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PERSPECTIVES IN ORNITHOLOGY

REFLECTIONS ACROSS HEMISPHERES: A SYSTEM-WIDE APPROACH TO NEW WORLD BIRD MIGRATION

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John Zimmer wrote in 1938, "It is not uncommon…to hear the statement made that South American birds do not migrate…. A few writers have noted the disappearance or reappearance of certain species at certain places and seasons, but there has been little evidence to show where the period of absence has been spent" (Zimmer 1938). Surprisingly, almost 60 years later, Stotz et al. (1996) echoed Zimmer: "Research is urgently needed on the winter distributions and habitat use of austral migrants…."

South America's austral migration system comprises species that breed in the south-temperate portion of the continent and move north toward tropical latitudes to overwinter. Unlike the other major New World migratory system—the Nearctic–Neotropical system, which comprises species that breed at north-temperate latitudes and move south to overwinter in Latin America—the austral system has received little attention. An obvious explanation for that disparity is the relative lack of financial resources for basic field research in South America, as compared with North America. In many ways, however, the challenge is far more than financial. Lack of infrastructure and a history of locally unstable political climates has made access to sites in South America quite variable.

Here, we argue the importance of understanding austral migration, both on its own merits and as a sister system to Nearctic–Neotropical migration. The two migratory systems are related because they share a common origin, the Neotropical avifauna. Most species of long-distance migrants in the New World are thought to have their evolutionary origins in the Neotropics (e.g. Cooke 1915, Levey and Stiles 1992, Rappole 1995, Joseph 1997, Chesser and Levey 1998). Thus, study of one system will inform study of the other. More generally, a broad view of New World migration—one that encompasses all directions and scales of seasonal movements—promises to reveal ecological and evolutionary mechanisms that may not be otherwise apparent (Levey 1994, Joseph 1997). Like searching for a lost object under a street-lamp because the light is brightest there, trying to untangle the complexities of migration by focusing on the most convenient or obvious migration system is at best restrictive and at worst misguided.

Our goal is to review current knowledge on South American austral migration and frame it in the context of New World migration. We start with a brief history of research on austral migration, then describe the similarities and differences between austral and Nearctic–Neotropical migration. We place New World migration in an evolutionary context and explain why such

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a perspective is necessary for understanding the causes and consequences of the processes underlying seasonal movements. We highlight intraspecific patterns of migration, such as partial migration, a condition in which a portion of the breeding population migrates at the end of the breeding season (Lack 1943, Berthold 2001). Although "austral" generally refers to Southern Hemisphere patterns, for the sake of brevity we here use the term "austral migration" in referring exclusively to birds that breed in southern South America and winter closer to or within tropical latitudes.

A Brief History of Austral Migration Research

Aside from regional publications that are largely unavailable, most literature on austral migration can be easily summarized. According to Chesser (1994), the first report was by de Azara (1802–1805), who reported changes in the abundance and composition of the avifauna of Paraguay and northeastern Argentina. Dabbene (1910) and Wetmore (1926) followed with descriptions of the seasonality of species occurrences. Zimmer (1938) provided the first overview of movements of several species throughout the year over the entire continent. The literature was then silent for almost 50 years. In the 1980s came the first report of winter site fidelity of an austral migration (McNeil 1982). Belton (1984, 1985) and Willis (1988) described austral migration patterns in southern Brazil, and Robinson et al. (1988) studied winter habitat occupancy of austral migrants in southeastern Peru.

In the 1990s, there was an awakening of interest in austral migration; museum records were mined for data, and species lists were systematically compiled and analyzed. Marantz and Remsen (1991) described the breeding and wintering range distributions of the Slaty Elaenia (*Elaenia strepera*). Hayes et al. (1994) described austral migrant occurrence and timing in Paraguay. Stotz et al. (1996) reviewed austral migrant habitat use, distribution, and conservation status; and Parker et al. (1996) provided a hypothetical list of complete and partial austral migrants. The most in-depth work to date is Chesser's (1994, 1995, 1997, 1998) study of the biogeography of austral migrant flycatchers (Tyrannidae), including the first comprehensive list of austral migrant species (Chesser 1994). Joseph (1996) studied winter distributions of migrants, later calling attention to the spectrum of New World migratory patterns (Joseph 1997). Chesser and Levey (1998) hypothesized evolutionary origins of austral migrants and Joseph et al. (2003) investigated the phylogeography and evolution of migration in Swainson's Flycatcher (*Myiarchus swainsoni*).

