



SPECIAL FEATURE: Advances in Neotropical Ornithology

Bird migration within the Neotropics

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ABSTRACT

Although the migration ecology of birds breeding in the Neotropics is still poorly studied relative to that of their counterparts breeding at north-temperate latitudes, studies conducted over the last 2 decades have revealed that migration in the Neotropics is much more common and diverse than previously thought. These studies have identified dozens of species that migrate latitudinally within South America, altitudinally within various mountain ranges, to and between Caribbean islands, and longitudinally across diverse ecosystems such as the Amazon rainforest. Advances in miniaturized tracking technologies, enormous citizen science databases, and powerful analytical approaches provide an unprecedented ability to detect and evaluate temporally and spatially fine-scale patterns, greatly facilitating the study of migratory patterns across tropical regions. We argue that a renewed effort in research on short- and long-distance bird migration within the Neotropics will allow (1) comparative studies that identify the emergent properties of migratory behavior, (2) identification of the convergent or unique mechanistic drivers of migration across diverse ecological settings, (3) formulation of effective conservation and management plans for migratory Neotropical birds, and (4) predictions about how migratory birds will respond to large-scale climatic changes within the Neotropics. Here, we review the current state of knowledge on Neotropical bird migration, with a focus on South America. We specifically examine similarities and differences in the observed migratory patterns of birds that breed in the Nearctic compared to the Neotropics and highlight key future research questions.

Keywords: altitudinal migration, conservation, intra-tropical migration, life history, migration drivers, Neotropical austral migration

La migración de las aves en el Neotrópico

RESUMEN

Aunque la ecología de la migración de las aves que se reproducen en el Neotrópico sigue poco estudiada en relación con las que se reproducen en las latitudes templadas boreales, los estudios realizados en las dos últimas décadas han revelado que la migración en el Neotrópico es mucho más común y diversa de lo que se pensaba. Esos estudios han identificado decenas de especies que migran latitudinalmente en América del Sur, altitudinalmente en varias cadenas montañosas, otros que migran hacia y entre las islas del Caribe, y otros que migran longitudinalmente a través de diversos ecosistemas como la selva Amazónica. Los avances en las tecnologías de rastreo miniaturizadas, las enormes bases de datos de ciencia ciudadana y poderosas técnicas analíticas proporcionan una capacidad sin precedentes para detectar y evaluar patrones temporales y espaciales a una escala fina, facilitando el estudio de los patrones migratorios en diferentes regiones tropicales. Sostenemos que un esfuerzo renovado en la investigación de la migración de aves a corta y larga distancia dentro del Neotrópico permitirá: (1) estudios comparativos que identifiquen las propiedades emergentes del comportamiento migratorio, (2) identificar los mecanismos convergentes o únicos de la migración a través de diversos escenarios ecológicos, (3) formular planes efectivos de conservación y manejo para las aves migratorias Neotropicales, y (4) predecir cómo responderán las aves migratorias a los cambios climáticos a gran escala dentro del Neotrópico. Aquí, revisamos el estado actual del conocimiento sobre la migración de las aves Neotropicales, con un enfoque en América del Sur. Examinamos específicamente las similitudes y diferencias entre los patrones observados de migración de aves que se reproducen en el Neártico vs. el Neotrópico y destacamos cuestiones claves para futuros estudios.

Palabras clave: causas de la migración, conservación, historia de vida, migración altitudinal, migración austral Neotropical, migración intra-tropical

INTRODUCTION

Given the vast area of the Neotropics, the diversity of its ecosystems, and its status as a biodiversity hotspot, it is perhaps no surprise that bird migration there is both common and highly diverse. Many birds that breed in the Neotropics regularly undergo annual migrations up and down mountains, latitudinally across thousands of kilometers between Patagonian temperate forests and tropical rainforests, between Caribbean islands, and across vast ecosystems such as the Amazon rainforest (e.g., [Chesser 1994](#), [Stotz et al. 1996](#)).

In general, bird migration is driven by the need to acquire seasonally available food resources to fuel such energetically demanding activities as molt and breeding, while avoiding stressful conditions (e.g., adverse weather, reduced food availability; [Boyle et al. 2010](#), [Somveille et al. 2015](#)). Because tropical habitats have long been considered aseasonal and stable, and because of the logistical difficulties of conducting tropical field work, large-scale movements of birds that breed in the tropics were, until recently, both unexpected and overlooked. As stated by [Zimmer \(1938\)](#), “It is not uncommon...to hear the statement made that South American birds do not migrate.” Today, we know that many tropical ecosystems are characterized by substantial spatial and temporal climatic variation, especially in rainfall, which almost certainly contributes to the predictable seasonal movements exhibited by various Neotropical birds that have long been assumed to be resident or nonmigratory. Indeed, “assumptions of sedentari-ness in tropical birds should be made with extreme caution” ([Winker et al. 1997](#)). These realizations, combined with advances in tracking technology, have spurred substantial recent interest in Neotropical bird migration. In particular, how common is migration and how might it differ from that of birds that breed at north-temperate latitudes?

Unfortunately, answers to such basic questions are limited by a lack of information about which taxa migrate, where they go, and the drivers of their diverse migration strategies. Moreover, detecting migration in New World birds that breed at tropical and south-temperate latitudes is often more difficult than in those that breed at north-temperate latitudes because most movements in the Neotropics occur over relatively short distances (e.g., hundreds, rather than thousands, of kilometers; [Chesser 1994, 1997](#); [Hayes et al. 1994](#), [Stotz et al. 1996](#)). Perhaps more problematic, partial migration is common ([Chesser 1994](#), [Winker et al. 1997](#), [Parker et al. 1996](#), [Jahn et al. 2004, 2012](#)), such that resident/nonmigratory individuals may “mask” movements of migratory individuals (e.g., Ash-throated Casiornis [*Casiornis fuscus*]; [Lees 2016](#); [Table 1](#)).

Nevertheless, a growing body of literature—especially in the last 2 decades ([Figures 1 and 2](#))—provides sufficient information to begin detection of general patterns. We limit this review to the migration of birds that breed in the Neotropical biogeographic region and focus on the migration of terrestrial bird species within South America because the vast majority of migration within the Neotropics occurs within South America ([Stotz et al. 1996](#)).

GENERAL PATTERNS OF BIRD MIGRATION IN THE NEOTROPICS

Numerous Neotropical birds respond to seasonality by making annual movements. Some species engage in true migratory behavior, defined as regular, directed movement between more than one well-defined area ([Berthold 2001](#), [Newton 2008](#)), whereas others exhibit irregular spatial and temporal movements, such as tracking spatial and temporal patterns of bamboo seed production (e.g., some *Sporophila* seedeaters, [Areta et al. 2013](#); Uniform Finch [*Haplospiza unicolor*], [Alves 2007](#)) and/or environmental conditions such as water levels (e.g., Wood Stork [*Mycteria americana*]; [Del Lama et al. 2015](#)).

Bird migration in the Neotropics does not appear to be shaped by major geographic barriers such as oceans or mountains. This fact may help facilitate movements across regions. However, ecological barriers to migration may be more subtle (e.g., large swaths of unsuitable habitat for an avifauna composed of highly specialized species, competition, and predation). For example, open country birds such as Fork-tailed Flycatchers (*Tyrannus savana*) must regularly cross Amazonia, the largest rainforest ecosystem in the world, to which they are likely less well adapted than to grasslands, because they primarily breed and overwinter in grassland habitats ([Jahn et al. 2016, 2019](#)). Likewise, recent research on White-crested Elaenias (*Elaenia albiceps chilensis*) has shown that they migrate quickly through desert and grassland environments during spring migration ([Cueto et al. 2016](#), [Bravo et al. 2017](#)) and stop over for an extended period before continuing to migrate ([Bravo et al. 2017](#)).

Here, we highlight that migration (a repeated annual movement) of bird species that breed in the Neotropics is more common than generally appreciated, encompassing a variety of less common migration types and that are often more subtle than at north-temperate latitudes.

Geographic Patterns

At least 4 types of annual migratory movement occur among birds that breed in the Neotropics: intra-tropical,

TABLE 1. Representative species of 4 major avian migration systems in the Neotropics.

