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TOWARDS A MECHANISTIC INTERPRETATION OF BIRD MIGRATION IN SOUTH AMERICA

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ABSTRACT.— Research to date has demonstrated that bird migration is comprised of highly diverse and plastic behavioural patterns. Our objective is to highlight the importance of studying mechanisms underlying these patterns in austral migrants. We focus on the high incidence of overlap in breeding and non-breeding ranges as a particularly thought-provoking pattern. We then explore the opportunities afforded by partial migration theory to elucidate the mechanisms underlying seasonal range overlap. We propose that a mechanistic understanding of migration in South America will both provide a deeper appreciation of the ecology, physiology and evolution of migratory species in the New World, and improve the scientific foundation for their conservation.

KEY WORDS: *mechanism, partial migration, population, range overlap, Tyrannus.*

RESUMEN. HACIA UNA INTERPRETACIÓN MECANÍSTICA DE LA MIGRACIÓN DE AVES EN AMÉRICA DEL SUR.— La investigación reciente sobre aves migratorias ha demostrado que constituyen un grupo que presenta comportamientos altamente diversos, plásticos y complejos. Nuestro objetivo general es resaltar la importancia de estudiar los mecanismos que generan los patrones que caracterizan la migración de aves en América del Sur. Para ello nos enfocamos en un patrón interesante (la alta incidencia de superposición en la distribución reproductiva y de invernada), analizando las oportunidades ofrecidas por la teoría de migración parcial para dilucidar los mecanismos que producen tal superposición. Proponemos que una comprensión mecanística de la migración de aves en América del Sur no solo proveería una apreciación más profunda sobre la ecología, la fisiología y la evolución de las especies migratorias del Nuevo Mundo, sino que también mejoraría los fundamentos científicos para su conservación.

PALABRAS CLAVE: *mecanismos, migración parcial, población, superposición de distribuciones, Tyrannus.*

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Research on various aspects of bird migration — from biogeography to ecology and physiology — has demonstrated that migratory behaviour is an extraordinarily diverse and complex phenomenon. For example, it can evolve relatively rapidly (Able and Belthoff 1998, Berthold 1999, Piersma et al. 2005), is phylogenetically flexible (Böhning-Gaese and Oberrath 1999), and can appear and disappear through time within a lineage (Zink 2002, Joseph et al. 2003, Outlaw et al. 2003) or even within an individual's lifetime (e.g., Schwabl and Silverin 1990). In the New World, a continuum of migratory strategies exists, from long-distance migrations undertaken by all populations of a species to short-distance

migrations undertaken by only some populations (Levey and Stiles 1992) or individuals (e.g., Ketterson and Nolan 1976). Migration can even play a central role in speciation (Winker 2000, Winker and Pruett 2006).

To solve persistent riddles about the evolution and regulation of migration requires teasing apart factors confounded in space and time. This is difficult to accomplish without a broad geographic scope. In the New World, almost all work on migration has been restricted to the north-temperate latitudes (Levey 1994, Jahn et al. 2004), with relatively little attention paid to migration within South America (austral migration, sensu Chesser 1994). Some species of Neotropical austral

migrants move annually between the temperate zone and tropical latitudes and some species migrate within either tropical or temperate latitudes of the continent (Joseph 1997). There are more than 220 species of Neotropical austral migrants, comprising the largest migratory system in the Southern Hemisphere (Chesser 1994). Recent literature on migration in South America principally explores biogeographic patterns (e.g., Chesser 1994, da Silva 1999, Capllonch and Lobo 2005), evolution (Joseph et al. 2003), habitat associations (e.g., Chesser 1995, Stotz et al. 1996, Jahn et al. 2002) and the timing of migratory movements (e.g., Hayes et al. 1994).

The geographical patterns of migration in the Neotropics are complex (Morton 1977, Winker et al. 1997, Bildstein 2004). In some species all populations migrate, but in others different populations migrate in the same or in different directions. Furthermore, all of these strategies can occur within one genus (e.g., genus *Tyrannus*, Fig. 1; Ridgely and Tudor 1994, Chesser 1995). This stands in sharp contrast to the situation in North America, where all the populations of migratory species generally move in the same direction during each season.

Given the diversity of migration strategies evident within South America, it is clear that the phrase "bird migration in South America" encompasses a multitude of inter- and intra-specific patterns at smaller scales than the overall pattern at the continental level would suggest. Thus, to better understand how migratory birds respond to competing ecological and physiological demands, it will be essential to form links between patterns observed at different spatial and temporal scales and among taxonomic (e.g., families and species) and biological levels of organization (e.g., genotypes, individuals, ecosystems) (Levin 1992).