Such theory-based research and geographically broad descriptions of austral migration have emerged recently. Meanwhile, descriptive work continues at the local scale, on which conclusions at broader geographic scales are based. In Argentina, for example, researchers have described habitat selection (Marone et al.1997) and seasonality (Marone 1992, Cueto and Lopez de Casenave 2000, Fraga 2001, Malizia 2001) of austral migrants. In Paraguay (Brooks 1997) and eastern Bolivia (Davis 1993; Jahn et al. 2002a, b), seasonality and other basic patterns of austral migration have been described.

Thus, in three paragraphs, we have summarized almost the entire literature on austral migration. Imagine trying to accomplish that for Nearctic–Neotropical migration.

An Imperfect Mirror Image

The basic pattern of migration is the same in both South and North America: species generally move toward the equator in fall (postbreeding) and away from it in spring (prebreeding). An interesting way to visualize this is to imagine migratory birds that breed in the Southern and Northern hemispheres moving in the same direction at the same time: north when the Northern Hemisphere is tilted toward the sun, and south when the Southern Hemisphere is tilted toward the sun (Fig. 1). Despite that reciprocity between hemispheres in direction and timing of migration, differences in relative size, position, and shape of land masses are significant. Those differences "distort" the mirror image that the two migratory systems might otherwise display.

First, because southern South America is smaller than northern North America, area effects help explain why there are fewer migrant species in South than in North America (Chesser 1994, Chan 2001). Estimates of the number of austral migrants range from 220 to 237 species (Chesser 1994, Stotz et al. 1996), as compared

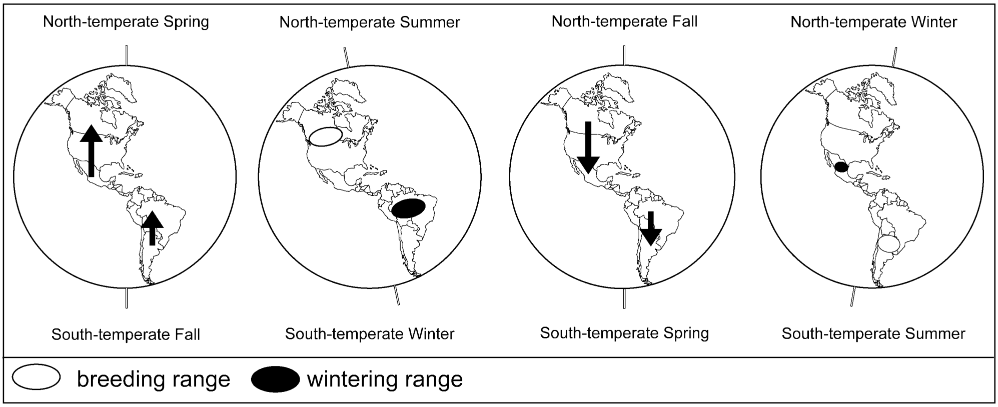

Fig. 1. Generalized seasonal movements and ranges of hypothetical populations of a Nearctic–Neotropical and a South American austral migrant species. The position of the sun is to the left of the diagram.

with 338 species of Nearctic–Neotropical migrants (Rappole 1995). That 1.5-fold difference may seem large; however, given that the land mass north of the Tropic of Cancer is ~5-fold larger than the land mass south of the Tropic of Capricorn, it is somewhat surprising that the difference in number of species is not greater. For such a relatively small area, temperate South America has a rich diversity of migratory species; we will return to this point.

