THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 122, 2020, pp. 1–18
DOI: 10.1093/condor/duaa055

SPECIAL FEATURE: Advances in Neotropical Ornithology

Habitat ecology of Nearctic–Neotropical migratory landbirds on the nonbreeding grounds

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Submission Date: March 23, 2020; Editorial Acceptance Date: August 18, 2020; Published October 14, 2020

ABSTRACT

Of the approximately 716 bird species that breed in North America, 386 (54%) are considered Nearctic–Neotropical migrants by the U.S. Fish and Wildlife Service. In the past 50 yr, scores of these migratory species, including some once considered common, have declined dramatically. Nearctic–Neotropical migrants normally spend 6–8 months in tropical habitats, making the identification, availability, and management of Neotropical habitats critical issues for their conservation. Yet, for most species, complete and nuanced information about their use of tropical habitats and the relative effects of breeding vs. wintering conditions on survival, productivity, and population trends is not available, though many studies point to Neotropical overwintering habitats as being a strong driver of population change. Particularly important for long-distance Nearctic–Neotropical migrants is an understanding of how "carry-over effects" arise and influence population trends when conditions on wintering grounds and tropical stopover areas affect subsequent reproductive performance on breeding grounds. For example, why some species show strong carry-over effects from tropical habitats while others do not is not fully understood. In recent years, many studies have offered insights into these issues by taking advantage of new scientific methods and technological innovations. In this review, we explore threats facing North American breeding birds that migrate to the Neotropics, summarize knowledge of habitat selection and use on the wintering grounds, describe how conditions at one point in the annual cycle may manifest in subsequent seasons or life history stages, and discuss conservation concerns such as climate change and the potential for phenological mismatch.

Keywords: carry-over effects, landbirds, migration, Nearctic–Neotropical migrants, phenological mismatch, wintering habitat

LAY SUMMARY

- More than half of the bird species that breed in North America, representing billions of birds, migrate to the Neotropics.
- In the past 50 years, scores of these species have declined dramatically.
- Migratory birds normally spend 6–8 months in tropical habitats, making the conservation of these species an international challenge. Yet, for most species, complete and nuanced information about their use of tropical habitats and the relative effects of breeding vs. wintering conditions on survival, productivity, and population trends is not available.
- Accelerating climate change is adding to the urgency of our gaining an understanding of the full annual and migratory cycle of these birds.
- In recent years, many studies have offered insights into these issues by taking advantage of new scientific methods and technological innovations.

Ecología del hábitat de las aves terrestres migratorias Neártico–Neotropicales en las zonas no reproductivas

RESUMEN

De las aproximadamente 716 especies de aves que se reproducen en América del Norte, el Fish and Wildlife Service de los EE. UU. considera que 386 (54%) son migratorias neártico-neotropicales. En los últimos 50 años, decenas de estas especies migratorias, incluidas algunas que hace poco se consideraban comunes, han disminuido drásticamente. Las aves migratorias neártico-neotropicales normalmente pasan entre seis y ocho meses en hábitats tropicales, lo que hace que la identificación, disponibilidad y manejo de los hábitats neotropicales sean temas críticos para su conservación. Sin embargo, para la mayoría de las especies, no se dispone de información completa y detallada sobre el uso de hábitats tropicales y los efectos relativos de las condiciones de reproducción vs. invernada en la sobrevivencia, la productividad y las tendencias de la población, aunque muchos estudios señalan que los hábitats de invernada neotropicales son un factor determinante de los cambios poblacionales. Es particularmente importante para los migrantes neárticos-neotropicales de larga distancia, es la comprensión de cómo surgen los "carryover effects" e influyen en las tendencias de la población cuando las condiciones en las zonas de invernada y en las zonas de escala tropical afectan el rendimiento reproductivo posterior en las zonas de reproducción. No se comprende completamente, por ejemplo, por qué algunas especies muestran fuertes "carry-over effects" desde los hábitats tropicales, mientras que otras no. En los últimos años, muchos estudios han ofrecido nuevas perspectivas sobre estas cuestiones aprovechando los nuevos métodos científicos e innovaciones tecnológicas. En este capítulo exploramos las amenazas a las que se enfrentan las aves reproductoras de América del Norte que migran al Neotrópico, resumimos el conocimiento del uso y la selección del hábitat en sus zonas de invernada, describimos cómo las condiciones en un punto del ciclo anual pueden manifestarse en las siguientes estaciones o etapas de la historia de la vida y discutimos problemas de conservación como el cambio climático y el potencial de desajuste fenológico.

Palabras clave: aves terrestres, carry-over effects, hábitat de invernada, migración, , migratorios Neártico–Neotropicales

INTRODUCTION

From a physiological perspective, long-distance migration is taxing (McWilliams and Karasov 2014). Birds must spend days or weeks gaining and storing energy to fly hundreds or thousands of kilometers over oceans, mountains, or deserts while avoiding adverse weather, predators, food shortages, and anthropogenic obstacles such as those posed by development (Hedenström 2008, Newton 2008, Longcore et al. 2013; Figure 1). When migrants arrive in the Neotropics, they may have to compete with conspecifics for resources, relegating less competitive individuals to lower quality habitat (Marra et al. 1993, Marra 2000, Studds and Marra 2005). Despite these challenges, the benefits of migration from the tropics to temperate zones (to exploit an abundance of spring and summer food resources) and back to the tropics (to escape harsh northern winter weather and lack of food) appear substantial, and these tradeoffs have shaped the remarkable life history strategies exhibited by Nearctic–Neotropical migratory birds (Alerstam 1990). While important knowledge about full annual cycle dynamics has increased greatly, our understanding of the specific drivers of population decline, especially in tropical wintering habitats, remains relatively poor (Runge and Marra 2005, Sherry et al. 2015).

This is no small matter: bird populations across the Americas are in trouble. A recent estimate from North America has put the loss at 25% of the continental avifauna—nearly 3 billion birds—in less than half a century (Rosenberg et al. 2019). Of ~716 bird species that breed in North America, 386 (54%) are considered Neotropical migrants by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2000), and migratory species might be particularly at risk compared with nonmigrants: Runge et al. (2015) noted that only 9% of migratory species are adequately covered by protected areas across all stages of their annual cycle, in comparison with 45% of nonmigratory birds.

Until conservation professionals better understand full annual cycle dynamics, such as how factors related to breeding in the Nearctic compared with wintering in the Neotropics drive population change, effective conservation action will be difficult, as efforts to conserve species by increasing or enhancing habitats during the less important parts of the cycle will have little effect on population size (Sherry and Holmes 1995, Sheehy et al. 2010, Rushing et al. 2016). Specifically, if a species is declining due to factors operating on the wintering grounds in the Neotropics rather than the temperate breeding grounds, conservation efforts on wintering grounds are likely to be most effective, and vice versa. (Note: although the term "winter" may refer to different calendar periods in temperate and tropical latitudes, the terms "winter" or "wintering" as we use them in this paper are synonymous with the nonmigratory, nonbreeding season of Nearctic–Neotropical migratory birds.)

This is an exciting time to study Nearctic–Neotropical migratory birds. A growing body of Latin American professionals and an increase in international, collaborative studies have led to more and deeper field studies in the tropics. For example, multiple studies in northern Colombia have drawn attention to the role tropical habitats play in enabling birds to prepare for (in spring) and recover from (in fall) long migratory flights across the Caribbean Sea (Bayly et al. 2013, 2019, Gómez et al. 2015). Multi-country initiatives are also becoming more common, shedding light on patterns of connectivity and variation in abundance at scales rarely studied in the past (González-Prieto et al. 2016, Bulluck et al. 2019), and Neotropical agroecosystems such as shade

FIGURE 1. The full annual cycle of Nearctic–Neotropical migratory birds. Although a generalized representation, most birds spend the majority of the year in the Neotropics. (Artwork by Lauren Helton, The Institute for Bird Populations.)

coffee and silvo-pastures have received attention as researchers have learned more about their use as winter habitat for migrants (McDermott and Rodewald 2014, Colorado and Rodewald 2017, González-Prieto 2018b, Narango et al. 2019).

Simultaneously, several studies have highlighted the importance of migration and stopover habitats (Bayly et al. 2012, Wolfe et al. 2014), a life history phase that is recognized as contributing to a large portion of annual mortality (Sillett and Holmes 2002, Rockwell et al. 2017). A relative explosion in the use of eBird in the Neotropics has opened the door to a plethora of questions regarding nonbreeding distributions (La Sorte et al. 2017) and movement patterns throughout the region (La Sorte et al. 2016b); and recent advances in tracking technology, such as miniaturized global positioning systems, light-level geolocators, and the Motus system (Taylor et al. 2016), are being used routinely to shed light on full annual cycle ecology and the connections between temperate and tropical habitats (Wikelski et al. 2007, Bridge et al. 2011, Taylor et al. 2016). Innovations in molecular genetics have also improved understanding of taxonomy and species distributions (Ruegg et al. 2014). Genome sequencing and isotopic signature study, among other techniques, have enabled subspecies or population differentiation as well as the linkage of breeding and wintering sites with migratory pathways and stopover sites (González-Prieto and Hobson 2013, Ruegg et al. 2014, Hobson et al. 2015b, González-Prieto et al. 2016, Ruegg et al. 2016).

Awareness of emerging and potentially grave threats has paralleled this rapid expansion of knowledge. Species declines due to habitat loss and fragmentation by anthropogenic causes are accelerating in many parts of the Neotropics (Rodriguez-Eraso et al. 2013, Ceballos et al. 2015), and a rapidly changing climate with potentially shifting bottom-up trophic effects that may affect the availability and phenology of food resources adds several layers of complexity. Thus, while advances in ornithology and technology have produced useful insights into the full annual cycle of Nearctic–Neotropical migratory birds, important questions remain, and the context for which bird conservation will be carried out in the 21st century and beyond is rapidly shifting. Recent findings by Rosenberg et al. (2019) have created renewed attention in the plight and loss of migratory bird populations, making a reexamination of the state of our knowledge timely. In this review, we aim to highlight important knowledge gaps and identify future directions for Neotropical migratory bird research and conservation.