Species	Breeding site	Nonbreeding site	Potential driver(s) of migration	References
Intra-Tropical Migrants				
Black Skimmer (<i>Rhynchops niger</i>)	southern Peru	northern Bolivia, southwestern Brazil	Nest site limitation due to flooding	Davenport et al. (2016)
Orinoco Goose (<i>Neochen jubata</i>)	southern Peru	northern Bolivia	Competition for nesting sites	Davenport et al. (2012)
Lesser Elaenia (<i>Elaenia chiriquensis</i>)	central and southern Brazil	central and western Amazonia	Arthropod (and fruit?) food availability	Marini and Cavalcanti (1990)
Rufous-thighed Kite (<i>Harpagus diodon</i>)	southeastern Brazil	Amazonia	Food availability	Lees and Martin (2015)
Altitudinal Migrants				
Violet-throated Metaltail (<i>Metallura baroni</i>)	higher altitudes of Ecuadorian Andes	lower altitudes of Ecuadorian Andes	Nectar (and arthropod?) food availability	Hobson et al. (2003)
Yellow-legged Thrush (<i>Turdus flavipes</i>)	higher altitudes of the Atlantic Rainforest	lower altitudes of the Atlantic Rainforest	Fruit and arthropod (other?) food availability	Castro et al. (2012)
Three-wattled Bellbird (<i>Procnias tricarunculatus</i>)	higher altitudes of Central America	lower altitudes in Central America	Fruit food availability	Powell and Bjork (2004)
Neotropical Austral Migrants				
South American Temperate–Tropical Migrants				
White-crested Elaenia (<i>Elaenia albiceps chilensis</i>)	Patagonian forests	Atlantic Rainforest and Brazilian interior	Fruit and arthropod food availability	Bravo et al. (2017)
Barn Swallow (<i>Hirundo rustica</i>)	central Argentina	northern South America	Arthropod food availability	Winkler et al. (2017)
Creamy-bellied Thrush (<i>Turdus amaurochalinus</i>)	south-central South America	central South America	Fruit and arthropod (and other?) food availability	Capllonch et al. (2008b)
Slaty Elaenia (<i>Elaenia strepera</i>)	southern Bolivia and northwestern Argentina	northern South America	Fruit and arthropod food availability	Marantz and Remsen (1991)
South American Cool–Temperate Migrants				
Chocolate-vented Tyrant (<i>Neoxolmis rufiventris</i>)	Patagonia	northeastern Argentina and Uruguay	Arthropod food availability	Farnsworth and Langham (2018)
Austral Nigrito (<i>Lessonia rufa</i>)	Patagonia	south-central South America	Arthropod food availability	Farnsworth et al. (2018)
Ruddy-headed Goose (<i>Chloephaga rubriceps</i>)	Patagonia	pampas grasslands	Temperature limitation/food availability	Blanco et al. (2003, 2006)
Longitudinal Migrants				
Cinnamon Warbling-Finch (<i>Pooecetes graminea</i>)	western Argentina	eastern Argentina	Seed food availability	Cueto et al. (2011)
Rosy-billed Pochard (<i>Nettion peposaca</i>)	central Argentina	eastern Brazil	Temperature limitation/food availability	Capllonch (2004)
Neotropic Cormorant (<i>Phalacrocorax brasilianus</i>)	central Argentina	eastern Brazil	Temperature limitation/food availability	Capllonch (2004)
Ash-throated Cassin's (<i>Cassin's fuscus</i>)	Caatinga ecoregion	Amazonia	Arthropod (and fruit?) food availability	Lees (2016)

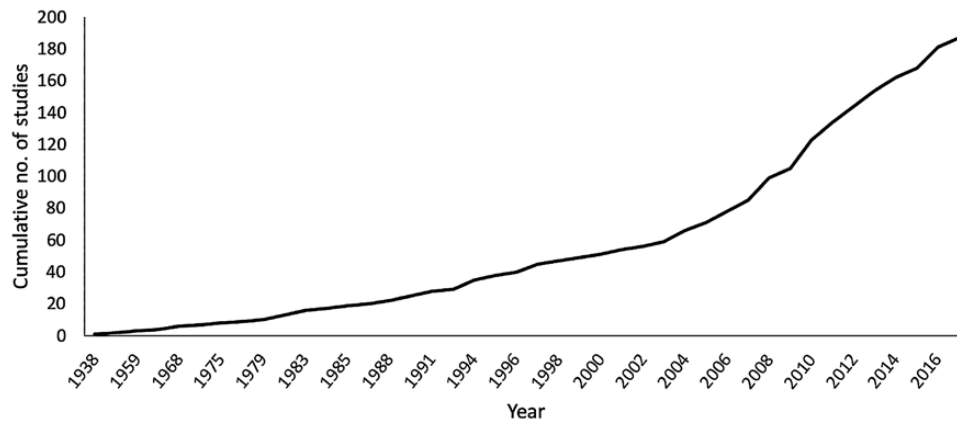


FIGURE 1. Cumulative number of published studies (total = 187) describing bird migration within the Neotropics (i.e. excluding studies of Nearctic–Neotropical migrants) by year (up to 2017). Data were compiled from a continuous review of the literature by the authors over the past 2 decades.

altitudinal, austral, and longitudinal migrations. These 4 broad types of migration are not mutually exclusive—some species exhibit multiple types of seasonal movement. For example, an altitudinal migratory hummingbird in Central America is also an intra-tropical migrant (e.g., Blue-tailed Hummingbird [*Amazilia cyanura*]; Fraser et al. 2010), as is a longitudinal migrant that spends its entire life within the tropics (e.g., Ash-throated Casiornis; Lees 2016; Table 1).

Intra-tropical migration is altitudinal, latitudinal, or longitudinal migration in the region between the Tropic of Cancer and the Tropic of Capricorn. Intra-tropical migration is increasingly recognized as common within such vast ecosystems as the Amazon rainforest and “llanos” grasslands of the Orinoco River Basin. For example, Azure Gallinules (*Porphyryla flavirostris*) breed in central and northeastern Amazonia and are hypothesized to move to southwestern Amazonia to spend the nonbreeding season (Remsen and Parker 1990). Likewise, Greater Anis (*Crotophaga major*) and Swallow Tanagers (*Tersina viridis*) are absent from much of Amazonia during the dry season, although where they go remains unknown (Stotz et al. 1996). Orinoco Geese (*Neochen jubata*) migrate across Amazonia (Davenport et al. 2012) as do Black Skimmers (*Rynchops niger cinerascens*), although some skimmers overwinter along the Pacific coast at south-temperate latitudes (Davenport et al. 2016). Intra-tropical bird migration may involve a complex set of movement steps and use of multiple staging sites (e.g., Three-wattled Bellbird [*Procnias tricarunculatus*]; Powell and Bjork 2004). Due to the complex nature of intra-tropical bird migration (i.e. often involving multiple, long stopovers and partial migration), the mechanisms underpinning it, as well as how many species engage in it, are still poorly understood. In just the last 5 yr in one country, Brazil, several species have been documented as intra-tropical migrants (e.g.,

Lees and Martin 2015, Lees 2016) that had previously been considered nonmigratory.

Altitudinal migration in the Neotropics is widespread (Bildstein 2004, Faaborg et al. 2010, Barçante et al. 2017; Table 1). We define it as seasonal movements between high-or low-elevation breeding grounds to areas at other elevations within the same or a different mountain range. These patterns are broadly recognized across broad geographic regions from Mexico (Nocedal 1994, Winker et al. 1997, Gómez de Silva et al. 1999, López-Segoviano et al. 2018), Central America (e.g., Stiles 1988, Blake and Loiselle 1991, 2002; Loiselle and Blake 1991, Levey and Stiles 1994, Rosselli 1994, Powell and Bjork 1995, 2004; Chaves-Campos et al. 2003, Boyle 2010, Fraser et al. 2010), northern South America (Hilty 1997), southern South America (Malizia 2001), the Andes Mountains (Hobson et al. 2003, Caziani et al. 2007, Merkord 2010, Villegas et al. 2016), and the Atlantic Rainforest (Davis 1945, Sick 1997, Bencke and Kindel 1999, Galetti 2001, Areta and Bodrati 2010, Bczuska 2017). Basic patterns, such as the timing of altitudinal movements and underlying mechanisms responsible for such movements, remain unknown for most populations (Boyle 2017). However, Barçante et al. (2017) found that frugivory and nectarivory are the predominant foraging guilds for the vast majority of altitudinal migrants in the Neotropics. More broadly, patterns likely vary according to species-specific physiological and life history tradeoffs (Merkord 2010, Boyle et al. 2011b, López-Segoviano et al. 2018), temporally variable resource availability (Loiselle and Blake 1991), and climatic events (e.g., escaping adverse weather; Boyle et al. 2010). Some of the most detailed work to date on both proximate and ultimate mechanisms driving altitudinal bird migration in the Neotropics has been conducted on altitudinal migrants in Central America (e.g., Powell and Bjork 2004, Boyle 2008a,