Second, temperate South America has a larger portion of its land mass situated near the equator than does North America, which means that South American birds need not migrate as far in fall as North American breeders, whose breeding grounds generally have more severe winter temperatures (Chan 2001). It also means that the ratio of breeding area to wintering area is low (<1), in contrast to the situation in the Northern Hemisphere, where there is far more breeding than wintering area. Both those factors likely explain the relative proximity of breeding and wintering ranges typical of many austral migrants (Chesser 1994, Hayes et al. 1994, Stotz et al. 1996). That, combined with the lack of topographic barriers to north–south migration in South America (Chesser 1994), provides another explanation for the relatively high species diversity of austral migrants. Likewise, one could argue that the species diversity of migrants in temperate North America is comparatively low because the source pool (Central and equatorial South America) is generally farther away and hindered in northward expansion by the Gulf of Mexico.

Continental position and shape could also be important factors promoting the higher incidence of partial migration in the Southern than in the Northern Hemisphere in the Americas. The general pattern of shorter distances between breeding and wintering grounds in South America, as compared with those in the Nearctic–Neotropical and Palearctic–African systems (Chesser 1994), and the lack of geographic barriers at the center of the continent (a situation associated with high levels of partial migration; Chan 2001), likely promote partial migration.

In terms of taxonomic affinities, South America's austral system is unique, in that one family, the Tyrannidae, accounts for 33% of all species, reflecting that family's overall predominance across the continent (Chesser 1994). In contrast, the most speciose families of Nearctic–Neotropical migrants comprise only 15% (Parulidae) and 9% (Tyrannidae) of all species in that system (Rappole 1995, American Ornithologists' Union 2003). In ecological terms, the majority of austral migrants are open-country breeders, whereas most Nearctic–Neotropical migrants tend to nest in more forested habitats (Chesser 1994). Nevertheless, migrant ecology between the systems is remarkably similar overall, given that both groups appear to be habitat generalists during the nonbreeding season in the tropics and that they are both composed primarily of species that depend on open water or that feed on active insects (Stotz et al. 1996).

Finally, we draw attention to a curious lack of correspondence in migratory patterns between the northern and southern migration systems. Many north-temperate breeding species overwinter in the south-temperate zone (e.g. Scolopacidae), but there are no south-temperate breeding migrant populations that "overwinter" in North America's summer (Chesser 1994). As far as we know, nobody has explored why that might be so. Cracking the mystery will require an evolutionary approach.

An Evolutionary Framework

Although migration has arisen multiple times via different evolutionary pathways (Berthold 2001), the consensus is that many species breeding in the temperate zone and overwintering in the tropics evolved from tropical ancestors (Sinclair 1983, Levey and Stiles 1992, Rappole 1995, Safriel 1995). Joseph (1997) and Chesser and Levey (1998) applied that hypothesis to the southern hemisphere, proposing a Neotropical origin for austral migrants. From that point of view, breeding in south-temperate latitudes may have been constrained by a relatively small breeding area, and fall migration back to the tropical ancestral home may have been limited by competition with nonmigratory conspecifics. Indeed, South America's austral migrants generally do not winter as far north as the tropics: only 32 species migrate in fall as far as Amazonia, and 14 north of the Amazon basin; and two-thirds have nonbreeding ranges that overlap the ranges of conspecific residents (Stotz et al. 1996). In contrast, almost one-quarter of Nearctic–Neotropical migrants winter south of Amazonia, and less than half have ranges that are nondisjunct (Stotz et al. 1996).

Applying an evolutionary framework to the study of migration, as proposed already by Gauthreaux (1982), can reveal why some species are migratory and others are not. For example, if small-scale seasonal movements by Neotropical species are viewed as an evolutionary precursor to austral migration (Levey and Stiles 1992, Chesser and Levey 1998), one can predict the extent of migration in various taxa. In particular, families containing many species that show small-scale seasonal movements within the tropics are more likely to also contain austral migrants than families whose species show no seasonal movements within the tropics. An untested application of that prediction lies within the Tyrannidae. Because so many species of flycatchers are austral migrants, we predict that closely related species and genera that are not austral migrants will display a high degree of seasonal movement within the tropics.