Habitat Conservation Concerns and Threats

With the worldwide human population already exceeding 7.6 billion and projected to reach 11 billion by the end of the 21st century, threats to birds will increase. Habitat is being lost, fragmented, and degraded due to the direct and indirect effects of an expanding agricultural footprint, climate change, environmental contaminants, invasive species, urban development, and myriad other threats. Forests in areas such as the Sierra Madre of Mexico and the heavily populated tropical Andes Mountains continue to be converted to other uses less sustainable to birds (Rodríguez-Eraso et al. 2013), threatening vulnerable species such as Cerulean Warbler (*Setophaga cerulea*), Wood Thrush (*Hylocichla mustelina*), Olive-sided Flycatcher (*Contopus cooperi*), and Canada Warbler (*Cardellina canadensis*), not to mention scores of (currently) more common species. Forest loss continues throughout much of the remaining large tracts of Central American wet and dry tropical forests, putting many migratory species at risk (Blandón et al. 2016). Meanwhile, the acceleration of forest habitat loss in the Amazon may affect populations of so far little known core wintering habitat of forest-dependent species such as Veery (*Catharus fuscescens*; Remsen 2001) and Connecticut Warbler (*Oporornis agilis*; Diniz et al. 2014). Other tropical habitats, including mangroves, which are important for many migratory warblers (Wunderle et al. 2014, Bulluck et al. 2019), and native grasslands (Vickery et al. 1999), are now rare in both North and South America, and are rapidly disappearing. However, certain types of land conversion of forest to agriculture or other uses may not be universally negative for Nearctic–Neotropical migratory birds. Some studies have shown increased avian diversity in mixed agroforestry landscapes (Bakermans et al. 2009, DeBeenhouwer et al. 2013, González-Prieto 2018b, Valdéz-Juárez 2018), although these benefits appear to accrue largely for habitat generalists. In addition, research has emphasized the potential for population-level impacts to occur during migration, especially at stopover sites (Baker et al. 2004, Faaborg et al. 2010, Cohen et al. 2015). Stopover habitat is being lost at similar rates to wintering habitat but, due to concentration effects at migratory bottlenecks, the impacts may be more widespread and affecting multiple populations. In general, these areas have received much less scientific and conservation attention than breeding and wintering areas.

Understanding Habitat Quality

Determining which conservation strategies work best for Nearctic–Neotropical migratory birds requires an understanding of what constitutes habitat quality. Conservation of migratory birds in the Neotropics has tended to focus on mitigating habitat loss (i.e. quantity), but habitat quality also merits discussion, and progress is ongoing (e.g., Johnson 2007, Faaborg et al. 2010). From studies in Jamaica on American Redstarts (*Setophaga ruticilla*), Johnson et al. (2006a) found that birds survive best from one winter to the next in habitats where they maintain body mass over the course of the dry season. Peele (2015) found that moderate elevation wet limestone forest had the highest estimates of annual survival, relatively early departure for spring migration, proportionately older males, and a near absence of transient individuals, all of which are indicators of high habitat quality. Early departure time in migration contributes to early arrival on the breeding grounds and enhanced reproductive success (Reudnik et al. 2009, Cooper et al. 2015). Shade coffee plantations are another higher elevation woodland habitat that provides abundant food and can constitute a refuge for wintering migratory birds in the Caribbean and Central America (see Wunderle and Arendt 2017). In a different context, Ruiz-Sánchez et al. (2017) found higher densities and smaller territory sizes for wintering Wilson's Warblers (*Cardellina pusilla*) in conserved cloud forests in southeastern Mexico compared with unprotected sites with lower forest cover, but without finding differences in body condition. This difference between habitat types suggests that density was mediated by food availability, with birds reducing territory size as resources increased. A similar finding was found in work on Swainson's Thrush (*Catharus ustulatus*) wintering in forest vs. shade coffee in Colombia (González-Prieto 2018b).

Body condition, which is often measured using body mass maintenance or gain, has been widely used to assess winter habitat quality (Smith et al. 2010, Colorado and Rodewald 2017), including during migration stopovers

(Buler et al. 2007, Bayly et al. 2016). More research is needed to understand precisely how to estimate winter body condition and its components in physiologically and ecologically meaningful ways.

In a comparison of stopover habitats in Colombia, Bayly et al. (2016) examined 7 potential parameters as possible indicators of habitat quality. Rate of body-mass change, foraging rate, recapture rate, bird density, and flock size were expected to show a positive correlation with habitat quality. In addition, more adults and more males and birds of higher body mass might be expected in higher quality habitats because of their ability to competitively exclude younger, smaller, or less experienced conspecifics and deny them access to resources. The authors found higher densities, body mass, foraging rates, and rates of mass change in pre-montane forest than in shade-coffee plantation for Tennessee Warbler (*Leiothlypis peregrina*) but no clear evidence for differences in age or sex ratios. For Gray-cheeked Thrush (*Catharus minimus*), forest provided higher body mass and mass gains, while shade coffee provided poorer fueling conditions (measured by fewer recaptures). These results point to the need to use multiple, independent indicators that are relevant to each species' ecology when assessing habitat quality.

Carry-Over Effects

Poor quality tropical habitat can have long-term negative effects on subsequent phases of an individual bird's annual cycle, a process known as seasonal carry-over (e.g., Norris and Taylor 2006, Hostetler et al. 2015). In some dry tropical habitats, arthropod abundance can be lower in the dry season, which has been linked to lower body mass (Cooper et al. 2015). In American Redstarts, the most extensively studied species with respect to carry-over effects, individuals occupying territories in dry scrub (as opposed to mangrove) were in worse physiological condition prior to the onset of spring migration, leading to delayed arrival times on the breeding grounds, which is known to affect a migratory bird's fitness (Marra and Holberton 1998). A decline in body condition of ~10% over the dry season was associated with a delay of almost 1 week in spring migration departure (Studds and Marra 2007). Experimental reductions in food availability led to lowered body condition and delayed departure (Cooper et al. 2015), and carbon isotope analysis revealed that former winter habitat of individual redstarts arriving in spring linked higher winter habitat quality to earlier male arrival and higher reproductive success (Norris et al. 2004). Similar findings have been made for Kirtland's Warbler (*Setophaga kirtlandii*; Rockwell et al. 2012) and Barn Swallow (*Hirundo rustica*; Saino et al. 2004).

Other research has shown that birds arriving later at spring stopover or breeding sites had stable isotope signatures associated with drier wintering habitat (Gonzalez-Prieto and Hobson 2013, Paxton and Moore 2015, Akresh et al. 2019). For Gray-cheeked Thrush on spring stopover at sites in northern Colombia, acquired fuel loads carried over influenced the subsequent pace of migration (less fuel meant a slower pace), and likely delayed arrival at the breeding grounds, possibly by weeks (Gómez et al. 2017).

Direct tracking studies confirm that, for several species, late departure from the wintering grounds correlates with late arrival at the breeding site (Stanley et al. 2012), and lab studies have shown a link between high energetic demands of flight endurance in females and subsequent lower quality of eggs (Skrip et al. 2016), either of which could reduce reproductive success.

By contrast, in Wood Thrush, a geolocator migration tracking study found that habitat quality at a wintering site in Belize and premigration body condition did not affect spring migration timing, speed, or arrival time at the breeding site (McKinnon et al. 2013). Wood Thrushes are relatively large-bodied and omnivorous, and individuals are consistent from year to year in their migration timing relative to the population average, suggesting an endogenous migration schedule (Stanley et al. 2012). Individuals in relatively poor condition may leave "on time" and then compensate at stopovers through differential habitat selection, diet, and/or duration of stopover. Some studies on smaller songbirds have also found that carry-over effects from tropical habitats can be weak. Research using stable isotopes for an Arctic-breeding population of Yellow Warbler (*Setophaga petechia*) did not detect any carry-over effects of nonbreeding habitat on arrival date or reproductive success (Drake et al. 2014). No carry-over effects were detected in one study of Magnolia Warblers (*Setophaga magnolia*) captured during spring migration (Boone et al. 2010). Thus, the American Redstart "model" may not apply equally well to all species, perhaps because of differences in body size, diet, habitat use, or migration strategy. Also, the gradients in tropical habitat quality occupied by some species may not be extreme enough to cause strong carry-over effects. For instance, body condition in Wilson's Warblers did not differ between a large protected cloud forest habitat and a small unprotected fragment (Ruiz-Sánchez et al. 2017).

Assessing the presence and extent of carry-over effects can be challenging because of the long timescales and vast distances over which individuals travel after leaving the tropics. Subtle carry-over effects could exist and have an important impact on population dynamics but are challenging to document (Imlay et al. 2019). Current tracking technology for small birds is limited to archival devices (those for which a bird must be recaptured in order to retrieve the information). It is thus only possible to measure carry-over effects for individuals who survive their entire round-trip migration, a fact which, in itself, may distort estimates. Further, linkages between breeding success and former wintering habitat can only be assessed indirectly through analysis of stable isotopes, which requires a strong moisture gradient across habitats to detect a signal. Here, too, only survivors who arrive at the breeding site can be sampled. Given these challenges, assessment of carry-over effects in a conservation context could instead focus on the underlying physiological mechanisms and signatures that drive population change (O'Connor and Cooke 2015). Direct assessment of physiological measures of stress and body condition could be used in short-term and cost-effective field studies (e.g., Marra and Holberton 1998) and lab studies (Skrip et al. 2016) as a proxy for forecasting the likely strength of carry-over effects.