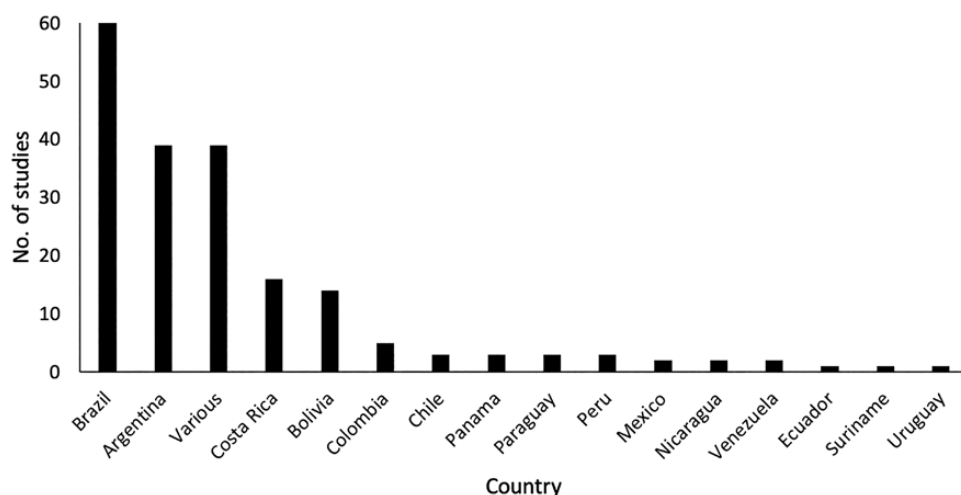


FIGURE 2. Number of published studies describing bird migration within the Neotropics (i.e. excluding studies of Nearctic–Neotropical migrants) by the country in which the data were collected. “Various” refers to studies conducted in more than one country and includes review papers. Data were compiled from a continuous review of the literature by the authors over the past 2 decades.

2010). Uniquely, altitudinal molt-migration has been documented in this region (Fraser et al. 2010).

Neotropical austral migration occurs when birds breed at south-temperate latitudes of South America then overwinter closer to the equator. This system is composed of 2 sub-types of migration (see below) and has been documented to occur in at least 220 species (Chesser 1994, Parker et al. 1996, Cueto and Jahn 2008, Zilio et al. 2014), one-third of which are tyrannid flycatchers (e.g., *Lathrotriccus*, *Tyrannus*, *Empidonomus*, *Elaenia*; Marantz and Remsen 1991, Chesser 1994, Stiles 2004, Capllonch and Zelaya 2006, Capllonch et al. 2009, Jahn et al. 2019). Some species are known to migrate along the Andes Mountains (e.g., ground-tyrants in the genus *Muscisaxicola*; Smith and Vuilleumier 1971, Capllonch 2007). The 2 sub-types of migration within this system are:

- **South American temperate–tropical migration** (sensu Joseph 1997; Table 1), in which birds breed in temperate latitudes of South America (i.e. south of the Tropic of Capricorn) then overwinter within tropical South America (i.e. north of the Tropic of Capricorn). Individuals in these populations make some of the longest distance movements in the Neotropics. For example, White-crested Elaenias make a one-way trip of >5,500 km between their breeding grounds in Patagonia and wintering grounds in northern Brazil (Jiménez et al. 2016, Bravo et al. 2017) and Barn Swallows (*Hirundo rustica*) make a round-trip journey of >8,700 km between Argentina and northern South America (Winkler et al. 2017). Some grassland species like seedeaters (*Sporophila* spp.) might move northward from a cool-temperate region of southern South America where they breed, reaching the *Pantanal*, *Cerrado*, and *Caatinga* in Brazil (Areta 2012, Repenning and Fontana

2013). A few species such as Black-bellied Seedeater (*S. melanogaster*) and Tropeiro Seedeater (*S. beltoni*) breed below the Tropic of Capricorn in Brazil and travel ~1,500 km to overwinter in the *Cerrado*, migrating only within Brazil (Da Silva 1999, Machado and Silveira 2010, Repenning and Fontana 2013, Suertegaray Fontana and Repenning 2014).

- **South American cool–temperate migration** (sensu Joseph 1997) occurs when birds do not leave the temperate zone of South America (i.e. south of the Tropic of Capricorn), generally breeding in southern Argentina and Chile and overwintering in Paraguay, Uruguay, southern Brazil, and central and northern Argentina and Chile (e.g., Patagonian Tyrant [*Colorhamphus parvirostris*], Chesser and Marín 1994; Cinnamon Warbling-Finch [*Poospiza ornata*], Cueto et al. 2011; Rufous-collared Sparrow [*Zonotrichia capensis australis*], Ortiz and Capllonch 2011; Ruddy-headed Goose [*Chloephaga rubidiceps*], Carboneras and Kirwan 2017; Table 1).

Longitudinal migration occurs when birds migrate east–west between breeding and wintering grounds. Such movements have been documented for waterbirds, many of which breed in freshwater wetlands, then overwinter along the Atlantic coast (e.g., Yellow-billed Pintail [*Anas georgica*]; Neotropic Cormorant [*Phalacrocorax brasilianus*], Rosy-billed Pochard [*Netta peposaca*]; Belton 1984, Capllonch 2004, Capllonch et al. 2008a reviewed by Antas 1994). Passerines also engage in this type of migration, the majority of which have been documented in the southern Atlantic Rainforest (e.g., Shear-tailed Gray-Tyrant [*Muscipipra vetula*], Areta and Bodrati 2008; Golden-rumped Euphonia [*Euphonia cyanocephala*]; Areta and Bodrati 2010; Yellow-legged Thrush [*Turdus flavipes*], Areta and Bodrati 2010; Table 1).

ORIGINS OF BIRD MIGRATION IN THE NEOTROPICS

Despite decades of debate and research, there is still little agreement on the origins of migration within and across lineages of Neotropical birds, or on the relationship between the evolution of intra-tropical bird migration and of New World bird migration generally. Two general questions have dominated the debate surrounding the evolution of bird migration: Is migration in birds ancestral or derived? And, where did migration in a given lineage originate? Very different conclusions have been reached regarding these issues, largely depending on which taxa, Neotropical or otherwise, were in question.

Early theoretical studies suggested that New World migrant birds are derived from resident ancestors (e.g., Cox 1968, 1985) or those tracking nectar and fruit food resources across tropical habitats (Levey and Stiles 1992, Chesser and Levey 1998, Boyle and Conway 2007). This idea has been partially supported by empirical studies (Joseph et al. 2003, Simpson et al. 2015, Licona-Vera and Ornelas 2017) and a recent study analyzing data from across the avian tree of life that concludes bird migration is a derived characteristic evolved from resident ancestors (Rolland et al. 2014). Other recent phylogenetic studies within lineages of New World birds have provided the alternate view that migration is the ancestral state and that resident behavior is derived (e.g., parulid wood-warblers: Winger et al. 2012, thrushes in the genus *Catharus*: Voelker et al. 2013; but see Zink and Gardner 2017).

For several reasons, the evolution of migration is best framed as modification of a complex and ancient suite of traits. First, given that migratory behavior is present in almost all major neognath bird families, migration is likely an ancient feature of avian lineages (Zink 2011). Second, migration is not a phenotypic trait but rather a cohort of traits that are under the control of linked genetic programs (e.g., timing of arrival at the destination and navigation; Zink 2002, 2011; Dingle 2006). Third, migratory behavior can evolve rapidly in birds (e.g., Berthold 1999, Piersma et al. 2005) and has done so multiple times within several New World lineages (*Vireo*: Cicero and Johnson 1998; tyrannid flycatchers: Chesser 2000, Joseph et al. 2003; parulid wood-warblers: Winger et al. 2012; thrushes in the genus *Catharus*: Outlaw et al. 2003, Voelker et al. 2013; bee hummingbirds: Licona-Vera and Ornelas 2017). Fourth, the capacity for migratory behavior may exist but not be expressed in nonmigratory populations (Zink 2002, 2011), with its expression and suppression depending on current environmental conditions (Zink and Gardner 2017), such that a clear-cut classification of “migratory” and “nonmigratory” populations is not straightforward. Finally, the factors responsible for subsequent modification of migratory behavior are not necessarily those initially responsible for the incipient stages of migration (Boyle and

Conway 2007). Thus, identifying the ancestral origins of migration likely depends on how far back in time one looks and/or how the evolutionary pressures shaping the migratory repertoire changed through space and time across a species’ range (Voelker et al. 2013).