Unfortunately, we are a long way from being able to test such predictions because so little is known about the extent of migration *on any scale* within South America. Figuring out which austral species migrate and where they go is greatly complicated by the fact that most have overlapping populations of migratory and resident individuals. Although such "partial migrant" species are an obstacle, they also present an opportunity to unravel the evolutionary pathway of austral migration. In particular, because partial migration is considered an evolutionary step toward migration (e.g. Cox 1985, Alerstam and Hedenström 1998, Berthold 1999), documenting the ecological, taxonomic, and geographic correlates of partial migration will reveal at least some of the processes driving the evolution of migration. South America is the best place for such a study, because partial migration typifies it more than any other system.

Intraspecific Patterns of South American Avian Migration

Partial migration is common worldwide (Lack 1943). In South America, ~70% of austral migrants have populations that migrate to south-temperate breeding grounds away from resident breeding populations (Stotz et al. 1996). We distinguish between two types, one in which some individuals migrate away from an otherwise nonmigratory (breeding) population in the temperate zone to overwinter nearer the equator (e.g. Vermilion Flycatcher [*Pyrocephalus rubinus*]), and one in which some individuals migrate away from an otherwise nonmigratory population in the tropics to breed in the temperate zone (e.g. Tropical Kingbird [*Tyrannus melancholicus*]). The first type, referred to as "partial migration," is well known. For example, Berthold (2001) reports that >60% of ~400 of Europe's breeding bird species are partial migrants. The proportion is 10% in South Africa (Dowsett 1988) and 36% in Australia (Chan 2001). The second type, which we term "population partial migration," is not as well appreciated. Forty-eight percent of Nearctic–Neotropical migratory species have conspecifics that breed in the Neotropics, whereas 23% of Palearctic–Paleotropical migratory species (breeding in the temperate Old World and migrating to tropical Africa) have populations that breed in the tropics (Rappole 1995). The fundamental difference between partial migration and population partial migration is that population partial migrants depart from a breeding population to breed elsewhere (i.e. the temperate zone), whereas partial migrants depart from a breeding population to overwinter elsewhere (i.e. the tropics). Nevertheless, the two are not mutually exclusive in a species, and it is possible that both operate in some austral migrant species.

The evolutionary significance of differentiating between these two types of migration rests on where the migratory behavior first appeared. If we assume that a species originated in the tropics, migration could result in a reproductively isolated population in the temperate zone, possibly leading to migration away from the tropics by all populations (e.g. via interspecific competition during the nonbreeding season; Cox 1985). That seems most plausible for population partial migrants. If, on the other hand, we assume that a species originated in the temperate zone and migration evolved toward tropical overwintering grounds, migratory and resident populations are likely not reproductively isolated. Partial migration in such cases can be driven by condition-dependent mechanisms (e.g. sex and dominance hierarchies; Ketterson and Nolan 1976, 1979). That seems most plausible for partial migrants. Recognizing the difference between the two patterns leads to a distinction between population-level (i.e. population partial migration) and individual-level (i.e. partial migration) processes. For example, a study on phenotypic plasticity in migratory birds would do better to focus on a partial migrant (in which individuals may migrate in an individual-level, condition-dependent manner) than on a population partial migrant species, in which migration is population-specific.

Unfortunately, such differences in the evolutionary histories of these intraspecific migratory patterns have been overlooked at times, at least partly as a result, we believe, of a north-temperate bias when considering migratory behavior. The matter is not trivial, because tests of possible causes of virtually any migratory pattern are designed on the basis of clear assumptions regarding the evolutionary origin of such mechanisms. If the assumption is made that a species first evolved within tropical latitudes, research on the ultimate causes of migration will focus on a species in which the migratory population migrates toward the temperate breeding zone, whereas research on the proximate causes of partial migration will focus on a population in which some individuals breed in the temperate zone and others migrate to tropical wintering grounds. If the assumption is made that a species first evolved as a temperate resident, the study location will be reversed.

For purposes of tracking the ecological and evolutionary pathways via partial migration to complete migration, the austral system is perhaps the best in the world. In many austral migrant species, the migratory individuals are those migrating out of the tropics (the putative ancestral home); whereas in systems with temperate partial migration, migratory individuals are migrating toward the tropics while sedentary conspecifics remain at temperate latitudes (where they presumably did not evolve). Furthermore, such a population-level pattern of migration in South America would presumably lead to a situation that optimizes conditions for population isolation and therefore speciation (see Joseph et al. 2003 for further discussion).