Studies of carry-over effects would benefit from the use of multiple intrinsic markers. Imlay et al. (2019) integrated stable isotopes, corticosterone levels, telomere dynamics, and body condition of 3 declining migratory species, Bank Swallow (*Riparia riparia*), Barn Swallow, and Cliff Swallow (*Petrochelidon pyrrhonota*), to show that environmental conditions in South American winter habitat resulted in carry-over effects. These included lower annual reproductive success through fewer surviving young, a lower incidence of double brooding, and poorer body condition for those overwintering on some habitats. This study highlights how the multi-marker analysis was vital for inferring the presence of carry-over effects undetectable using a single marker.

Migration Stopover

Although most migration stopover regions and their habitats in the Neotropics are not well identified (Bayly et al. 2018), researchers are beginning to understand how habitat loss or conversion can negatively affect migratory behavior (Bayly et al. 2019). This theme becomes particularly relevant when one considers how some regions and the associated stopover habitats concentrate much of the global population of certain species into areas a fraction of the size of their breeding or wintering grounds. This occurs for Gray-cheeked Thrush in Colombia's Sierra Nevada de Santa Marta (Gómez et al. 2019) and in the Darién region of Panama (Cárdenas-Ortiz et al. 2017, 2020), the latter funneling birds from a region spanning >5,000 km east to west in North America into a narrow corridor barely 100 km wide. The loss of geographically restricted migration/stopover habitats could therefore have a disproportionate effect on some species. In addition, the utility of some stopover sites is still coming into focus. Pyle et al. (2018) studied the postbreeding movements of 140 species captured at more than 900 Monitoring Avian Productivity and Survivorship (MAPS) stations over a 25-yr period to investigate latitudinal, longitudinal, and elevational shifts from breeding to molting grounds. They found evidence for postbreeding movements to molting areas (many of which were migratory stopover sites) among a variety of North American landbirds, including many migratory species previously assumed to molt on breeding grounds. Movements were heterogeneous, both within and among species, and included areas in the Neotropics; the monsoon region of northwestern Mexico is particularly important in this regard. Logistical challenges notwithstanding, the role of migration stopover sites in the full annual cycle of Nearctic–Neotropical migratory birds merits considerably more attention than it has received to date.

Wintering Habitat Dynamics

Because different breeding or wintering populations do not face the same pressures, and neither increase nor decline at the same rates (Wilson et al. 2018), population-specific information is needed to better inform conservation efforts. Genetically derived population delineations and newly described migration routes are contributing to our understanding of migratory connectivity and habitat use by specific populations of many species (Ruegg et al. 2016). For example, the Willow Flycatcher (*Empidonax traillii*) is a relatively common, widely distributed species across its North American breeding range, although the *extimus* subspecies, which nests in northwestern Mexico and the southwestern United States, is U.S. federally Endangered. Recent work is homing in on the wintering areas used by the breeding population of *extimus* (Ruegg et al. 2020), which would enable conservation strategies to be focused where they are most needed. Similar work using stable isotopes has revealed how wintering Canada Warbler populations are structured across the tropical Andes of Colombia (Gonzalez et al. 2016), making it possible to identify deforestation in the eastern Andes of Colombia as one of the main drivers of declines occurring in eastern but not western breeding populations of this species (Wilson et al. 2018). An isotopic study of the likely breeding origins of Golden-winged Warbler (*Vermivora chrysoptera*) captured throughout their wintering range (Hobson et al. 2016) revealed how steeply declining breeding populations are migrating largely to mountainous regions of northern Colombia and Venezuela. Dramatic declines of Appalachian populations of this species have been linked to disproportionate forest loss on this population's wintering grounds in northern South America (Kramer et al. 2018).

An expanding topic of research is how intraspecific habitat use should be taken into account when evaluating habitat quality and designing appropriate conservation strategies. In many species, males tend to outcompete females or first-year birds in certain habitats (Latta and

Faaborg 2002, Studds and Marra 2005, Wunderle et al. 2014), something that can lead to differential carry-over effects (Marra and Holmes 2001, Drake et al. 2013), while also raising the question about what types of habitat are being conserved. In many species, a proportion of individuals will remain on the same territory throughout the winter, even returning to the same territory in subsequent years (e.g., see Koronkiewicz et al. 2006), though one striking pattern that has emerged from recent wintering studies is the frequency of prolonged stopover behaviors or the use of multiple wintering grounds for some species. In a review of geolocator studies, McKinnon et al. (2013) found that 6 of 11 species studied used secondary wintering areas. Other studies have shown that migrants frequently move among habitats in winter, indicating that behavioral transience is more frequent than previously appreciated (Gómez and Bayly 2010, Peele et al. 2015, Ruiz Gutierrez et al. 2016). Some habitats show an increase in migrant density through the winter, others a decrease (Hilty 1980, Johnson 1980, Lefebvre et al. 1992, Gómez and Bayly 2010), suggesting that individuals possess the capacity to track seasonal changes in food or other resources. Perhaps the species that best exemplifies the range of movement patterns during the nonbreeding season is Bobolink (*Dolichonyx oryzivorus*). Renfrew et al. (2011) noted that "…movements during the…annual cycle of the Bobolink… can be characterized as a continuum, with occasional stops lasting no more than two months". Bobolinks exhibit prolonged periods of stasis in Venezuela and Colombia, which appear to provide fuel for migratory flights both north and south, while stationary periods in Bolivia and Argentina are closest to the traditional concept of wintering areas, but are also used for undergoing an extensive prealternate molt before returning northward (Pyle 1997, Renfrew et al. 2011).

Despite the variation in observed behaviors, similar pressures can be expected to be acting on habitat selection, such as resource abundance (Somveille et al. 2018), relative "safety" (Cuadrado 1997), and prior knowledge (Forrester 2015). Because resources fluctuate with precipitation, moisture gradients may strongly influence the choice of wintering sites (Smith et al. 2010). The timing and seasonality of precipitation should be accounted for, too (Studds and Marra 2007, Rockwell et al. 2017). However, birds wintering in, for example, tropical dry forests may be selecting attributes not directly related to moisture, such as seasonality in resource abundance. Indeed, net annual precipitation by itself may not explain variation in site use, with seasonality in rainfall patterns potentially playing an important role.

Site selection may also be influenced by evolutionary pressures, such as niche conservatism, the tendency of species to retain certain ecological characteristics or behaviors. In a novel study comparing environmental niche breadth (the 2-dimensional space defined by a set of environmental variables such as mean temperature and average precipitation) between the breeding and nonbreeding periods in Wood Warblers, Gomez et al. (2016) found that migratory warblers were more likely than tropical resident species to track a niche across the year. This suggests that site selection is likely constrained in many species and may also explain why so many Nearctic–Neotropical migratory birds converge on the highlands of Central and South America during the winter (Robinson et al. 1995), where they experience temperatures and precipitation similar to their breeding grounds. Even during migration, some species appear to track the conditions of their environmental niche. For example, Cerulean Warblers use stopover habitats in montane forests in Central America, which tend to mirror many environmental conditions encountered on their breeding grounds (Welton et al. 2012).

On the breeding grounds, most migratory species exhibit high territoriality and between-year site fidelity. A mixture of year-to-year fidelity and territoriality can be advantageous in reducing food search costs (Stamps et al. 2005) and increasing the effectiveness of acquiring food (Greenwood et al. 1982). Given the investments in time and energy required to obtain and hold a winter territory, species with multiple and widely separated wintering sites may not be truly territorial. Here, we reviewed multiple winter territoriality studies for 18 species/subspecies (Table 1). Of those, 7 used multiple wintering areas and, of these 7, 4 had no winter territorial behavior, and 3 had unknown winter territorial behavior. However, high site fidelity has been described even in non-territorial species. In the typically "non-territorial" Prothonotary Warbler (*Protonotaria citrea*), a marked population wintering in coastal scrub in northeastern Costa Rica yielded an estimated year-to-year recapture probability of 0.42 (Wolfe et al. 2013) whereas highly territorial species such as the Willow Flycatcher show an average winter site fidelity of ~68% (Koronkiewicz et al. 2006). It appears that some species may switch modes of territoriality within or between seasons and changes in territoriality between seasons coincide with a switch from an insect-based diet on the breeding grounds to a fruit-based diet on the wintering grounds (Wolfe et al. 2014).

Interspecific competition also plays a role in tropical habitat selection by Nearctic–Neotropical migrants, and may contribute to population limitation, although this topic is relatively poorly understood. Most studies of migratory populations have focused on single species, which tends to neglect migrant–migrant or migrant–resident interactions. The breeding currency hypothesis (Greenberg 1995), supported empirically by Johnson et al. (2005, 2006b), emphasizes that competition from resident birds may have selected for migrants to winter in relatively

TABLE 1. Nearctic–Neotropical migrant species where the use of multiple winter sites or winter territoriality has been documented.