What is apparent from these studies is that migration is a highly complex behavior requiring a broad suite of adaptations; its expression can be highly plastic through time (i.e. quickly evolving or disappearing within a population) and space (e.g., involving population-specific migration distances or routes). It can also be highly variable at the individual level, depending on the age, sex, and body condition of individuals in partially migratory populations (e.g., Boyle 2010). Migration also appears to be highly conserved across the avian tree of life, such that the genetic architecture necessary to express migration under the right conditions may be present in numerous resident taxa. Viewed cumulatively, these lines of evidence strongly suggest that migration is present in many more populations of Neotropical birds than we currently appreciate.

Similar to work on the evolutionary origins of migration, there has been much research into, but little consensus regarding, the geographical origins of New World bird migration. Some have suggested a tropical or “southern home” origin (e.g., Levey and Stiles 1992, Rappole 1995, Joseph et al. 1999, Outlaw et al. 2003, Rappole and Jones 2003, Licona-Vera and Ornelas 2017), a temperate or “northern home” origin (Winger et al. 2012, Voelker et al. 2013, Winger et al. 2014), or a subtropical origin (i.e. southwestern North America; Cox 1985). In the genus *Catharus*, migration may have initially originated in North America, with migrants colonizing tropical latitudes and subsequently losing migratory behavior, establishing tropical, resident populations (Voelker et al. 2013). Later, migration reappeared in those resident populations, allowing them to recolonize North America, such that the migratory routes and winter destinations we observe today may have changed throughout evolutionary history (Voelker et al. 2013; also see the “shifting home hypothesis” as applied to Palearctic–Paleotropical bird migration; Louchart 2008). More recently, evidence has emerged showing that bird migration in the New World has been gained and lost multiple times (e.g., in New World flycatchers; Gomez-Bahamón et al. 2020), with migratory populations breeding in North America reverting to an ancestral tropical state during glacial maxima (Zink and Gardner 2017). Given the complex evolutionary history of New World bird migration, as well as the evolution of biodiversity gradients generally, the evolution and regulation of bird migration within the Neotropics is likely to be a long and complex story.

DRIVERS OF BIRD MIGRATION IN THE NEOTROPICS

Despite extensive research on why birds migrate in the New World, there is little consensus about the underlying environmental drivers of migration in most species. Arguably, the least understood in this respect are intra-tropical migrants. Early work proposed a combined role of seasonality and interspecific competition, leading to partial migration and eventually obligate migration (Cox 1968, 1985). The role of diet also dominated the discussion, especially as it became increasingly apparent that intra-tropical migrants track food resources, such as fruit and nectar (e.g., Morton 1977, Loiselle and Blake 1991, Levey and Stiles 1992). The “evolutionary precursor hypothesis” proposed that, because many frugivorous tropical birds track spatial and temporal availability of fruit, they are pre-adapted for migration (Levey and Stiles 1992), especially those inhabiting edge and canopy microhabitats (Chesser and Levey 1998). More recent research has refined this hypothesis, suggesting that large fluctuations in food resources such as nectar and fruit drive the initial evolution of migratory behavior, regardless of habitat or diet (i.e. the “resource variability hypothesis”; Boyle and Conway 2007, also see Outlaw and Voelker 2006).

Furthermore, competition for food resources may have played an important role in the evolution of migration at tropical latitudes, with competition and potential exclusion of migrants by residents (Cox 1968), selecting migrants for dietary specialization (Boyle et al. 2011a). Evaluating this possibility and refining our understanding of the role of diet in the evolution and regulation of migration within the Neotropics (and in the New World more generally) would be greatly aided by comparative studies of resident vs. migrant diets in different seasons (especially the nonbreeding season), as well as the nutritional importance of different food sources throughout the year (Boyle et al. 2011a). Given that, depending on taxon, birds in the Neotropics actively track a broad variety of food resources, such as fruit (tyrannid flycatchers, Guaraldo et al. 2016, Bravo et al. 2017; thrushes, Bczuska 2017) and seeds (e.g., seedeaters in the genus *Sporophila*, Remsen and Hunn 1979, Ortiz and Capllonch 2007, Machado and Silveira 2010, Repenning and Fontana 2013, Suertegaray Fontana and Repenning 2014), understanding how food availability drives Neotropical bird movements will require a broad body of research on the spatial and temporal availability of resources used by migrants.

Due to the central role that food plays in driving avian migratory patterns in general, understanding the environmental drivers of food resource availability is key to elucidating the ultimate causes of bird migration. Because seasonality at tropical latitudes is primarily defined in terms of rainfall (e.g., Poulin et al. 1992, Wikelski

et al. 2000, Oliveira and Marquis 2002, Gottsberger and Silberbauer-Gottsberger 2006), the availability of food resources that intra-tropical and many austral migrants depend upon is likely to be primarily driven by seasonal precipitation cycles. Indeed, rainfall in the tropics is the primary driver of the timing of leafing, flowering, and fruiting (van Schaik et al. 1993, Wright 1996, Gottsberger and Silberbauer-Gottsberger 2006, Myneni et al. 2007, Araujo et al. 2017) and arthropod abundance (Develey and Peres 2000, Pinheiro et al. 2002, Cotton 2007, Amorim et al. 2009, Jahn et al. 2010b, Araujo et al. 2017). Not surprisingly, molt and breeding schedules of many tropical birds are synchronized by patterns of annual precipitation (e.g., Poulin et al. 1992, Jahn et al. 2010b, Araujo et al. 2017), and many migrants within the tropics and Southern Hemisphere track rainfall (Hockey 2005, Dingle 2008, Jahn et al. 2010a, MacPherson et al. 2018). Such tracking of rain and subsequent productivity in the tropics also applies to at least some Nearctic–Neotropical migrants during their nonbreeding season visit to tropical latitudes, such as Bobolinks (*Dolichonyx oryzivorus*, Renfrew et al. 2013, but see Stutchbury et al. 2016). Similarly, the overwinter movements of Veeries (*Catharus fuscescens*) in Amazonia appear to be driven by flood pulses (Heckscher et al. 2011, 2015; Pinho et al. 2017). Comparisons of how birds in these different migratory systems track climate and resources over time could offer insights into the early evolution of bird migration across the New World.

Nevertheless, the magnitude and variation of the relationship between food availability and rainfall is likely to vary according to local habitat (e.g., dry forest vs. rainforest) and type of food, thus driving regional differences in migration strategies (Hockey 2005). For example, tropical fruit availability is often only weakly linked to timing of rainfall in humid tropical montane forests (Loiselle and Blake 1991, Develey and Peres 2000), and fruit availability in those systems can be highly spatiotemporally variable (e.g., Morellato et al. 2000, Chaves-Campos 2004), even at the microhabitat level (e.g., higher in treefall gaps than in forest understory; Levey 1988a). More consistent patterns of fruit availability in relation to precipitation may predominate in relatively dry tropical ecosystems (e.g., dry scrub, Poulin et al. 1992; Caatinga, Araujo et al. 2017), where movements of birds (e.g., Ash-throated Casiornis in the Caatinga; Lees 2016) are often more predictable than in humid montane forests. Viewed cumulatively, spatio-temporal variation in resource availability—specifically the predictability of resource pulses—may be a strong predictor of annual movements in Neotropical birds.