Our objective is to demonstrate that research on the mechanisms generating specific patterns of bird migration in South America is a prerequisite to gaining a better theoretical foothold, as well as for the ability to formulate sound, proactive conservation and management strategies. We use as an example the high incidence of seasonal range overlap in the distributions of South American migratory bird populations to highlight the power of existing theory on intrapopulation variation in migratory behaviour to explain such patterns.

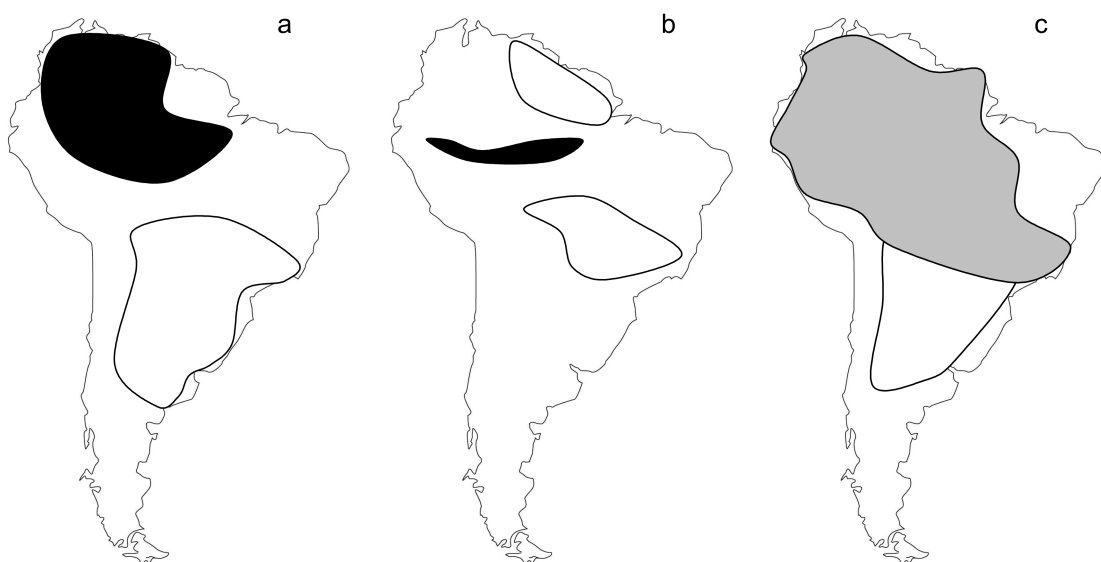


Figure 1. Generalized seasonal distributions of *Tyrannus savana savana* (a), *Tyrannus albogularis* (b), and *Tyrannus melancholicus melancholicus* (c) in South America. Black polygons represent seasonal non-breeding ranges, white polygons represent seasonal breeding ranges and the gray polygon represents area of overlap in which permanent residents as well as non-breeding (i.e., overwintering) migratory individuals from the south occur together. Adapted from Chesser (1995).

A FOCUS ON MECHANISMS

Studying mechanisms — the proximate relationships between what an individual experiences and how it responds — is the key to being able to explain the causes for observed patterns, advancing both basic science (i.e., explanations, predictions, the formulation of original questions) as well as practical applications (i.e., conservation and environmental planning and management). Such rewards will only result from studies that are focused on specific questions and employ testable hypotheses (Vuilleumier 2004).

Tests of mechanistic hypotheses (i.e., how component parts of the phenomenon interrelate) — rather than phenomenological explanations (i.e., models that extrapolate future trends based on past trends) — are useful for interpreting the reasons for changes observed in a pattern (e.g., migratory timing or direction) (Koehl 1989), especially in light of the magnitude and speed of contemporary anthropogenic changes in global biogeochemical cycles (Lubchenco 1998). From an applied perspective, knowing where species are located during the entire annual cycle is necessary to formulate a basic conservation plan. However, an understanding of the factors influencing survival and reproduction at smaller spatial scales enables a more effective conservation strategy. For example, Marra et al. (1998) demonstrated that the quality of habitats occupied by *Setophaga ruticilla* individuals during the non-breeding season can affect their physical condition and thus their arrival date on North American breeding ranges, which has consequences for their reproductive success. In this case, knowledge of the life-history consequences of habitat use opens the door to the formulation of more detailed conservation priorities.