Species	Multiple winter sites	Winter territoriality
Purple Martin (*Progne subis*)	Yes [1]	No [2]
Tree Swallow (*Tachycineta bicolor*)	No [3]	No [4]
Barn Swallow (*Hirundo rustica*)	No [5]	No [6]
Red-eyed Vireo (*Vireo olivaceus*)	No [8]	No [7]
Bobolink (*Dolichonyx oryzivorus*)	Yes [10]	No [9]
Veery (*Catharus fuscescens*)	Yes [12]	Unknown [11]
Swainson's Thrush (coastal; *C. ustulatus*)	Yes [14]	Unknown [13]
Swainson's Thrush (inland; *C. ustulatus*)	No [14]	Unknown [13]
Eastern Kingbird (*Tyrannus tyrannus*)	Yes [16]	No [15]
Western Kingbird (*T. verticalis*)	Yes [18]	Unknown [17]
Scissor-tailed Flycatcher (*T. forficatus*)	No [20]	No [19]
Gray Catbird (*Dumetella carolinensis*)	No [22]	Yes [21]
Golden-winged Warbler (*Vermivora chrysoptera*)	No [24]	Yes [23]
Kirtland's Warbler (*Setophaga kirtlandii*)	No [26]	Yes [25]
Prothonotary Warbler (*Protonotaria citrea*)	Yes [28]	No [27]
Ovenbird (*Seiurus aurocapilla*)	No [30]	Yes [29]
Wood Thrush (*Hylocichla mustelina*)	No [32]	Yes [31]
Western Yellow-billed Cuckoo (*Coccyzus americanus occidentalis*)	No [34]	Unknown [33]

References: 1. Fraser et al. (2012), 2. Hill (1993), 3. Bradley et al. (2014), 4. Eliott (1939), 5. Hobson et al. (2015a), 6. Bing (1993), 7. Callo et al. (2013), 8. Cimprich et al. (2020), 9. McKinnon et al. (2013), 10. Renfrew et al. (2020), 11. Hobson and Kardynal (2015), 12. Heckscher et al. (2020), 13. Delmore et al. (2012), 14. Mack and Yong (2020), 15. Cormier et al. (2013), 16. Fitzpatrick (1980), 17. Jahn et al. (2013), 18. Gamble and Bergin (2020), 19. Jahn et al. (2013), 20. Regosin (2020), 21. Ryder et al. (2011), 22. Rappole and Warner (1980), 23. Kramer et al. (2017), 24. J. D. Wolfe personal observations, 25. Cooper et al. (2017), 26. Sykes and Clench (1998), 27. Wolfe and Johnson (2015), 28. Post (1978), 29. Hallworth et al. (2015), 30. Faaborg and Arendt (1984), 31. Stanley et al. (2012), 32. Evans et al. (2020), 33. Sechrist et al. (2012), 34. Hughes (2020).

poor habitats (e.g., migrants leave niches empty for part of the year; Johnson and Sherry 2001). A study on "morphological space" (ecological space as defined by morphological niches and traits) in the Mexican Neotropics by Malpica et al. (2017) supports this hypothesis using seasonal changes in morphological niche-packing and niche-volume.

Breeding Season vs. Wintering Season Limitation

A largely unanswered question for most Nearctic–Neotropical migratory species and populations is what annual cycle phase (breeding, wintering, or migration) is the strongest driver of population change. This gap in knowledge may impact conservation planning, as any efforts to improve habitat in the less limiting season will have little effect in the more limiting season (Sherry and Holmes 1995). Several studies have provided evidence for either breeding or wintering season limitation for certain species. Rappole et al. (2003) argued that, for the U.S. federally Endangered Golden-cheeked Warbler (*Setophaga chrysoparia*), based on both the availability and use of breeding and nonbreeding habitat, nonbreeding habitat in Mexico and Central America is likely more limited than breeding habitat in Texas. Using migratory networks and population modeling, Taylor and Stutchbury (2016) argued that Wood Thrush is more limited by quantity of habitat in winter than in summer. A full life-cycle model for Canada Warbler implicated habitat loss in the tropical eastern Andes as the primary driver of population declines (Wilson et al. 2018). DeSante et al. (2018) found that population change for Golden-crowned Kinglet (*Regulus satrapa*) was driven primarily by decreases in adult survival in nonbreeding areas, and population changes for "Western" Flycatcher (*Empidonax difficilis/occidentalis*) and Warbling Vireo (*Vireo gilvus*) were driven primarily by changes to first-year survival of young during the nonbreeding season. By contrast, Sherry et al. (2015) argue that, for American Redstart, both winter and summer could be simultaneously driving population change. DeSante et al. (2018) had similar findings for Orange-crowned Warbler (*Oreothlypis celata*). DeSante et al. (2015) conducted one of the largest scale studies to address this question, using 15 yr of demographic data from the MAPS program to examine the demographic drivers of population change for 158 species of passerines and near passerines. Wintering habitat was the primary driving factor in population change for many, if not most, of these species.

Climate Change and Habitat Loss

Impacts to Neotropical habitats from climate change, a topic of enormous importance and breadth, is covered only briefly here. Although some impacts to Nearctic–Neotropical migrant and resident bird species are relatively easy to predict (e.g., for species with limited ranges and narrow habitat requirements), many are unforeseeable because of, for example, the many migratory species whose habitat needs on their wintering grounds are still largely unknown. As temperature and rainfall patterns shift, habitats will inevitably change, and trophic interactions of primary producers, and secondary and tertiary consumers, will be disrupted; it is therefore likely that many species now considered to have stable populations will become vulnerable.

Under most climate change scenarios, significant areas of habitat for migratory landbirds, including forests, grasslands, and shrublands, will be greatly altered. In some models, habitat loss may increase bird extinctions caused by climate change by 50% and the expected 3.5°C surface warming by the year 2100 may result in 600–900 extinctions of landbird species, 89% of which occur in the tropics (Şekercioğlu et al. 2002). In one of the most extensive studies to date, Langham et al. (2015) described the habitat-based climate limitations ("climate envelopes") for 588 North American species, hundreds of them Nearctic–Neotropical migrants, pinpointing the range of temperatures, rainfall, and other climate characteristics of their habitats. Results indicate that 314 species (53%) will lose more than 50% of their current climatic range by 2080. Although the models examined habitats almost exclusively in North America (plans call for expanding the study to the Neotropics), nonbreeding range in tropical Mexico for Baird's Sparrow (*Ammodramus bairdii*), for example, is predicted to shrink by 97% by 2050. In addition, the greatly constricted geography of the Central American Isthmus may amplify any habitat losses due to climate change.

Most climate change scenarios forecast increased frequency and strength of storms such as hurricanes and typhoons, a prediction that was bolstered in 2017 when, within a few weeks, hurricanes Irma, Jose, and Maria battered the Caribbean and southeastern U.S. devastating human lives and homes, but also habitat for resident and migratory birds (Wunderle Jr. 2017), as much of the impact occurred during fall migration and early stopover and wintering ground arrival. While many migratory species may sense falling air pressure that precedes a large storm and alter their migration patterns (Dänhardt and Lindström 2001), others cannot and may suffer significant mortality (Dionne et al. 2008). The impacts are still being assessed, but it is already known that the effects on nonbreeding habitats for many Nearctic–Neotropical migrants were widespread and severe.

One of the first studies that identified the potential for the El Niño-Southern Oscillation (ENSO) to impact migrant birds by affecting their Neotropical habitats was conducted by Sillett et al. (2000), who found a correlation between El Niño events in Jamaica, which are associated with droughts in the Caribbean Basin, and reductions in Black-throated Blue Warbler (*Setophaga caerulescens*) annual adult survival, presumably because these droughts impact the availability of food needed to survive the winter and to fuel spring migration to breeding grounds. Subsequently, Wilson et al. (2011) found support for negative impacts of Caribbean drought, especially centered on Cuba, on Breeding Bird Survey population trends in eastern North America in American Redstarts. Similar effects of winter season drought in the Caribbean have been suggested for Ovenbirds (*Seiurus aurocapila*; Brown and Sherry 2006), Northern Waterthrush (*Seiurus noveboracensis*; Smith et al. 2010), and the endangered Kirtland's Warbler (Wunderle and Arendt 2017). For migratory species from western North America, Lamanna et al. (2012) found that annual survival of Swainson's Thrush was strongly influenced by ENSO-related weather changes during one or more periods of its annual cycle. The clear message from this body of research is that ENSO-related droughts impact habitats, and therefore populations, in a variety of birds, probably via food supply. Droughts will likely increase in magnitude with intensification of climate change.

Phenological Mismatch

Phenology, the timing of seasonal life-cycle events, is fundamental to species' ecology and life history, providing a valuable indicator of environmental impacts on ecosystems (IPCC 2014). Climate-driven changes in habitat phenology can impact migratory bird populations through disruption or "mismatch" of previously synchronized trophic interactions (Sherry and Holmes 1996). Mismatch in habitat conditions between Neotropical wintering and stopover habitats may impact wintering body condition, overwinter survival, and spring departure (Marra and Holberton 1998, Strong and Sherry 2000) with carry-over effects on reproductive success (Norris et al. 2004) and migration timing (Paxton and Moore 2015) for migrating birds. For example, Neotropical habitat quality has been associated with an overlap of wintering migrants with invertebrate prey abundance (Strong and Sherry 2000), which is influenced by winter precipitation (McKellar et al. 2013, Rockwell et al. 2017), highlighting that a predictable or seasonally stable optimal window plays an important role in bird movements and habitat selection on the wintering grounds (Parrish and Sherry 1994, Kresnik and Stutchbury 2014).

Phenological information from the Neotropics is not representative of the large land area and biodiversity of the region (Mendoza et al. 2017, Merrick et al. 2019), despite the fact that most climate projections suggest that tropical biomes will experience among the greatest increases in extreme heat and precipitation events (Garcia et al. 2014), with concurrent changes to the abundance and phenological timing of pollen, fruits, seeds, and insects expected in these habitats as well.

Mismatch may be most significant for long-distance migrants (La Sorte and Fink 2017), especially species which depend on highly seasonal food resources that have a narrow temporal distribution of availability and potential for "match" (Both et al. 2010), as well as species with more restricted diets (Mallord et al. 2017). Research on wintering habitat ecology has revealed interactions of habitat type and habitat structure, food availability, and bird movements, although research is lacking on long-term distributional patterns that could reveal phenological mismatches. Age- and sex-related habitat segregation within wintering bird populations adds complexity to the task of fully understanding the implications of phenological mismatch (Parrish and Sherry 1994, Kresnik and Stutchbury 2014). Although there is significant variation in phenotypic plasticity for responding to interannual variation and trends, there are likely distributional limits to most populations and species (Fraser et al. 2019), which, if trends continue, may soon be exceeded. Links between variation in local and hemispheric weather and climate factors, trophic-associated habitat quality, and avian responses should be considered within the context of phenological mismatch across species assemblages and inherent latitudinal differences in the ecological processes and mechanisms involved.

