirds, as well as in meeting their habitat needs throughout the hemisphere.

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More information about WHSRN can be found at http://www.manomet.org/WHSRN/.

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