Classifying Types of Austral Migration

There are many types of austral migrants. Distinguishing among them is an important first step in understanding their evolutionary ecology, as demonstrated in the previous section with partial migrants. This theme of embracing the full range of migratory movements has been championed by many ornithologists, both temperate and tropical (e.g. Levey 1994, Rappole 1995, Berthold 2001). In the context of austral migration, Joseph (1997) called attention to the danger of using one broad nomenclature for a general migratory pattern, when in fact various species-specific patterns exist.

The challenge of distinguishing among different types of austral migrants is unusually daunting, in large part, because of South America's shape, latitudinal position, and topography. As mentioned above, the relatively large tropical–subtropical area, small temperate area, and lack of east–west barriers result in a situation where most birds on the continent have many migratory options. Practically nothing is known about which options are taken by which species, but it is likely that the entire spectrum is represented. Although interspecific patterns (e.g. migratory route use, habitat use) will probably be the first to emerge with further research, distinguishing between the various intraspecific, population-level migration strategies employed will require research capable of gathering detailed information locally (e.g. age and sex of individuals exhibiting different migratory behaviors) across various landscapes at a wide range of sites. To draw attention to the various possibilities and help focus research on teasing them apart at the population level, we define the following intraspecific patterns of austral migration, divided into population- and intrapopulation-level phenomena. Although intraspecific patterns of austral migration are generally poorly known, we provide examples of species in which the phenomenon could at least potentially occur, given the general migratory pattern of the species.

Population-level

(1) Complete migration: All individuals of a population migrate in both fall and spring (e.g. Cinnamon-bellied Ground-Tyrant [*Muscisaxicola capistratus*]).

(2) Leapfrog migration: Some populations consist solely of permanent residents, with migratory populations flying over or around them (e.g. White-banded Mockingbird [*Mimus triurus*]).

(3) Postbreeding displacement migration: After breeding, southern populations migrate toward the equator and displace conspecifics, which then migrate closer to the equator to overwinter (e.g. Southern Martin [*Progne elegans*]).

(4) Breeding displacement migration: One population migrates to breed at the wintering location of other conspecifics, which are then displaced to breed at higher latitudes (e.g. Creamy-bellied Thrush [*Turdus amaurochalinus*]).

(5) Population partial migration: Migration of some individuals toward south-temperate latitudes to breed, with some individuals residing year-round in the Neotropics (e.g. Lesser Elaenia [*Elaenia chiriquensis*]).

(6) Temperate population partial migration: Migration of some breeding populations toward tropical latitudes to overwinter, with other populations overwintering in south-temperate latitudes (e.g. Black-crowned Monjita [*Xolmis coronatus*]).

Intrapopulation-level

(1) Partial migration: Migration of some individuals toward tropical latitudes to overwinter, with some individuals of the same population residing year-round in the south-temperate zone (e.g. White-winged Black-Tyrant [*Knipolegus aterrimus*]).

(2) Dual partial migration: Migration of some individuals northward and some southward, away from a permanent resident population in the tropics (e.g. White-throated Kingbird [*Tyrannus albogularis*]).

(3) Leapfrog partial migration: Migration of some individuals between a seasonal breeding range and a seasonal wintering range, overflying populations in which some individuals are migratory and others permanent residents (e.g. Crowned-Slaty Flycatcher [*Empidonomus aurantioatrocristatus*]).

Suggestions for Future Research

In light of the pervasive and acute habitat alterations occurring on the South American continent (e.g. Stotz et al. 1996), knowledge of basic ecology, such as resource use and timing of migration in austral migrants, as well as population trends and relative abundances at various spatial scales, is imperative for the success of long-term conservation efforts. Such information has been collected for decades in North America (reviewed in Gauthreaux 1996) and has proved useful for understanding migratory birds' requirements. Standardized equivalents beyond the local scale do not exist for South America; not only is it unclear whether most populations of migratory species are declining, it is impossible with current data to even explore such a possibility. Although our existing knowledge of the ecology of austral migrants points to most having low habitat-specificity (Stotz et al. 1996), increasing alteration of various habitats on the continent by humans (e.g. dry forests; Gentry 1977, 1993), as well as the more general threat of global climate change (e.g. Berthold 2001), may pose significant threats to South America's migrants. An example of a threatened group is the *Sporophila* seedeaters, which are faced with habitat alteration (Stotz et al. 1996) and, in some cases, capture for the pet trade. For many species, ranges are "still surprisingly imperfectly known" (Ridgely and Tudor 1989).