Priority Habitats

The preceding sections explained why tropical habitats are so pivotal in the full annual cycle of migratory birds, while hinting at the finding that some vegetation types occupied by migrants may be of greater importance than others. We still have much to learn about the relative use and quality of tropical habitats, but our current knowledge is sufficient to draw attention to specific habitats that are both important to declining species and are themselves under threat. Multiple studies have converged on the conclusion that humid pre-montane forests in the tropical Andes provide habitat for a suite of steeply declining species including Cerulean Warbler, Canada Warbler, Golden-winged Warbler, and Olive-sided Flycatcher (Colorado et al. 2012, Kramer et al. 2017, Céspedes and Bayly 2018, Wilson et al. 2018). The tropical Andes span a broad elevation range, with multiple peaks above 5,000 m; by contrast, migratory birds occupy a relatively restricted elevation band primarily between 1,000 and 2,000 m. These intermediate elevations have undergone extreme transformations (Rodríguez-Eraso et al. 2013), making way for coffee plantations, cattle pastures, and human settlements (Correa Ayram et al. 2015). It is no surprise then that Andean forests in Venezuela, Colombia, and, to a lesser extent, Ecuador and Peru, are considered a priority for the conservation of migratory landbirds. In addition, the relative impacts of habitat loss from climate change (discussed below) may be greatly amplified in such areas.

In Central America, the forested highlands have also been recognized as critical habitat for several species. Humid broadleaf forests in mountainous regions between 500 and 2,500 m of Costa Rica, Panama, Nicaragua, and Honduras are habitat for Golden-winged Warblers (Bennett et al. 2016), while highland pine-oak forests (1,100–2,400 m) in northern Central America are occupied by Golden-cheeked Warblers (Rappole et al. 2000). Bicknell's Thrush (*Catharus bicknelli*) also winter in humid montane broadleaf forests in the Greater Antilles (McFarland et al. 2013). While a disproportionate number of declining and threatened species are associated with montane forest, lowland habitats also have a role. Humid lowland broadleaf forests in Central America provide high quality habitat for Wood Thrush and Kentucky Warbler (*Geothlypis formosa*), among others, while mangroves, especially black mangrove (*Avicennia germinans*) stands, hold a high diversity and richness of migrants in Central America (Gómez and Bayly 2010) and the Caribbean. In northern South America, occupancy, emigration, and extinction rates all point to mangroves and wooded wetlands as vital habitats for the declining Prothonotary Warbler (Bulluck et al. 2019).

Studies examining the factors driving presence/abundance, as well as comparing habitat quality, reveal a common pattern among several migratory species, an increasing probability of occurrence or abundance in more humid and more mature forests (Johnson et al. 2006a, McFarland et al. 2013, Ruiz-Sanchez et al. 2017, Céspedes and Bayly 2018). For example, increasing canopy height not only results in higher densities of Canada Warblers in the Andes (Céspedes and Bayly 2018) but also a lower rate of extinction from the wetland habitats occupied by Prothonotary Warblers (Bulluck et al. 2019). It follows that the loss of mature forests is likely to negatively impact a range of species. Nonetheless, many migratory landbirds will occupy transformed tropical habitats and are not forest-dependent. Shade-coffee plantations, for example, are widely recognized as a better alternative to many other possible land uses (Komar 2006, González-Prieto 2018a) and may even support similar densities of migrants as the forests they replaced (Bakermans et al. 2009).

How transformed tropical habitats compare with natural habitats is a topic that has received relatively limited attention (González-Prieto 2018b), despite its considerable importance when it comes to deciding between land-sharing or land-sparing approaches (Chandler et al. 2013) for migratory bird conservation. For American Redstarts wintering in Jamaica, coastal mangroves are of higher quality than either shade coffee or citrus plantations (Johnson et al. 2006a). By contrast, Bakermans et al. (2009) concluded that shade coffee was of equal or higher quality than nearby primary forest in Venezuela based on the density of migrants. While density alone is not necessarily a reliable measure of habitat quality, the degree of variation in density between shade coffee and forest among different migrants is noteworthy. Canada Warblers, for example, are more abundant in forest (Céspedes and Bayly 2018), while the mean abundance of Blackburnian Warblers (*Setophaga fusca*) and Tennessee Warblers per mixed species flock was higher in coffee (McDermott and Rodewald 2014). These mixed results highlight the role shade coffee plays as a wintering habitat but it is notable that during migration, when energy needs are elevated, birds departing from or stopping over in forest have been found to fuel faster, attain larger energy reserves, and migrate in longer stages (Bayly et al. 2016, 2019, González-Prieto 2018b).

The quality of other agricultural systems that include shade trees should be further explored, including cocoa (Schroth and Harvey 2007), cardamom, silvo-pastures (McDermott and Rodewald 2014), and mixed native hardwood plantations (Bennett 2018).

The Future of Neotropical Habitats for North American Migrants

The last few decades have underscored the, sometimes contradictory, trends in the study and conservation of North American breeding birds on their stopover and wintering grounds in the Neotropics. Enormous strides have been made in our understanding of movements, population dynamics, habitat use, and successful conservation practices. Tracking devices are becoming smaller and cheaper every year and, in the near future, scientists may have mapped the movements and seasonal habitats of every species that migrates between North America and the tropics. The development of new population models, and the spread of eBird, the Monitoring Overwinter Survival program, and other community science programs, are providing valuable insights into how birds move on their wintering grounds. Concurrently, Latin American and Caribbean governments and homegrown conservation movements have become empowered and capable of successfully carrying out complex and comprehensive research and conservation initiatives, and among the public, the importance of birds and their conservation has grown considerably (see Dayer et al. 2020).

But will all of these improvements lead to better outcomes for the "birds of two worlds"? Many of the threats that have been well documented for decades, such as habitat loss and fragmentation, invasive species, pollution, and urbanization, continue apace and have, in many areas, accelerated. Add to these emerging threats factors such as climate change and the associated impacts of sea level rise and phenological mismatch, and it can be difficult to remain optimistic about the future of Nearctic–Neotropical migratory birds.

If the negative trends are to be reversed and the positive ones preserved, large reserves and protected areas will be more important than ever. But these areas need to be designed with a multitude of factors in mind, such as the full cooperation of local stakeholders, the complexities of political and social realities, and—crucially—the potential changes to the landscape that climate change will bring. Networks of protected areas need to incorporate extensive topographical diversity, cover wide elevation ranges, have high connectivity, and integrate human-dominated landscapes into conservation schemes, something which is not currently universally done (Langham et al. [2015], for example, found no strong associations between projected climate sensitivities and existing conservation priorities). Many Nearctic–Neotropical migratory bird species vulnerable to climate change are not currently considered threatened with extinction, often due to lack of knowledge, so systematically and regularly gathering information on the ecology and current and future distributions of these species is an urgent matter. One of the goals of the international bird conservation consortium Partners in Flight is "keeping common birds common" (Rosenberg et al. 2016).

In addition, while many countries in the Neotropics have established protected areas, they lack the financial resources to actively manage them, and many remain "paper parks"—lines on a map with no de facto protection—while habitat loss goes on around and sometimes inside their borders. Because a relatively high percentage of land in the Neotropics is privately owned (and therefore not legally protected in the long term), land-sharing systems that incorporate primary forest and a diversity of other habitats will be a key component of future conservation initiatives. Because locally based, long-term tropical bird monitoring and conservation programs based on adaptive management are essential to help protect birds against the myriad threats they face, local conservation efforts need to be bolstered with all the resources cooperating countries and non-governmental organizations can muster. And, because the birds we all care about traverse much of the hemisphere in their annual migrations, cooperation and resources must come from all countries in the hemisphere.

ACKNOWLEDGMENTS

Thanks to the anonymous reviewers who evaluated this manuscript, and to Morgan Tingley, Rodney Siegel, and Peter Pyle who reviewed early drafts of this manuscript. N.J.B. thanks the team of researchers in SELVA, especially Camila Gómez and Ana María Gonzalez, whose PhD thesis contributed important ideas to this paper.

Funding statement: Multiple grants from the National Science Foundation and Tulane University supported the work of T.S. N.J.B. thanks the funders who made the body of work in Colombia possible, including the Cornell Lab of Ornithology and Environment and Climate Change Canada.

Ethics statement: All research and writing that went into the preparation of this manuscript followed the guidelines of the Committee on Publication Ethics (COPE).

Author contributions: S.A. and J.D.W. conceived the idea, design, experiment (supervised research, formulated question or hypothesis). S.A., J.D.W., J.K., T.S., B.J.M.S., N.J.B., and A.R.-S. wrote the paper.
Conflict of interest statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

LITERATURE CITED

Akresh, M. E., D. I. King, and P. P. Marra (2019). Examining carry-over effects of winter habitat on breeding phenology and reproductive success in Prairie Warblers *Setophaga discolor*. Journal of Avian Biology e02025.

Alerstam, T. (1990). Bird Migration. Cambridge University Press, Cambridge, UK.

Baker, A. J., P. M. Gonzalez, T. Piersma, L. J. Niles, I. de Lima, S. do Nascimento, P. W. Atkinson, P. Collins, N. A. Clark, C. D. T. Minton, et al. (2004). Rapid population decline in Red Knots: Fitness consequences of decreased refueling rates and late arrival in Delaware Bay. Proceedings of the Royal Society of London, Series B 271:875–882.

Bakermans, M. H., A. C. Vitz, A. D. Rodewald, and C. G. Rengifo (2009). Migratory songbird use of shade coffee in the Venezuelan Andes with implications for conservation of Cerulean Warbler. Biological Conservation 14211:2476–2483.

Bayly, N. J., C. Gómez, and K. A. Hobson (2013). Energy reserves stored by migrating Gray-cheeked Thrushes at a spring stopover site in northern Colombia are sufficient for a long distance flight to North America. Ibis 155:271–283.

Bayly, N. J., C. Gómez, C., K. A. Hobson, A. M. González, and K. V. Rosenberg (2012). Fall migration of the Veery (*Catharus fuscescens*) in northern Colombia: Determining the energetic importance of a stopover site. The Auk 129:449–459.