This hypothesis on the availability of resources and migration timing is largely supported in humid tropical montane forests, where fruiting phenology is consistent across elevations, beginning in the lowlands and

progressing upslope (Loiselle and Blake 1991, Castro et al. 2012), where altitudinal migratory frugivores track fruit availability (Levey 1988b, Loiselle and Blake 1991). In Central America, a large proportion (>25%) of altitudinal migrants are frugivorous or nectarivorous (Levey 1988b, Blake et al. 1990, Blake and Loiselle 2000), tracking temporal availability of fruit and nectar across elevational gradients (Stiles 1985, Levey 1988b, Loiselle and Blake 1991, Hobson et al. 2003). Further support for the idea that migratory birds track predictable resource availability in the Neotropics comes from research on altitudinal bird migration in the Andes (Herzog et al. 2003), the Sierra Madre Occidental mountains of Mexico (López-Segoviano et al. 2018), and the Atlantic Rainforest (Castro et al. 2012). More research across taxa is needed on the relationship between climate, food availability, and patterns of bird movement in the Neotropics, especially since a given species may specialize on a narrow range of fruit resources. For example, Yellow-legged Thrushes appear to specifically track fruiting palms (Castro et al. 2012), as do frugivorous parrots in eastern Amazonia (Moegenburg and Levey 2003).

At south-temperate latitudes (e.g., Patagonia), seasonality related to fluctuations in temperature is likely the main driver of bird migration (Joseph 1996, Chesser 1998). Climate at south-temperate latitudes is generally more buffered than that at comparable north-temperate latitudes (Paruelo et al. 1998, 2007) due to the stabilizing effect of the oceans that make up the majority of the Southern Hemisphere (Yom-Tov et al. 1994, Dingle 2008). Nevertheless, at south-temperate latitudes of South America, there is a clear pattern across many species of Neotropical austral migrants of breeding during the warmer austral summer and being absent in the winter (e.g., tyrannid flycatchers; Chesser 1998, 2005).

In addition to seasonality of climate and food availability, other postulated drivers of intra-tropical migration are avoidance of nest predation (Boyle 2008a), intra-specific competition for roosting sites (Stutchbury et al. 2016), nest site availability associated with flood pulses (e.g., in Black Skimmers; Davenport et al. 2016), and cavity nest site limitation (e.g., in Orinoco Geese, Davenport et al. 2012). After breeding, competition for increasingly limited food during the nonbreeding season may account for the migration of insectivorous birds (e.g., Jahn et al. 2010a). In addition to avoidance of nest predation (Boyle 2008a), altitudinal migration of numerous species may be driven by avoidance of severe weather (Boyle et al. 2010) and potentially be facilitated by mutualistic interactions within mixed-species flocks (Merkord 2010; reviewed by Barçante et al. 2017). This diversity of observed patterns and presumed underlying mechanisms suggests that the drivers of migration are often species- and/or habitat- specific.

Ultimately, the proximate mechanisms underpinning avian migratory patterns across the Neotropics are likely to depend on a combination of (1) intrinsic factors, such as diet, age, and sex; and (2) extrinsic factors, such as climate and level of competition for resources, the strength of which can vary between habitat types and years (e.g., Bell 2005, Hockey 2005). Thus, proximate drivers of bird migration in the Neotropics and elsewhere may be population-specific and vary tremendously between ecoregions and years (e.g., depending on the phase of the El Niño/La Niña Southern Oscillation).

MIGRATORY STRATEGIES OF BIRDS IN THE NEOTROPICS

All migratory birds must accomplish several basic activities in an annual cycle: reproduction, molt, and migration. Accomplishing these in an efficient and timely manner involves tradeoffs (Hedenström 2008). For example, because feather molt is energetically expensive (Lindström et al. 1993, Murphy 1996), migratory schedules (Rohwer et al. 2005), use of stopover sites (Leu and Thompson 2002), and migration distances (Barta et al. 2008) can be largely influenced by the degree and timing of molt. When tradeoffs are poorly managed, consequences may be severe; overlapping molt and migration, for instance, may lower feather quality and potentially affect fitness (Norris et al. 2004). Thus, most migratory bird species that breed in North America and Europe do not overlap the timing of migration and molt. Instead, short-distance migrants in these regions undergo a pre-basic molt before fall migration, whereas long-distance migrants generally molt before fall migration, during stopover along the fall migratory route, or in the wintering area (e.g., Svensson and Hedenström 1999, Rohwer et al. 2005, Newton 2011, Butler 2013).

An increasing number of intra-tropical migrants are known to undergo molt-migration, in which individuals migrate to a specific region to undergo molt (e.g., Lesser Elaenia [*Elaenia chiriquensis*], Guaraldo et al. 2016; Fork-tailed Flycatcher, Jahn et al. 2016; altitudinal molt-migration of the Blue-tailed Hummingbird, Fraser et al. 2010; see Ryder and Wolfe 2009). Although the relationship between molt and migration is known for some migratory birds in the Neotropics (e.g., White-crested Elaenia, Cueto and Gorosito 2018), information on the annual timing of breeding, molting, and migration remains sparse for most Neotropical species, precluding a comprehensive evaluation of whether their annual cycles differ substantially from better-studied migratory populations at north-temperate latitudes (but see Wolfe et al., this volume).

Nevertheless, evidence suggests that the tradeoffs between investing in molt and migration in the Neotropics are less pronounced than in most long-distance,

intercontinental migrants. Tropical breeders exhibit overall slower and more protracted molt schedules (Helm and Gwinner 1999, Collar 2005, Ryder and Wolfe 2009) and tend to overlap molt and breeding to a higher degree than birds breeding at north-temperate latitudes (e.g., Foster 1975, Johnson et al. 2012, Jahn et al. 2017, but see Silveira and Marini 2012, Repenning and Fontana 2011, Wolfe et al., this volume). Such a slower, and presumably more flexible, molt strategy at tropical latitudes suggests that selective pressures shaping the timing and energetic demands of molt are relaxed in the tropics. The potential reduced cost of molt and/or constraints on its timing could facilitate a greater degree of either molt-breeding or molt-migration overlap in Neotropical migratory birds compared to their north-temperate counterparts. Although some evidence exists for this possibility (Jahn et al. 2017), the fact that flexibility in molt timing is widespread across resident and migratory birds (Hall and Tullberg 2004) suggests that a variety of options are available to Neotropical migratory birds (reviewed by Jahn et al. 2017).

In addition to molt, reproductive strategies may mold avian migratory behavior. Studies in Europe and North America show that reproductive success decreases over the breeding season (e.g., Verboven and Visser 1998). As such, earlier spring arrival can increase individual reproductive success by increasing the probability of a successful brood or by providing sufficient time for multiple broods (Smith and Moore 2005, reviewed by Kokko 1999). Thus, for north-temperate breeding birds, the timing of arrival on the breeding grounds can have important fitness consequences and may be under selection (Smith and Moore 2005). This is especially the case for males, which must often compete for breeding territories and mates, resulting in protandrous spring migration (reviewed by Morbey and Ydenberg 2001, Tøttrup and Thorup 2008) where males arrive first. In contrast, birds that breed at tropical and south-temperate latitudes exhibit an overall slower life history strategy than their northern counterparts because they lay smaller and fewer clutches in a given year (e.g., Yom-Tov et al. 1994, Martin et al. 2000, Auer et al. 2007, Jetz et al. 2008, Jahn et al. 2017), have an extended breeding season (e.g., Rowley and Russell 1991), experience lower intrasexual competition on the breeding grounds (Garamszegi et al. 2008), have higher rates of adult survival (Rowley and Russell 1991, Johnston et al. 1997), and experience higher levels of nest predation (reviewed by Wiersma et al. 2007, Robinson et al. 2010b). Additionally, tropical breeding birds often have lower metabolic rates than north-temperate counterparts (Robinson et al. 2010b). As a result, although intra-tropical migrants may have reduced fitness as a result of arriving late to the breeding grounds (Bejarano and Jahn 2018), the consequences of arriving later may be less severe at tropical and south-temperate latitudes than at north-temperate latitudes.