Studying the mechanisms that regulate the components of a system also allows patterns to be placed within an evolutionary context. As pointed out by Moore and Aborn (2000), research about habitat selection during migration has historically focused on describing habitat use rather than examining the mechanisms through which selection acts. Thus, to elucidate the processes responsible for observed patterns, it is important to consider the evolutionary history of a species as well as contemporary constraints. Taking just such

an approach, Böhning-Gaese and Oberrath (2003) concluded that contemporary habitat preferences of migrants have been strongly influenced by the historical occupation of relatively open habitats in Africa (by ancestors of Holarctic migrants) and of Neotropical forests (by ancestors of Nearctic migrants), as well as by contemporary processes.

Nevertheless, an ability to understand the causes of patterns evident at the population level demands research on processes occurring at the individual level (Koehl 1989). This is because the evolutionary mechanisms that generate population-level migratory patterns originate from variation among individuals. Thus, a focus on the individual is essential for formulating and testing hypotheses about the evolution of migration (Bell 2000). Research focused at the level of the individual requires consideration of the ecological constraints encountered by individuals on different scales throughout their annual cycle. For example, a bird that forages on a scale of hundreds of meters may migrate hundreds of kilometers to search for similar resources at another site. Thus, migratory species are affected by processes occurring on vastly different temporal and spatial scales (e.g., Alerstam and Åkesson 2003). Forming links between these disparate scales is one of the central challenges not only of migrant bird ecology, but of science in general (Levin 1992).

Finally, since migratory behaviour is an attribute regulated by a suite of characters (e.g., physiological, social; Piersma et al. 2005), it is important to formulate hypotheses about these characters within an explicitly phylogenetic context (Zink 2002). In South America, the diversity of movement patterns, even within a single species (e.g., *Myiarchus swainsoni*; Joseph et al. 2003), may be a complex and long-term response to changing environmental conditions on the continent. However, diverse migratory behaviours can also appear on much shorter time scales. One notable example is the appearance of populations of *Hirundo rustica* that are beginning to reproduce within their historical non-breeding range, particularly in the coastal zone of the province of Buenos Aires, Argentina (Martínez 1983).

We now have the opportunity to design studies within South America to test theories formulated in other migration systems. With

such an approach, we can both enrich our understanding of migration within South America and test the explanatory power of extant theories across migratory systems. We can begin to answer such questions as: do similar ecological, physiological, and genetic mechanisms underlie all migratory systems?; does migration within South America operate under different "rules" than in other systems? For example, the capacity for nocturnal compass orientation is highly conserved phylogenetically in migratory birds around the world (Piersma et al. 2005). In mid- and high-latitudes, migratory birds can use a magnetic inclination compass for orientation, but this system cannot function at equatorial latitudes (Wiltschko and Wiltschko 1995). Thus, what alternative cues can migrants use to orient and navigate in equatorial South America? Clearly, research in this area will allow us to test extant mechanistic theories as well as formulate new hypotheses about the migrations of birds.

In the next section, we use the seasonal overlap of ranges to launch a discussion of how to distinguish between populations of migratory species, as well as how to study the mechanisms operating within these populations.

RANGE OVERLAP

What patterns characterize bird migration within South America? Stotz et al. (1996) and Chesser (1994) identified several key features: (1) taxonomic composition (in South America, the family Tyrannidae makes up nearly a third of all migratory species on the continent); (2) distance of migration (within South America, most migrants move over shorter distances than do Nearctic-Neotropical migrants); (3) proportion of migratory species along a latitudinal gradient (in South America, the gradient of increasing number of migratory species with latitude is less dramatic than in North-temperate latitudes); and (4) range overlap (approximately two-thirds of Neotropical austral migrants — 159 species — exhibit overlap in population ranges across seasons; i.e., migrants of one population migrate to areas already occupied by conspecifics that do not migrate). Although these four patterns are coarse-grained and described at a continental scale, they offer a point of departure from which to look for more specific patterns (Stotz et al. 1996). We focus on the pattern of range

overlap among populations as an interesting pattern to explore the mechanisms that may underlie it.

Several biogeographical explanations have been offered to explain the causes of range overlap. Chesser (1994) offered two hypotheses. First, given that the South American continent is wider towards the equator, birds moving northwards towards the equator after the breeding season could experience a reduction in interspecific competition as a consequence of lower population densities due to the increasing land area, reducing their need to continue migrating northward. Second, there are no evident geophysical barriers to the east of the Andean Cordillera to segregate breeding and non-breeding ranges. In a similar vein, Hayes et al. (1994) proposed that the diminished land area at high latitudes corresponded to a reduced capacity to sustain breeding populations of migratory species, thus producing relatively short migrations between tropical and temperate latitudes.