Bayly, N. J., C. Gómez, K. A. Hobson, and K. V. Rosenberg (2016). Prioritizing tropical habitats for long-distance migratory songbirds: An assessment of habitat quality at a stopover site in Colombia. Avian Conservation and Ecology 11:5. http://dx.doi.org/10.5751/ACE-00873-110205

Bayly, N. J., K. V. Rosenberg, C. Gómez, and K. A. Hobson (2019). Habitat choice shapes the spring stopover behaviour of a Neotropical songbird. Journal of Ornithology 160:377–388.

Bayly, N., K. Rosenberg, W. Easton, C. Gómez, J. Carlisle, D. Ewert, A. Drake, and L. Goodrich (2018). Major stopover regions and migratory bottlenecks for Nearctic–Neotropical landbirds within the Neotropics: A review. Bird Conservation International 28:1–26.

Bennett, R. (2018). Nonbreeding ecology and conservation of migratory landbirds with a focus on the Golden-winged Warbler (*Vermivora chrysoptera*). Ph.D. dissertation, Cornell University, Ithaca, NY, USA.

Bennett, R.E., A. Rothman, K.V. Rosenberg, and F. Rodriguez (2016). Golden-winged Warbler nonbreeding season conservation plan. In Golden-winged Warbler Status Review and Conservation Plan (A. M. Roth, R. W. Rohrbaugh, T. Will, and D.A. Buehler, Editors). U.S. Forest Service, Washington, D.C., USA. pp. AP10–AP16. https://www.fws.gov/migratorybirds/pdf/management/focal-species/Golden-wingedWarbler.pdf.

Bing, M. D. (1993). A million swallows and more. Honeyguide 39:147–148.

Blandón, A. C., S. B. Perelman, M. Ramírez, A. López, J. Obdulio, and C. S. Robbins (2016). Temporal bird community dynamics are strongly affected by landscape fragmentation in a Central American tropical forest region. Biodiversity Conservation 25:311.

Boone, A. T., P. G. Rodewald, and L. W. DeGroote (2010). Neotropical winter habitat of the Magnolia Warbler: Effects on molt, energetic condition, migration timing, and hematozoan infection during spring migration. The Condor 112:115–122.

Both, C., C. A. M. Van Turnhout, R. G. Bijlsma, H. Siepel, A. J. Van Strien, and R. P. B. Foppen (2010). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proceedings of the Royal Society of London, Series B 277:1259–1266.

Bradley, D. W., R. G. Clark, P. O. Dunn, A. J. Laughlin, C. M. Taylor, C. Vleck, L. A. Whittingham, D. W. Winkler, and D. R. Norris (2014). Trans-Gulf of Mexico loop migration of Tree Swallows revealed by solar geolocation. Current Zoology 60:653–659.

Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, P. H. R. Kays, J. F. Kelly, and W. D. Robinson (2011). Technology on the move: Recent and forthcoming innovations for tracking migratory birds. BioScience 61:689–698.

Brown, D. R., and T. W. Sherry (2006). Food supply controls physical condition of a long-distance migrant bird wintering in the tropics. Oecologia 149:22–32.

Buler, J. J., F. R. Moore, and S. Woltmann (2007). A multi-scale examination of stopover habitat use by birds. Ecology 88:1789–1802.

Bullock, S. H., and J. A. Solis-Magallanes (1990). Phenology of canopy trees of a tropical deciduous forest in Mexico. Biotropica 22:22–35.

Bulluck, L., E. Ames, N. Bayly, J. Reese, C. Viverette, J. Wright, A. Caguazango, and C. Tonra (2019). Habitat-dependent occupancy and movement in a migrant songbird highlights the importance of mangroves and forested lagoons in Panama and Colombia. Ecology and Evolution 19:11064–11077.

Callo, P. A., E. S. Morton, and B. J. Stutchbury (2013). Prolonged spring migration in the Red-eyed Vireo (*Vireo olivaceus*). The Auk 130:240–246.

Cárdenas-Ortiz, L., N. J. Bayly, C. J. Colorado, and K. A. Hobson (2017). Fall migration and breeding origins of Canada Warbler moving through northern Colombia. Journal of Field Ornithology 88:53–64.

Cárdenas-Ortiz, L., N. J. Bayly, K. J. Kardynal, and K. A. Hobson (2020). Defining catchment origins of a geographical bottleneck: Implications of population mixing and phenological overlap for the conservation of Neotropical migratory birds. The Condor: Ornithological Applications 122:1–13. https://doi.org/10.1093/condor/duaa004.

Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, and T. M. Palmer (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science Advances 2015:e1400253.

Chandler, R. B., D. I. King, R. Raudales, R. Trubey, C. Chandler, and C. Arce (2013). A small-scale land-sparing approach to conserving biological diversity in tropical agricultural landscapes. Conservation Biology 27:785–795.

Cimprich, D. A., F. R. Moore, and M. P. Guilfoyle (2020). Red-eyed Vireo (*Vireo olivaceus*), version 1.0. In Birds of the World

(P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.reevir1.01

Cohen, E. M., Z. Németh, T. J. Zenzal, Jr., K. L. Paxton, R. Diehl, E. H. Paxton, and F. R. Moore (2015). Spring resource phenology and timing of songbird migration across the Gulf of Mexico. In Phenological Synchrony and Bird Migration: Changing Climate and Seasonal Resources in North America (E. M. Wood and J. L. Kellermann, Editors). Studies in Avian Biology 47:63–82.

Colorado, G. J., and A. D. Rodewald (2017). Patterns of change in body condition in wintering Neotropical-Nearctic migratory birds in shaded plantations in the Andes. Agroforest Systems 91:1129–1137.

Colorado, G. J., P. B. Hamel, A. D. Rodewald, and D. Mehlman (2012). Advancing our understanding of the non-breeding distribution of Cerulean Warbler (*Setophaga cerulea*) in the Andes. Ornitología Neotropical 23 (Supplement):309–317.

Cooper, N. W., M. T. Hallworth, and P. P. Marra (2017). Light-level geolocation reveals wintering distribution, migration routes, and primary stopover locations of an endangered long-distance migratory songbird. Journal of Avian Biology 48:209–219.

Cooper, N. W., T. W. Sherry, and P. P. Marra (2015). Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. Ecology 96:1933–1942.

Cormier, R. L., D. L. Humple, T. Gardali, and N. E. Seavy (2013). Light-level geolocators reveal strong migratory connectivity and within-winter movements for a coastal California Swainson's Thrush (*Catharus ustulatus*) population. The Auk 130:283–290.

Correa Ayram, C. A., M. E. Mendoza, A. Etter, and D. R. Pérez Salicrup (2015). Habitat connectivity in biodiversity conservation: A review of recent studies and applications. Progress in Physical Geography: Earth and Environment 40:7–37.

Cuadrado, M. (1997). Why are migrant Robins (*Erithacus rubecula*) territorial in winter? The importance of the anti-predatory behaviour. Ethology Ecology and Evolution 9:77–88.

Dänhardt, J., and Å Lindström (2001). Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. Animal Behaviour 62:235–243.

Dayer, A. A., E. A. Silva-Rodríguez, S. Albert, M. Chapman, B. Zukowski, J. T. Ibarra, G. Gifford, A. Echeverri, A. Martínez-Salinas, and C. Sepúlveda-Luque (2020). Applying conservation social science to study the human dimensions of Neotropical bird conservation. The Condor: Ornithological Applications 122:1–15. https://doi.org/10.1093/condor/duaa021.

De Beenhouwer, M. R. Aerts, and O. Honnaya (2013). A global meta-analysis of the biodiversity and ecosystem service benefits of coffee and cacao agroforestry. Agriculture, Ecosystems and Environment 175:1–7.

Delmore, K. E., J. W. Fox, and D. E. Irwin (2012). Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. Proceedings of the Royal Society of London, Series B 279:4582–4589.

DeSante, D. F., D. R. Kaschube, and J. F. Saracco (2015). Vital rates of North American landbirds. The Institute for Bird Populations, Point Reyes Station, CA, USA. www.VitalRatesOfNorthAmericanLandbirds.org.

DeSante, D. F., D. R. Kaschube, and J. F. Saracco (2018). Population changes and their demographic drivers in landbirds of western North America: An assessment from the Monitoring Avian Productivity and Survivorship program. In Trends and Traditions: Avifaunal Change in Western North America (W. D. Shuford, R. E. Gill Jr., and C. M. Handel, Editors). Studies of Western Birds 3:269–293.

Diniz, F. C., J. D. Wolfe, M. Anciães and P. C. Stouffer (2014). New record of Connecticut Warbler (*Oporornis agilis*) in Central Amazonian Brazil. Cotinga 36:127–128.

Dionne, M., C. Maurice, J. Gauthier, and F. Shaffer (2008). Impact of Hurricane Wilma on migrating birds: The case of the Chimney Swift. The Wilson Journal of Ornithology 120:784–792.

Drake, A., C. A. Rock, S. P. Quinlan, M. Martin, and D. J. Greer (2014). Wind speed during migration influences the survival, timing of breeding, and productivity of a Neotropical migrant, *Setophaga Petechia*. PLoS One 9:e97152.

Drake, A., C. Rock, S. P. Quinlan, and D. J. Green (2013). Carry-over effects of winter habitat vary with age and sex in Yellow Warblers *Setophaga petechia*. Journal of Avian Biology 44:321–330.

Eliott, J. (1939). Wintering Tree Swallows at Jones Beach, fall and winter 1938 and 1939. Bird Lore 41:11–16.

Evans, M., E. Gow, R. R. Roth, M. S. Johnson, and T. J. Underwood (2020). Wood Thrush (*Hylocichla mustelina*), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.woothr.01

Faaborg, J., and W. J. Arendt (1984). Population sizes and philopatry of winter resident warblers in Puerto Rico. The Journal of Field Ornithology 55:376–378.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, et al. (2010). Conserving migratory land birds in the New World: Do we know enough? Ecological Applications 20:398–418.

Fitzpatrick, J. W. (1980). Wintering of North American Tyrant Flycatchers in the Neotropics. In Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation (A. Keast and E. S. Morton, Editors). Smithsonian Institution Press, Washington, D.C., USA. pp. 67–78.