We believe that the most fundamental challenge in correcting this situation is one of critical mass—the few South American ornithologists interested in migration are widely scattered and faced with an enormous and complex migration system about which even the most basic information is lacking. Thus, a top priority should be to establish a dialogue to prioritize needs, set research goals, and establish collaborative ties across countries and continents. If a collective vision is clearly articulated, the next significant challenge—securing financial resources—will be less difficult.

As a first step in that direction, a symposium on austral migration was held at the VII Neotropical Ornithological Congress at Termas de Puyehue, Chile, in October 2003. To the best of our knowledge, it was the first such symposium. Even within the context of major symposia on migrant birds, contributions about austral migration seem to be almost totally absent (e.g. most recently at the "Birds of Two Worlds" symposium; see Acknowledgments). (It is important to note that this absence is due not to neglect by the organizers but rather to the almost total absence of researchers publishing on austral migration in international journals.) The major goal of the austral migration symposium in Chile was to bring together researchers from South and North America to share ideas and techniques and to help foster collaborative projects (see Acknowledgments).

Perhaps the most effective way to promote migratory bird research and conservation in South America would be to establish an international, multi-agency consortium that focuses on and promotes research, conservation, and management of austral migrants. An obvious and successful model is Partners in Flight, which brings together disparate government agencies (e.g. Bureau of Land Management, Department of Defense, Fish and Wildlife Service, Forest Service), academic institutions, and nongovernmental organizations (e.g. American Bird Conservancy, National Audubon Society, The Nature Conservancy). It is international and emphasizes representation from organizations in Canada, United States, and several Central American countries.

In this context, we note that a diverse array of avian ecology projects are already underway across South America. Those projects have untapped potential for providing basic data on austral migrants across a broad geographic range. A strong collaborative effort could unite such projects and provide standardized methodologies for monitoring migrant populations. In some cases, valuable information on austral migration has already been collected, albeit unintentionally. Museum records are an especially promising but relatively unexplored example. What is lacking is a means of compiling such information for analysis and dissemination. In the same way that synthesis of data from museums yielded much information on seasonality and ranges of austral migrant species (e.g. Chesser 1995), collating information from existing field studies could elucidate important details of migration from across the continent. Collecting, compiling, and synthesizing of such data would best be carried out under the auspices of a network of scientists, who could champion the need to collect specific data on migration in a highly standardized manner.

Use of novel technologies, such as online interactive databases, would greatly facilitate the maintenance of a migration research and research-monitoring network in South America (see Vuilleumier [2003] for similar and further suggestions for future research in Neotropical ornithology). For example, during the 2004 fall migration in South America, a group of ornithologists led by Jennifer Johnson of Swarthmore College conducted nocturnal migratory bird censuses by moon-watching. Ornithologists from each country entered data into an online database, thus compiling continent-wide information. Because New World migratory birds generally move in the same direction in the same season, this effort simultaneously monitored the migration of north-temperate as well as south-temperate breeders. Such collaborative efforts could open doors for the use of a variety of new technologies for migration research in South America. Stable-isotope analysis, satellite telemetry, and weather radar, which have been recently and widely applied in studies on Nearctic–Neotropical migrants, are known and largely available in South America (e.g. stable hydrogen isotope; K. Hobson et al. unpubl. data), though their potential remains virtually untapped.

Finally, we believe that opening a new avenue to the study of avian migration will not only lead to improved understanding of the "hows and whys" of austral migration, but is a chance to make great strides in our understanding of migration in general. Zimmer's (1938) remark, which opened this article, on the poor state of knowledge of bird migration in South America at the middle of the 20th century, continues to ring true. In the present century, we have an opportunity to produce a much clearer picture—and possibly a new paradigm—of New World bird migration.

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