This slower life history strategy typical of birds in the Southern Hemisphere may be partially explained by variation between hemispheres in the availability of food resources for breeding. The Southern Hemisphere's climate—temperature, in particular—is overall more seasonally buffered than that of most of the Northern Hemisphere (Yom-Tov et al. 1994, Paruelo et al. 1998, 2007; Dingle 2008), such that food resources for birds breeding in the Southern Hemisphere may be available for a longer period of the annual cycle. This prolonged resource availability/greater stability has been suggested to lead to greater flexibility in the length of the breeding period (Rowley and Russell 1991, but see de Paiva and Marini 2013). Additionally, primary productivity at tropical and south-temperate latitudes is highly variable between years (e.g., in southern Brazil; Nobre et al. 2006), even more so than at north-temperate latitudes (Goetz et al. 2000). Such a combination of slow life history strategies, seasonally buffered environmental conditions, and relatively high unpredictability in productivity between years may mean that, compared to their northern counterparts, birds migrating within the Neotropics generally experience lower selective pressure to arrive as early as possible on the breeding grounds. This combination of environmental variation and variation in life history strategies employed by birds across regions offers a chance to use a comparative approach to test hypotheses regarding the drivers of migratory strategies.

DO LIFE HISTORY STRATEGIES PREDICT MIGRATORY STRATEGIES?

We largely lack a conceptual framework to study the ecological and evolutionary processes that shape migratory strategies of birds around the planet, including the suite of physiological and life history characteristics associated with different migratory lifestyles. Here, we present a synthetic framework to conceptualize which mechanisms underpin individual- and population-level migration processes across latitudes within the New World. This framework is also applicable to other regions of the globe.

According to optimal migration theory, birds on migration are time-, energy-, or predation-selected (Alerstam and Lindström 1990, Åkesson and Hedenström 2007, Hedenström 2008). If birds migrating within the Neotropics are indeed under lower selective pressure to arrive as early as possible on the breeding grounds (see previous section), then they should employ a slower spring migration strategy, whereas migratory birds breeding at similar latitudes in the Northern Hemisphere may have a faster, more time-selected strategy (Jahn and Cueto 2012; Figure 3). If life history strategies mold spring migration strategies, migration to Neotropical breeding grounds may not be as risky a period of the annual cycle as spring migration to north-temperate latitudes, which

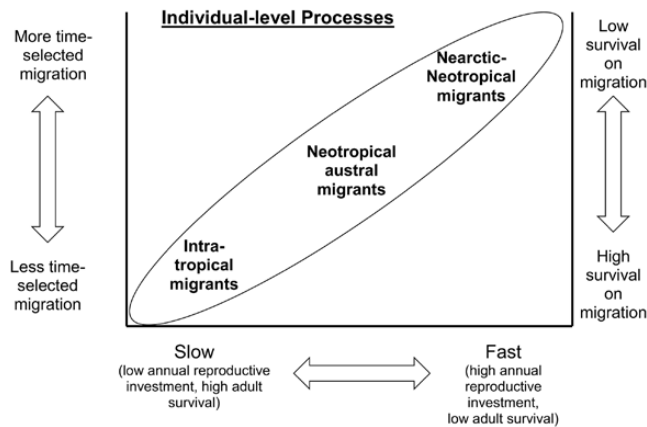


FIGURE 3. Predicted individual spring migratory strategies as a function of avian life history strategies across migratory systems. For polygynous migratory species in which sex-specific breeding roles are highly differentiated (e.g., lekking species), males within each migratory system would be at the faster end of the migratory strategy spectrum (i.e. employing a more time-selected migratory strategy) with the opposite pattern in females.

has been shown to be a period of high adult mortality (e.g., Sillett and Holmes 2002, Rushing et al. 2017; Figure 3). Such a continuum of migratory strategies may even exist within the Neotropics, because migratory birds breeding at south-temperate latitudes of South America are often characterized by a slightly faster (and potentially riskier) life history strategy compared to species breeding in tropical South America (e.g., larger clutch sizes, Jetz et al. 2008, Jahn et al. 2017; higher adult survival, Bulit and Massoni 2011). As such, Neotropical austral migrants should have a more time-selected spring migratory strategy than intra-tropical migrants (Figure 3).

Nevertheless, migratory strategies are shaped in complex ways by a diverse combination of intrinsic (e.g., energetic condition) and extrinsic (e.g., climate) factors that also depend on a given individual's age and/or sex (e.g., Boyle 2008b, Jahn et al. 2010a, Bejarano and Jahn 2018). For example, in polygynous migratory species in which sex-specific roles are highly differentiated and in which there is high competition for females (e.g., lekking species such as manakins and bellbirds), males may be much more time-selected on spring migration than females (i.e. they are selected to arrive earlier on breeding grounds than females in order to acquire a territory/lek site; Figure 3). These predictions may not be applicable when comparing migrants with extremely different migration distances (e.g., an altitudinal migrant vs. an intercontinental migrant) because a long-distance migrant may be more time-selected on migration simply because of the distance it must cover. Seasonal (spring vs. fall migration) and annual (e.g., phase of an El Niño/La Niña cycle, Paxton et al. 2014) effects would also need to be accounted for when testing these predictions.

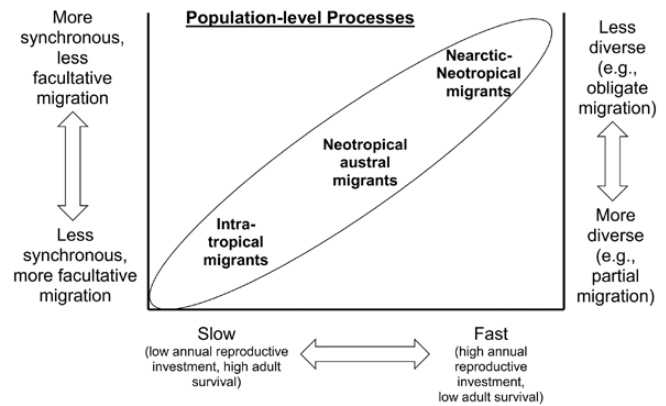


FIGURE 4. Predicted population-level migratory patterns as a function of avian life history strategies. Synchronicity represents the variation in departure and arrival dates between individuals of a population. Facultative migration refers to migration in a population occurring only under certain circumstances (e.g., in some years but not others; Newton 2012).

Variation in life history strategies between populations breeding in the Neotropics and those at north-temperate latitudes may also translate into population-level differences in migratory patterns (Figure 4). Birds that use more stopovers on migration and migrate relatively slowly (as we postulate occurs within the Neotropics) may have a lower selection threshold in terms of the adaptations (e.g., morphological, physiological) they need to migrate successfully. As a result, permanent resident Neotropical birds may more readily adopt migratory behavior than resident birds breeding at north-temperate latitudes, leading to partial migration in Neotropical populations. If so, partial migration (flexible or rigid, see Watts et al. 2018) should be more common in intra-tropical migrants, whereas obligate migration, in which migration timing, direction, and distance are relatively constant between years (Newton 2012, Watts et al. 2018), should be more common in migrants breeding at north-temperate latitudes (Figure 4). Additionally, birds breeding at south-temperate and low latitudes typically have a prolonged breeding season compared to those breeding at north-temperate and high latitudes (e.g., Rowley and Russell 1991, Hemborg et al. 2001, Garamszegi et al. 2008). Such a pattern could translate to higher variation between individuals in departure and arrival dates, compared to conspecifics breeding at north-temperate latitudes (Figure 4; Jahn and Cueto 2012).

In summary, given that intra-tropical migrants and those breeding at south-temperate latitudes experience a different set of environmental conditions and employ different life history strategies than their north-temperate counterparts, they are likely to employ different migration strategies and exhibit different population-level migratory patterns. Exceptions likely exist, depending on a variety of factors, such as breeding latitude. For example,

White-crested Elaenias on spring migration to Patagonian breeding grounds appear to migrate at similar rates to those of related species at north-temperate latitudes (Bravo et al. 2017). Additionally, flexibility in annual routines (i.e. timing of breeding, migration, molt; Ramenofsky and Wingfield 2007) diminishes with the number of migratory life history stages and sub-stages expressed throughout the year (i.e. number of breeding or molt events, Wingfield 2008). Thus, a migrant that expresses more life history stages (e.g., double-brooding) and cannot overlap them may be more time-limited than one with fewer life history stages, regardless of its position on the “fast–slow” life history strategy continuum or the latitude at which it breeds.