Forrester, T. D., D. S. Casady, and H. U. Wittmer (2015). Home sweet home: Fitness consequences of site familiarity in female black-tailed deer. Behavioral Ecology and Sociobiology 69:603–612.

Fraser, K. C., A. Shave, E. de Greef, J. Siegrist, and C. J. Garroway (2019). Individual variability in migration timing can explain long-term, population-level advances in a songbird. Frontiers in Ecology and Evolution 7. https://doi.org/10.3389/fevo.2019.00324.

Fraser, K. C., B. J. Stutchbury, C. Silverio, P. M. Kramer, J. Barrow, D. Newstead, N. Mickle, B. F. Cousens, J. C. Lee, D. M. Morrison, and T. Shaheen (2012). Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. Proceedings of the Royal Society of London, Series B 279:4901–4906.

Gamble, L. R., and T. M. Bergin (2020). Western Kingbird (*Tyrannus verticalis*), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.weskin.01

Garcia, R. A., M. Cabeza, C. Rahbek, and M. B. Araújo (2014). Multiple dimensions of climate change and their implications for biodiversity. Science 344:6183.

Gómez, C., and N. J. Bayly (2010). Habitat use, abundance and persistence of Neotropical migrant birds in a habitat matrix in northeast Belize. Journal of Field Ornithology 81:237–251.

Gómez, C., E. A. Tenorio, P. Montoya, and C. D. Cadena (2016). Niche tracking migrants and niche switching residents: Evolution of climatic niches in New World warblers (Parulidae). Proceedings of the Royal Society London B 283:20152458.

Gómez, C., N. J. Bayly, D. R. Norris, S. A. Mackenzie, K. V. Rosenberg, P. D. Taylor, K. A. Hobson, and C. D. Cadena (2017). Fuel loads acquired at a stopover site influence the pace of intercontinental migration in a boreal songbird. Scientific Reports 7:3405.

Gómez, C., S. L. Guerrero, A. M. FitzGerald, N. J. Bayly, K. A. Hobson, and C. D. Cadena (2019). Range-wide populations of a long-distance migratory songbird converge during stopover in the tropics. Ecological Monographs 89:e01349.

Gómez, C., V. Gómez-Bahamón, L. Cárdenas-Ortiz, and N. J. Bayly (2015). Distribution of Nearctic–Neotropical migratory birds along a South American elevation gradient during spring migration. The Wilson Journal of Ornithology 127:72–86.

González-Prieto, A. M. (2018a). Conservation of Neotropical migrants: The coffee connection revisited. Avian Conservation and Ecology 13:19. https://doi.org/10.5751/ACE-01223-130119.

González-Prieto, A. M. (2018b). The relative importance of native forest and shade-grown coffee plantations for habitat use, individual fitness and migration strategies of overwintering Neotropical migrant songbirds in Colombia. Ph.D. thesis, College of Graduate and Postdoctoral Studies, Department of Biology. University of Saskatchewan, Saskatoon, Canada.

González-Prieto, A. M., and K. A. Hobson (2013). Environmental conditions on wintering grounds and during migration influence spring nutritional condition and arrival phenology of Neotropical migrants at a northern stopover site. Journal of Ornithology 154:1067–1078.

Gonzalez-Prieto, A. M., N. J. Bayly, G. J. Colorado, and K. A. Hobson (2016). The topography of the Andes mountains shapes the wintering distribution of a migratory bird. Diversity and Distributions 23:118–129.

Greenberg, R. (1995). Insectivorous migratory birds in tropical ecosystems: The breeding currency hypothesis. Journal of Avian Biology 26:260–264.

Greenwood, P. J., and P. H. Harvey (1982). The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13:1–21.

Hallworth, M. T., T. S. Sillett, S. L. Van Wilgenburg, K. A. Hobson, and P. P. Marra (2015). Migratory connectivity of a Neotropical migratory songbird revealed by archival light-level geolocators. Ecological Applications 25:336–347.

Heckscher, C. M., L. R. Bevier, A. F. Poole, W. Moskoff, P. Pyle, and M. A. Patten (2020). Veery (*Catharus fuscescens*), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.veery.01.

Hedenström, A. (2008). Adaptations to migration in birds: Behavioural strategies, morphology and scaling effects. Philosophical Transactions of the Royal Society of London 363:287–99.

Hill, J. R. (1993). A Giant Martin roost on the Amazon River. Purple Martin Update 4:5–7.

Hilty, S. L. (1980). Flowering and fruiting periodicity in a premontane rainforest in Pacific Colombia. Biotropica 12:292–306.

Hobson, K. A. , and K. J. Kardynal (2015). Western Veeries use an eastern shortest-distance pathway: New insights to migration routes and phenology using light-level geolocators. The Auk: Ornithological Advances 132:540–550.

Hobson, K. A., K. J. Kardynal, S. L. Van Wilgenburg, G. Albrecht, A. Salvadori, M. D. Cadman, F. Liechti, and J. W. Fox (2015a). A continent-wide migratory divide in North American breeding Barn Swallows (*Hirundo rustica*). PloS One 10:e0129340.

Hobson, K. A., S. L. Van Wilgenburg, E. H. Dunn, D. J. T. Hussell, P. D. Taylor, and D. M. Collister (2015b). Predicting origins of passerines migrating through Canadian migration monitoring stations using stable-hydrogen isotope analyses of feathers: A new tool for bird conservation. Avian Conservation and Ecology 10:3. http://dx.doi.org/10.5751/ACE-00719-100103.

Hobson, K. A., S. L. Van Wilgenburg, A. M. Roth, R. E. Bennett, N. J. Bayly, L. Chavarría-Duriaux, G. J. Colorado, P. Elizondo, C. G. Rengifo, and J. D. Ritterson (2016). Golden-winged Warbler migratory connectivity derived from stable isotopes. In Golden-winged Warbler Ecology, Conservation, and Habitat Management (H. M. Streby, D. E. Andersen, and D. A. Buehler, Editors). Studies in Avian Biology (no. 49), CRC Press, Boca Raton, FL, USA 193–203.

Hostetler, J. A., T. S. Sillett, and P. P. Marra (2015). Full-annual-cycle population models for migratory birds. The Auk: Ornithological Advances 132:433–449.

Hughes, J. M. (2020). Yellow-billed Cuckoo (*Coccyzus americanus*), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.yebcuc.01.

Imlay, T. L., F. A. Angelier, K. A. Hobson, G. Mastromonaco, S. Saldanha, and M. L. Leonard (2019). Multiple intrinsic markers identify carry-over effects from wintering to breeding sites for three Nearctic–Neotropical migrant swallows. The Auk: Ornithological Advances 136:1–15.

Intergovernmental Panel on Climate Change (IPCC) (2014). Climate change 2014: Synthesis report. Contribution of working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Jahn, A. E., V. R. Cueto, J. W. Fox, M. S. Husak, D. H. Kim, D. V. Landoll, J. P. Ledezma, H. K. Lepage, D. J. Levey, M. T. Murphy, et al. (2013). Migration timing and wintering areas of three species of flycatchers (*Tyrannus*) breeding in the Great Plains of North America. The Auk 130:247–257.

Johnson, M. D. (2007). Measuring habitat quality: A review. The Condor 109:489–504.

Johnson, M. D., A. M. Strong, and T. W. Sherry (2006b). Migrants in tropical bird communities: The Balanced Breeding Limitation hypothesis. Journal of Avian Biology 37:229–237.

Johnson, M. D., and T. W. Sherry (2001). Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. Journal of Animal Ecology 70:546–560.

Johnson, M. D., T. W. Sherry, A. M. Strong, and A. Medori (2005). Migrants in Neotropical bird communities: An assessment of the breeding currency hypothesis. Journal of Animal Ecology 74:333–341.

Johnson, M. D., T. W. Sherry, R. T. Holmes, and P. P. Marra (2006a). Assessing habitat quality for a wintering songbird in natural and agricultural areas. Conservation Biology 20:1433–1444.

Johnson, T. B. (1980). Resident and North American migrant bird interactions in the Santa Marta highlands, northern Colombia. In Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation (A. Keast and E. S. Morton, Editors). Smithsonian Institution Press, Washington, D.C., USA. pp. 239–247.

Komar, O. (2006). Ecology and conservation of birds in coffee plantations: A critical review. Bird Conservation International 16:1–23.

Koronkiewicz, T. J., M. K. Sogge, C. Van Riper, and E. H. Paxton (2006). Territoriality, site fidelity, and survivorship of Willow Flycatchers wintering in Costa Rica. The Condor 108:558–570.

Kramer, G. R., D. E. Andersen, D. A. Buehler, P. B. Wood, S. M. Peterson, J. A. Lehman, K. R. Aldinger, L. P. Bulluck, S. Harding, J. A. Jones, J. P. et al. (2018). Population trends in Vermivora warblers are linked to strong migratory connectivity Proceedings of the National Academy of Sciences USA 115:E3192–E3200.

Kramer, G. R., H. M. Streby, S. M. Peterson, J. A. Lehman, D. A. Buehler, P. B. Wood, D. J. McNeil, J. L. Larkin, and D. E. Andersen (2017). Nonbreeding isolation and population-specific migration patterns among three populations of Golden-winged Warblers. The Condor: Ornithological Applications 119:108–121.

Kresnik, R. J., and B. J. M. Stutchbury (2014). Space-use strategies of wintering Ovenbirds in Belize: Causes and consequences. Journal of Field Ornithology 85:274–288.

La Sorte, F. A., and D. Fink (2017). Migration distance, ecological barriers and en-route variation in the migratory behaviour of terrestrial bird populations. Global Ecology and Biogeography 26:216–227.

La Sorte, F. A., D. Fink, P. J. Blancher, A. D. Rodewald, V. Ruiz-Gutierrez, K. V. Rosenberg, W. M. Hochachka, P. H. Verburg, and S. Kelling (2017). Global change and the distributional dynamics of migratory bird populations wintering in Central America. Global Change Biology 23:5284–5296.