To test mechanistic hypotheses on the pattern of range overlap, however, we must know something about the variation in migratory distance among individuals, since different strategies among individuals may be present across the species' range. In essence, seasonally overlapping ranges obscure any pattern of exactly where migratory individuals pass the non-breeding season (Stotz et al. 1996). Some populations may even be migrating within the area of overlapping ranges. For example, within any one species, there may be populations that are completely resident, as well as some that are partially migratory (i.e., some individuals of a population migrate; Fig. 2). Thus, the area of overlap may "mask" substantial variation in migratory movements among populations. Furthermore, migrant and resident individuals may be partitioning the area of overlap in different ways. For example, Tellería and Pérez-Tris (2004) studied habitat associations in *Erithacus rubecula*, a European migrant species comprised of migratory populations whose non-breeding distribution overlaps with the distribution of resident populations in the south of the continent. They found that residents and migrants were physiologically different and occupied distinct habitats during the period of overlap. Consequently, in order to study the mechanisms underlying range

overlap, it will be important to differentiate between populations and to define their "connectivity": the origin and destination of migratory populations (for a review, see Webster et al. 2002). Once the migratory patterns of populations have been characterized as migratory, resident, or partially migratory, research can turn to the question of which processes underlie their migratory pattern.

Information on connectivity of populations and, at a local scale, on habitat use by different individuals (i.e., migrants vs. residents) has obvious relevance for conservation policy. For example, if one population is in decline in the breeding area, knowledge of where it spends the non-breeding season within the area of overlap can greatly help to pinpoint the part of the life cycle in which the greatest threats to the survival of that population occur.

We now focus on some ideas about how to study mechanisms that operate on an intra-population level and produce population-level patterns. We use partial migration as an example (Fig. 2). For a recent review of other population-level migration patterns, see Boulet and Norris (2006).

PARTIAL MIGRATION

Partial migration is perhaps the most common type of bird migration in the world (Berthold 2001). From an evolutionary standpoint, partial migration is thought to be an intermediate step in the evolution of complete migratory behaviour in birds (Berthold 1999). Consequently, studying the processes that produce partial migration could be a key to understanding more about the proximate and ultimate processes that govern migratory movements in species with overlapping ranges.

Before discussing the processes producing partial migration, it is important to distinguish between population-level partial migration and intra-population partial migration. In population-level partial migration, some populations of a species migrate and other populations do not. For example, in *Tyrannus savana*, the nominate subspecies is a Neotropical austral migrant, while another subspecies (*Tyrannus savana sanctaemartae*) remains as permanent resident in the northern part of the continent (Chesser 1995, Stiles 2004). This population-level variation in migration

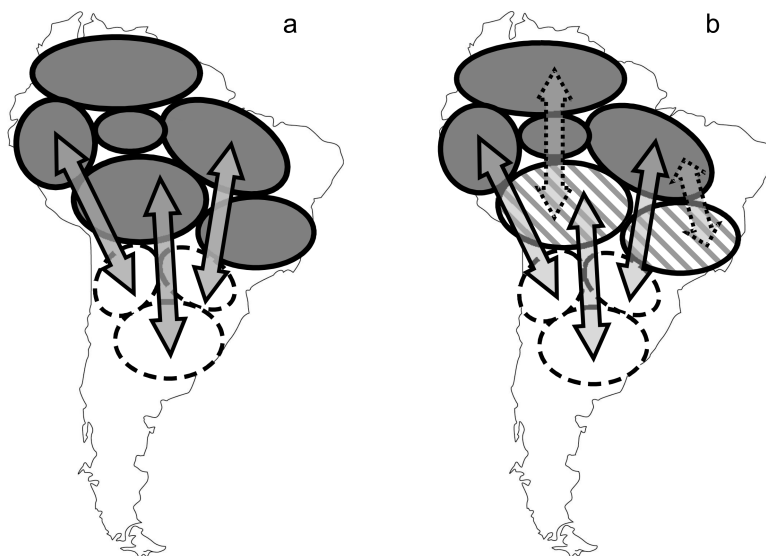


Figure 2. Two hypothetical patterns of population-level migration of *Tyrannus melancholicus melancholicus*: (a) migration exclusively of populations between a seasonal breeding area and an area of range overlap, and (b) migration of populations between a seasonal breeding area and an area of overlap, as well as partial migration of some populations within the area of overlap. Gray areas: populations of permanent residents, hatched areas: partially migratory populations, white areas: completely migratory populations, dashed arrows: partial migration, closed arrows: complete migration.

characterizes at least 70% of the migratory species in South America (Parker et al. 1996). In the case of intra-population partial migration, some individuals of the same population migrate after the breeding season and others do not (*sensu* Lack 1943; for a review, see Berthold 2001, Jahn et al. 2004). Differences in migratory behaviour between individuals in the same population have been widely documented in other migratory systems but have not yet been documented in South America. Hereafter, when we refer to "partial migration", we consider specifically intra-population partial migration.