CONSERVATION OF MIGRATORY BIRDS IN THE NEOTROPICS

Increasing threats to numerous migratory bird species, combined with a lack of information on their complex annual cycles, precludes detailed and effective conservation of migratory bird populations across the planet (Wilcove and Wikelski 2008). Although migratory birds in the Neotropics often use secondary vegetation (including natural successional and degraded primary habitats; Blake and Loiselle 1992, Stotz et al. 1996), many exceptions exist. For example, altitudinal migrants can be more abundant in mature forest than in second growth (Blake et al. 1990), and numerous grassland migrants require pristine habitat (Jahn et al. 2017). Furthermore, because we understand little about the life histories, annual cycles, and population dynamics of many migratory species in the Neotropics, assumptions about the level of threat to their populations should be made with caution, especially in an era of rapid climate change. Two examples highlight the plight that migrants face in the Neotropics.

(A) The Ruddy-headed Goose is a South American cool-temperate migrant that occurs in 2 populations: one of permanent residents on the Malvinas/Falkland Islands, and one of migratory individuals that breed in Patagonia of Argentina and Chile and overwinter in central Argentina (Ibáñez and Petracci 2014, Carboneras and Kirwan 2017; Table 1). In 1931, the Ruddy-headed Goose was declared an agricultural pest in Argentina and was persecuted through state-sponsored programs (Ibáñez and Petracci 2014, Petracci et al. 2016), and the size of the mainland population has fallen precipitously (Canevari 1996, Petracci et al. 2016). Although it is no longer considered a pest species in Argentina, illegal hunting continues (Petracci and Carrizo 2017) and its population size has continued to decline. Between 1999 and 2006 alone, there was a 41% decrease in the adult population (Petracci and Carrizo 2017). The

latest estimate of the mainland population size is between 900 and 1,178 individuals (Blanco et al. 2006). Two recent studies have found that the 2 populations are highly genetically distinct (Bulgarella et al. 2014, Kopuchian et al. 2016), which may warrant a taxonomic revision (Kopuchian et al. 2016). The species is now listed in Argentina as “Critically Endangered” (López-Lanús et al. 2008, Ibáñez and Petracci 2014), yet basic information such as where populations overwinter is lacking, making effective conservation impossible (Cossa et al. 2017).

(B) Bare-throated Bellbird (*Procnias nudicollis*), an Atlantic forest endemic, is listed as “Vulnerable” by the IUCN (Birdlife International 2016) and thought to be undergoing rapid population declines from habitat loss and the commercial cagebird trade (Kirwan and Green 2011, Birdlife International 2016). This charismatic species breeds in the eastern highlands of the Atlantic Rainforest from October to January, then migrates to geographically unknown nonbreeding areas. Davis (1945) hypothesized that it likely moves to lowland habitats, making it an altitudinal migrant. Without basic information on the timing and extent of this bird’s migration, we may miss complex seasonal patterns of habitat use and underestimate the minimum critical area required for its protection, as 2 empirical studies on similar altitudinal migrants have found. In Central America, the Resplendent Quetzal (*Pharomachrus mocinno*) and Three-wattled Bellbird employ complex, multi-stage altitudinal migrations across protected and non-protected areas (Powell and Bjork 1995, 2004). Failure to account for seasonal movements across areas with different threats to survival can affect the efficacy of conservation strategies for such species (Powell and Bjork 2004).

Numerous other migratory birds in the Neotropics likely face similar threats as Ruddy-headed Geese and Bare-throated Bellbirds, yet we know little about which species and populations are most immediately threatened. Some threats are likely to be more local (e.g., window strikes, electrocution from power lines, wind turbines; CEMAVE 2016), whereas others, such as rapid climate change, habitat degradation, and pesticides, can affect migrants across large swaths of their range. At north-temperate latitudes, changes in migration phenology (or behavioral plasticity) tend to be associated with species that have more generalized diets, shorter migration distances, and a greater number of broods per year (Végyvári et al. 2010), potentially placing them at lower risk to future climate changes. Additionally, the level of migratory connectivity across a species’ range (i.e. the proportion of individuals of a given breeding population that overwinter together; Webster et al. 2002, Webster and Marra 2005) also influences the

degree to which a migratory species may be at risk due to climate and habitat change (Taylor and Norris 2010, Fudickar and Ketterson 2018). In contrast, the probability of a phenological mismatch (i.e. the mismatch between a bird's annual clock and the phenology of its environment) may be greater for long- than short-distance migrants because long-distance migrants are less able to detect phenological changes occurring at their destination (Jones and Cresswell 2010). Whether these characteristics make migratory birds in the Neotropics more or less vulnerable to climate change remains unclear. However, humid forests in Amazonia are sensitive to decreases in rainfall (Hilker et al. 2014), such that future predicted drying of this region (Malhi et al. 2009) has the potential for widespread ecosystem effects.

Conservation of migratory birds is not only important to preserve these unique species, but also to ensure the long-term viability of the ecosystems they inhabit. Migratory birds in the Neotropics provide key ecosystem services, such as seed dispersal (Amico and Aizen 2005, Blendinger et al. 2012), pest control (Mazia et al. 2004), and pollination (Smith-Ramírez and Armesto 1998). Intra-tropical and altitudinal migrants that act as seed dispersers (e.g., bellbirds) even have the potential to shape the structure of the tropical forests they inhabit (Galetti et al. 2013). In Patagonian forests, the White-crested Elaenia is the primary seed disperser for fleshy-fruited shrub species during its austral summer visit to the region (Armesto et al. 1987, Amico and Aizen 2005), playing a principal role in forest regeneration there (Cavallero et al. 2013, Bravo et al. 2015). Additionally, migration may promote speciation across the avian tree of life, given that migratory species often generate resident/nonmigratory species and are characterized by a lower extinction rate (Rolland et al. 2014). An increasing number of studies in the New World have shown that loss of migration may lead to nonmigratory tropical populations (e.g., Outlaw et al. 2003, Winger et al. 2012, 2014; Voelker et al. 2013), which may not be surprising, given that migration can disappear rapidly (Pulido and Berthold 2010).

FUTURE DIRECTIONS FOR RESEARCH ON BIRD MIGRATION IN THE NEOTROPICS

Given the gaps in our knowledge of both basic patterns and mechanisms underlying bird migration in the Neotropics, we highlight 5 major areas that we believe will advance both our understanding of bird migration in the Neotropics and, more broadly, the emergent patterns of migration across latitudes.

Patterns of Migration

Descriptive studies are urgently needed to answer questions such as:

- Which species migrate? Because partial migration is so common in the Neotropics, understanding population-specific patterns is imperative (e.g., Somenzari et al. 2018). Species may be composed of both migratory and resident populations, and within migratory populations, migration can be age- or sex-dependent (Jahn et al. 2010a).
- What is the migratory connectivity of species within the Neotropics? For example, we know little about where any given population of most austral migrant species overwinter. Such information is essential to understanding how migratory bird populations change over time (Rushing et al. 2016).
- What is the phenology of migration within a given population? Addressing this question involves understanding seasonal departure and arrival schedules, as well as the speed of migration among age and sex classes.

Proximate and Ultimate Drivers of Migratory Behavior

Once a basic description of the migratory behavior in a given population is achieved, questions about the mechanisms underpinning migratory patterns can be addressed. Examples include:

- Why does a given population (or subset of individuals within a population) migrate? Understanding the proximate drivers of bird migration in the Neotropics (e.g., food resource availability, nest site limitation) is necessary for developing a broad body of theory on the evolution and regulation of Neotropical migration systems (e.g., altitudinal, longitudinal). These kinds of mechanistic studies will undoubtedly advance our understanding of the underpinnings of bird migration around the globe.
- Which migratory strategy (i.e. time-, energy-, or predator-selected; Alerstam and Lindström 1990, see above) is most relevant in a given population, and why? Because some migrants are likely to be more time-limited than others, comparisons of the annual cycle of migrants in different systems could provide key insights into the pressures molding a given migratory strategy. For example, because birds that breed at low latitudes often exhibit lower annual fecundity (e.g., nestling survival) than those at higher latitudes (Robinson et al. 2010b), one would expect that birds in the former group should exhibit a less time-selected spring migratory strategy (Figure 3; Jahn and Cueto 2012).