The first studies on partial migration tended to be descriptive or to focus on evolutionary, population-level processes (e.g., Lack 1943, 1954, Kalela 1954, Cohen 1967, von Haartman 1968, Biebach 1983). More recently, emphasis has moved towards identifying and weighing the differences between individuals. Within this context, "migrant" and "resident" are considered to be alternative strategies with different benefits for different individuals in a population (e.g., Swingland 1983). Individual asymmetries (e.g., age, size) are postulated to determine migratory status because of differences in competitive advantage between individuals. Lundberg (1987) contributed to this framework by adding the parameter of frequency-dependent choice, in which individuals of different social rank (e.g., juveniles low in the social hierarchy) decide whether to migrate, depending upon the relative frequencies of the dominant and subdominant individuals in the population with which they have to compete. Indeed, factors such as age, sex and social status in a population have been shown to determine migratory behaviour (e.g., Gauthreaux 1982, Schwabl 1983, Adriaensen and Dhondt 1990). For example, Able and Beltoft (1998) demonstrated that among *Carpodacus mexicanus* migrating within North America, younger individuals were characterized by a higher tendency to migrate. These demographic and social conditions are often tightly linked to such parameters as competitive ability, physiological tolerance and habitat associations, which in turn are postulated to affect migratory status (Ketterson and Nolan 1983, Cristol et al. 1999, Tellería and Pérez-Tris 2004). Thus, a test of the relationship between these parameters (e.g., physiological tolerance,

social dominance) and migratory strategy (e.g., migratory timing, migratory distance) produces mechanistic models on the causes of such patterns as range overlap. It follows that identifying demographic (e.g., age, sex), social (e.g., dominance), and morphological (e.g., body size) differences between individuals is a prerequisite to studying the processes responsible for variation in the migratory behaviour among individuals of a partially migratory population (i.e., whether or not an individual migrates).

What, then, are some specific, testable mechanistic hypotheses that can begin to tease apart potential causes for range overlap? Partial migration is one class of the broader category of differential migration, in which individuals within a population undertake migrations of varying distances (e.g., Ketterson and Nolan 1976). In partial migrants, the distance travelled by some members of the population falls at an extreme of a gradient: zero migration (i.e., residence). Thus, since partial migration is a class of differential migration (Alerstam and Hedenström 1998), much of the theory about differential migration is applicable to partial migration and vice versa. A great variety of theories attempt to explain partial and differential migration, but the majority are variations on three general hypotheses (Bell 2005). The first one is the Dominance Hypothesis. Subdominants are poor competitors for available food; when there are not sufficient resources for all the individuals in a population, subdominants are therefore more likely to migrate in order to avoid competition with dominant individuals. Supporting data are principally indirect, based upon the observation that in different species younger individuals or females are subdominant and migrate longer distances (e.g., *Junco hyemalis*; Ketterson and Nolan 1976). The second hypothesis is the Arrival Time Hypothesis. Individuals that establish territories at the beginning of the breeding season are less likely to migrate as far because a short migration distance ensures a rapid return to the breeding range and access to the best territories. For example, in a study of *Anser caerulescens*, Bêty et al. (2004) found a significant relationship between the arrival date on the breeding grounds and the probability of reproducing (although excessively early arrivals suffered from negative climatic

effects). Finally, the third hypothesis is the Body Size Hypothesis. In accordance with the relationship between body surface area and volume, larger individuals can better withstand lower temperatures and endure food limitations, giving them a lower probability of migrating away for the winter. For example, in *Carpodacus mexicanus*, females are socially dominant, but also smaller in size and tend to migrate further than males (Belthoff and Gauthreaux 1991). Studies evaluating these hypotheses have generally failed to produce data that predict migratory distance (e.g., *Junco hyemalis*; Ketterson and Nolan 1985). Future research in South America could test the explanatory power of these hypotheses in a context independent of the North-temperate system within which the hypotheses were originally formulated.

FUTURE DIRECTIONS

Given the challenge of understanding the mechanisms underlying such a complex system, it is timely to note several themes that may put this type of research in perspective.

Comparisons among common taxa in the New World

Current theory postulates a Neotropical origin for migratory species in the New World, both Nearctic-Neotropical and Neotropical austral migrants (Levey and Stiles 1992, Rappole 1995, Joseph 1997, Chesser and Levey 1998, Joseph et al. 1999, Böhning-Gaese and Oberrath 2003). A review of the data from Parker et al. (1996) reveals that at least 34 families, 56 genera and 23 species have populations of both Nearctic-Neotropical and Neotropical austral migrants. For example, *Pyrocephalus rubinus* have populations that are Nearctic-Neotropical migrants and other populations that are Neotropical austral migrants (Parker et al. 1996). Intraspecific comparisons of populations employing different strategies (Neotropical austral vs. Nearctic-Neotropical migration) are therefore possible and have the advantage of avoiding the confounding effects of phylogeny that commonly haunt interspecific comparative studies. Specifically, intraspecific research among populations of one species rather than comparisons between species decreases the effects of a shared phylogenetic history, which is problematic because it leads to a lack of inde-

pendence in the parameters being compared (e.g., Gittleman and Luh 1992, Garland and Adolph 1994).

Conducting comparative studies among migratory systems offers the additional benefit of avoiding the circular logic of attempting to test a hypothesis explaining the causes of a pattern in the same system within which the hypothesis was originally developed. For example, within South America, at least two distinct migratory sub-systems have evolved (Joseph 1997). Extant hypotheses can be evaluated in each sub-system independently.

Available techniques and technologies

The complexity of migration within South America demands an interdisciplinary research approach, incorporating a variety of techniques and technologies (Alerstam and Åkesson 2003, Barlein 2003). What tools can be applied to migration research in South America? New technologies exist that can supply data on diverse temporal scales (between years, months, or days), spatial scales (meters or kilometers), and between levels of biological organization (cellular, organismal, population-level). One particularly exciting new tool is stable isotope analysis, which can be used to determine the origins of migratory individuals (see Hobson 2005 for a review, and Torres Dowdall et al. 2006, in this volume). Base isotope maps do not currently exist for most isotopes throughout the whole of South America, but may be available in the near future.

International collaboration

Because migratory species confront varying constraints throughout the annual cycle (Sillert and Holmes 2002), and since events in one season can exert substantial influence over processes in subsequent seasons (e.g., Marra et al. 1998, Norris et al. 2004), research should be conducted throughout all phases of the annual cycle. This may most easily be accomplished by establishing collaborative international networks of researchers and conservation practitioners (e.g., Barlein 2003). Such associations could standardize methods and share data about the same species and populations. These activities will be essential for advancing the study of patterns and mechanisms (see Stiles 2004 for suggestions

and interesting questions), as well as advancing the conservation of populations of migratory species that cross political boundaries.

Research at the individual level

We emphasize the value of collecting individual-specific data (e.g., through colour-banding and genetics). Mechanisms apparent at the population level originate at the individual level; therefore, descriptive studies conducted at the individual level, such as McNeil's (1982) work documenting winter site fidelity in *Elaenia parvirostris*, are particularly useful to guide the development and testing of mechanistic hypotheses.

CONCLUSION

Numerous questions are wide-open lines of research — both descriptive and hypothesis-based — in South America. Much progress has been made on other continents about problems that remain unsolved in South America, such that existing bodies of theory, technologies and methods could be readily applied to research on South American migration. Interesting questions concerning the evolution of migration for which we know little in South America include: (1) biogeography (what is the relationship between speciation rates and migratory behaviour across clades?, how does this relationship compare in South America to other migratory systems?); (2) ecology (what is the winter ecology of Neotropical austral migrants?, what is the relationship between migratory timing and biotic vs. abiotic factors?); (3) physiology (do Neotropical austral migrants employ a similar navigation system as migrants in other systems?, what are the energetic constraints to migration in South America relative to other systems?); (4) life-history (which part of the life cycle is most limiting in terms of reproductive success and survival?, are there carry-over effects for reproductive success between seasons?). The answers to such questions will provide a basis upon which to ask more questions and further develop more detailed, mechanistic hypotheses. Given the complexity that characterizes austral migration, our understanding of New World bird migration will be greatly enriched when we undertake a multidisciplinary approach that incorporates both descriptive and theoretical research to

elucidate the origins and maintenance of migratory patterns in South America.

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