Altitudinal migration is common in North and South America, offering a chance for geographically and taxonomically broad comparative work (Barçante et al. 2017, Boyle 2017). Furthermore, numerous congeneric species, of genera such as *Anas*, *Buteo*, *Progne*, *Turdus*, and *Zonotrichia*, occur in both the Nearctic–Neotropical

and Neotropical migration systems, and some migratory genera are shared between migration systems in South America and Africa (e.g., [Hockey 2000](#), [Nagy et al. 2017](#)), offering a testbed for comparative research. Within the Neotropics, comparisons can be made between groups of birds exhibiting different movement strategies, such as between resident and migratory congeners ([Guaraldo et al. 2016](#)), between populations migrating different distances ([Aharon-Rotman et al. 2016](#)), or between those that have to cross significant barriers vs. those that do not ([Nwaogu and Cresswell 2016](#)). At a molecular level, identifying the genes that control the expression of migratory behavior by comparing migratory vs. resident populations (e.g., [Fudickar et al. 2016](#)) or by contrasting those that exhibit different migratory behaviors (e.g., [Mueller et al. 2011](#), [Johnston et al. 2016](#)) hold promise for revealing intriguing insights into the evolution of bird migration.

- What is the evolutionary history of migration within a given population? The few phylogenetic studies that have been conducted on migratory birds in the Neotropics have shown that the expression of migration can be highly plastic, as in flycatchers in the genus *Muscisaxicola* ([Chesser 2000](#)) and in the genus *Myiarchus* ([Joseph et al. 2003](#)), indicating a need for phylogenetic comparisons at low taxonomic levels (e.g., among subspecies; [Kondo and Omland 2007](#)).

Adaptations for Migration

- What are the morphological, physiological, and cognitive adaptations for migration in Neotropical birds? In terms of morphology, studies from the Northern Hemisphere have concluded that migrants often have longer, more pointed wings ([Voelker 2001](#), [Baldwin et al. 2010](#), [Outlaw 2011](#)) and a smaller body size (e.g., [Sol et al. 2005](#)) than permanent residents. Furthermore, birds that migrate longer distances have more pointed wings than those that migrate shorter distances ([Winkler and Leisler 1992](#), [Marchetti et al. 1995](#)), possibly because increased wing pointedness improves flight efficiency ([Bowlin and Wikelski 2008](#)). Because most species migrating in South America travel shorter distances than their North American counterparts ([Stotz et al. 1996](#), [Dingle 2008](#)), morphological adaptations to migration are likely to differ between the 2 groups. From a behavioral perspective, evidence exists that some species may be pre-adapted to migrate, as in Palearctic species that are behaviorally less flexible in their foraging repertoire and are therefore forced to migrate to spend the winter away from the breeding grounds ([Sol et al. 2005](#)). The nervous and endocrine systems of tropical birds may also be pre-adapted for migration, because at least some tropical breeding residents ([Hau et al. 1998](#)),

as well as intra-tropical migrants ([Styrsky et al. 2004](#)), can detect even small changes in photoperiod, which is known as a cue for migrants to prepare for migration (reviewed by [Newton 2008](#)). Thus, intra-tropical migrants may use similar cues to prepare for migration as their north-temperate counterparts.

Mapping specific behavioral (e.g., pre-migratory fattening), physiological (e.g., antioxidant capacity; [Jenni-Eiermann et al. 2014](#)) and morphological traits (e.g., wing pointedness; e.g., [Provinciati et al. 2018](#)), as well as genes associated with migratory behavior (e.g., [Franchini et al. 2017](#)) onto phylogenies will go a long way toward understanding the evolution of bird migration in the Neotropics ([Zink 2011](#)).

The Relationship Between Migration and Other Life History Strategies

- How do events experienced in one season affect a migrant's performance in subsequent seasons (i.e. carryover effects)? For example, the quality of habitat used by a migratory bird during the nonbreeding season can affect its body condition (e.g., [Marra et al. 1998](#), [Bearhop et al. 2004](#), [Inger et al. 2010](#)), migratory timing ([Studds and Marra 2005](#)), survivorship ([Marra and Holmes 2001](#)), and breeding success ([Inger et al. 2010](#)). Thus, for migratory populations, a basic understanding of the mechanisms that influence individual fitness and population regulation requires information on carryover effects and on the migratory connectivity of the population ([Harrison et al. 2011](#), [Marra et al. 2015](#), [Rushing et al. 2016](#)). If the annual routines of Neotropical migratory birds are indeed more flexible than those of species breeding at north-temperate latitudes (see above), then the tradeoffs between investing in different activities such as molt and migration may be weaker in the Neotropics ([Jahn and Cueto 2012](#)).
- What time of year or which events are most limiting to population size ([Sillert and Holmes 2002](#), [Klaassen et al. 2014](#), [Rushing et al. 2017](#))? Employing a given migratory strategy (i.e. time-, energy-, or predator-selected strategies, see above) or having to cross significant barriers (e.g., deserts, mountains) likely affects survival on migration, such that the risk that migration poses likely varies significantly between populations and between individuals of different age classes and sexes.

Evolution and Regulation of Migration

- Which genes control migratory behavior in different migratory systems? Comparing the genes that are expressed prior to and during migration and comparing such processes with those occurring in residents will likely provide key insights into how migration is

regulated at the molecular level (e.g., [Franchini et al. 2017](#)). Population genomics may even help us understand how vulnerable migratory birds are to climate change ([Bay et al. 2017](#)). Additionally, comparisons between migratory systems could provide important insights into the evolution of migration. For example, if it were found that the same genes are expressed in intra-tropical migrants and Nearctic–Neotropical migrants when they make mid-winter movements while in the Neotropics, such results would provide support for the possibility that one evolved from the other ([Stutchbury et al. 2016](#)).

Although achieving meaningful answers to these questions may seem like a daunting task, novel techniques and technologies are available that offer unprecedented opportunities to address them and to assess the tradeoffs that migrant birds face throughout the year ([Marra et al. 2015](#)). Applying theoretical models (e.g., migratory network models: [Norris and Taylor 2006](#); population dynamics: [Rushing et al. 2016, 2017](#); climate change vulnerability: [Culp et al. 2017](#)) to different migratory systems could help elucidate the ecological and physiological constraints faced by migrants. Collecting the data needed to run such models is aided by novel technologies that allow a comprehensive understanding of minute details of even the smallest migratory birds at almost any time of year. Powerful citizen science databases, such as eBird (e.g., [Lees 2016](#), [LaSorte and Fink 2017](#)), now provide continent-level abundance data throughout the year, molecular and chemical tracers allow detailed descriptions of population migratory connectivity ([Ruegg et al. 2016](#)), and miniaturized, electronic tracking technologies provide detailed, quantitative data on individual migratory timing, rates, and routes (e.g., [Robinson et al. 2010a](#), [Kays et al. 2015](#), [López-López 2016](#), [Jahn et al. 2019](#)). Such devices can now even be outfitted with auxiliary technologies, such as accelerometers to understand hourly behavioral patterns ([Hedenström et al. 2016](#), [Bäckman et al. 2017](#)). Combining individual behavioral data, population-level movement data collected through citizen science, and data on environmental conditions such as ecosystem productivity and weather, allows an in-depth understanding of how migrants track environmental resource gradients throughout the year (e.g., [Bridge et al. 2015](#), [Hallworth and Marra 2015](#), [LaSorte and Fink 2017](#), [Thorup et al. 2017](#), [Fudickar and Ketterson 2018](#)).

In conclusion, incorporating classical and state-of-the-art techniques, while adopting a multidisciplinary approach to test theoretical concepts drawn from across disciplines, offers the best chance to effectively address the descriptive and mechanistic questions listed at the beginning of this section. Research to date shows that bird migration is highly plastic at both individual (e.g., between sexes/ages) and population levels (i.e. at different latitudes and in different

ecosystems), and is shaped by a variety of selective pressures related to ecology (e.g., microhabitat use, diet) and life history strategy (e.g., annual reproductive investment). Thus, answering the above questions will necessarily involve an innovative and varied approach. In particular, comparisons across migration systems provide a novel and powerful test of hypotheses ([Hockey 2005](#), [Jahn and Cueto 2012](#), [Stutchbury et al. 2016](#), [Boyle 2017](#)). Over half of the world's migratory bird species have declined in the last 30 yr ([Kirby et al. 2008](#)) as a result of habitat destruction and climate change ([Wilcove and Wikelski 2008](#), [Jones and Cresswell 2010](#)), such that answers are urgently needed. Given the lack of reliable data on the mechanisms underpinning movements of birds in the Neotropics, and information on the risks to their survival ([Faaborg et al. 2010](#), [Jahn and Cueto 2012](#)), the time is ripe for research on the fascinating but poorly understood phenomenon of Neotropical bird migration.

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