La Sorte, F. A., D. Fink, W. M. Hochachka, and S. Kelling (2016a). Convergence of broad-scale migration strategies in terrestrial birds. Proceedings of the Royal Society B 283:20152588.

La Sorte, F. A., W. M. Hochachka, A. Farnsworth, A. A. Dhondt, and D. Sheldon (2016b). The implications of mid-latitude climate extremes for North American migratory bird populations. Ecosphere 7:e01261.

Lamanna, J. A., T. L. George, J. F. Saracco, M. P. Nott, and D. F. DeSante (2012). El Niño-Southern Oscillation influences annual survival of a migratory songbird at a regional scale. The Auk 129:734–743.

Langham, G. M., J. G. Schuetz, T. Distler T, C. U. Soykan, and C. Wilsey (2015). Conservation status of North American birds in the face of future climate change. PLoS One 10:e0135350.

Latta, S. C., and J. Faaborg (2002). Demographic and population responses of Cape May Warblers wintering in multiple habitats. Ecology 83:2502–2515.

Lefebvre, G., B. Poulin, and R. McNeil (1992). Abundance, feeding behavior, and body condition of Nearctic warblers wintering in Venezuelan mangroves. The Wilson Bulletin 104:400–412.

Longcore, T., C. Rich, P. Mineau, B. MacDonald, D. G. Bert, L. M. Sullivan, E. Mutrie, S. A. Gauthreaux, Jr., M. L. Avery, R. L. Crawford, et al. (2013). Avian mortality at communication towers in the United States and Canada: Which species, how many, and where? Biological Conservation 158:410–419.

Mack, D. E., and W. Yong (2020). Swainson's Thrush (*Catharus ustulatus*), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.swathr.01.

Mallord, J. W., C. J. Orsman, A. Cristinacce, T. J. Stowe, E. C. Charman, and R. D. Gregory (2017). Diet flexibility in a declining long-distance migrant may allow it to escape the consequences of phenological mismatch with its caterpillar food supply. Ibis 159:76–90.

Malpica, A., S. Covarrubias, R. Villegas-Patraca, L. Herrera-Alsina (2017). Ecomorphological structure of avian communities' changes upon arrival of wintering species. Basic and Applied Ecology 24:60–67.

Marra, P. P. (2000). The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. Behavioral Ecology 11:299–308.

Marra, P. P., and R. L. L. Holberton (1998). Corticosterone levels as indicators of habitat quality: Effects of habitat segregation in a migratory bird during the non-breeding season. Oecologia 116:284–292.

Marra, P. P., and R. T. Holmes (2001). Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. The Auk 118:92–104.

Marra, P. P., T. W. Sherry, and R. T. Holmes (1993). Territorial exclusion by a long-distance migrant warbler in Jamaica: A removal experiment with American Redstarts (*Setophaga Ruticilla*). The Auk 110:565–572.

McDermott, M. E., and A. D. Rodewald (2014). Conservation value of silvopastures to Neotropical migrants in Andean forest flocks. Biological Conservation 175:140–147.

McFarland, K. P., C. C. Rimmer, J. E. Goetz, Y. Aubry, J. M. Wunderle, Jr., A. Sutton, J. M. Townsend, A. Llanes Sosa, and A. Kirkconnell (2013). A winter distribution model for Bicknell's Thrush (*Catharus bicknelli*): A conservation tool for a threatened migratory songbird. PLoS One 8:e53986.

McKellar, A. E., P. P. Marra, S. J. Hannon, C. E. Studds, and L. M. Ratcliffe (2013). Winter rainfall predicts phenology in widely separated populations of a migrant songbird. Oecologia 172:595–605.

McKinnon E. A., C. Q. Stanley, and B. J. M. Stutchbury (2015). Carry-over effects of nonbreeding habitat on start-to-finish spring migration performance of a songbird. PLoS One 10:e0141580.

McKinnon, E. A., K. C. Fraser, and B. J. Stutchbury (2013). New discoveries in landbird migration using geolocators, and a flight plan for the future. The Auk 130:211–222.

McWilliams, S. R., and W. H. Karasov (2014). Spare capacity and phenotypic flexibility in the digestive system of a migratory bird: Defining the limits of animal design. Proceedings of the Royal Society B 281:20140308.

Melaas, E. K., D. Sulla-Menashe, and M. A. Friedl (2018). Multidecadal changes and interannual variation in springtime phenology of North American temperate and boreal deciduous forests. Geophysical Research Letters 45:2679–2687.

Mendoza, I., C. A. Peres, and L. P. C. Morellato (2017). Continental-scale patterns and climatic drivers of fruiting phenology: A quantitative Neotropical review. Global and Planetary Change 148:227–241.

Merrick, T., S. Pau, M. L. S. P. Jorge, T. S. F. Silva, and R. Bennartz (2019). Spatiotemporal patterns and phenology of tropical vegetation solar-induced chlorophyll fluorescence across Brazilian biomes using satellite observations. Remote Sensing 11:1746. https://doi.org/10.3390/rs11151746.

Molleman, F., T. Remmel, and K. Sam (2016). Phenology of predation on insects in a tropical forest: Temporal variation in attack rate on dummy caterpillars. Biotropica 48:229–236.

Narango, D. L., D. W. Tallamy, K. J. Snyder, and R. A. Rice (2019). Canopy tree preference by insectivorous birds in shade-coffee farms: Implications for migratory bird conservation. Biotropica 51:387–398.

Newton, I. (2008). The Migration Ecology of Birds. Elsevier, London, UK.
Norris, D. R., P. P. Marra, G. J. Bowen, L. M. Ratcliffe, J. A. Royle, and T. K. Kyser (2006). Migratory connectivity of a widely distributed songbird, the American Redstart (*Setophaga ruticilla*). Ornithological Monographs 61:14–28.
Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society B 271:59–64.
Norris, D. R., and C. M. Taylor (2006). Predicting the consequences of carry-over effects for migratory populations. Biology Letters 2:148–151.
O'Connor, C. M., and S. J. Cooke (2015). Ecological carry-over effects complicate conservation. Ambio 44:582–591.
Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology 13:1860–1872.
Parrish, J. D., and T. W. Sherry (1994). Sexual habitat segregation by American Redstarts wintering in Jamaica: Importance of resource seasonality. The Auk 111:38–49.
Paxton, K. L., and F. R. Moore (2015). Carry-over effects of winter habitat quality on en route timing and condition of a migratory passerine during spring migration. The Journal of Avian Biology 46:495–506.
Peele, A. M. (2015). Population regulation of a long-distance migratory bird population in the non-breeding season: a test of buffer and crowding effects. Ph.D. dissertation, Tulane University, New Orleans, LA, USA.
Peele, A. M., P. P. Marra, T. S. Sillett, and T. W. Sherry (2015). Combining survey methods to estimate abundance and transience of birds among tropical non-breeding habitats. The Auk: Ornithological Advances 132:926–937.
Perfecto, I. R., A. Rice, R. Greenberg, and M. van der Voort (1996). Shade coffee: A disappearing refuge for biodiversity. BioScience 46:598–608.
Post, W. (1978). Social and foraging behavior of warblers wintering in Puerto Rican coastal scrub. The Wilson Bulletin 90:197–214.
Pyle, P. (1997). Identification Guide to North American Birds: Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA, USA.
Pyle, P., J. F. Saracco, and D. F. DeSante (2018). Evidence of widespread movements from breeding to molting grounds by North American landbirds. The Auk: Ornithological Advances 135:506–520.
Rappole J. H., D. I. King, and J. Diez (2003). Winter- vs. breeding-habitat limitation for an endangered avian migrant. Ecological Applications 13:735–742.
Rappole, J. H., and D. W. Warner (1980). Ecological aspects of migrant bird behavior in Veracruz, Mexico. In Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation (A. Keast and E. S. Morton, Editors). Smithsonian Institution Press, Washington, D.C., USA. pp. 353–393.
Rappole, J. H., D. I. King, and J. H. V. Rivera (2003). Coffee and conservation. Conservation Biology 17:334–336.
Rappole, J. H., M. A. Ramos, and K. Winker (1989). Wintering Wood Thrush movements and mortality in southern Veracruz. The Auk 106:402–410.
Rappole, J., King, D. and P. Leimgruber (2000). Winter habitat and distribution of the endangered Golden-cheeked Warbler (*Dendroica chrysoparia*). Animal Conservation 3:45–59.
Regosin, J. V. (2020). Scissor-tailed Flycatcher (*Tyrannus forficatus*), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.sctfly.01.
Remsen, Jr., J. V. (2001). True wintering range of the Veery (*Catharus fuscescens*): Lessons for determining winter ranges of species that winter in the tropics. The Auk 118:838–848.
Renfrew, R. B., D. Kim, N. Perlut, J. Smith., J. Fox, and P. P. Marra (2013). Phenological matching across hemispheres in a long-distance migratory bird. Diversity and Distributions 19:1008–1019.
Renfrew, R. B., S. J. Frey, and J. Klavins (2011). Phenology and sequence of the complete prealternate molt of Bobolinks in South America. The Journal of Field Ornithology 82:101–113.
Renfrew, R., A. M. Strong, N. G. Perlut, S. G. Martin, and T. A. Gavin (2020). Bobolink (*Dolichonyx oryzivorus*), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.boboli.01.
Reudink M. W., P. P. Marra, T. K. Kyser, P. T. Boag, K. M. Langin, and L. M. Ratcliffe (2009). Non-breeding season events influence sexual selection in a long-distance migratory bird. Proceedings of the Royal Society B 276:1619–1626.
Reynolds, M. D., B. L. Sullivan, E. Hallstein, S. Matsumoto, S. Kelling, M. Merrifield, D. Fink, A. Johnston, W. M. Hochachka, N. E. Bruns, et al. (2017). Dynamic conservation for migratory species. Science Advances 3:e1700707.
Ricklefs, R. E., and D. B. Miles (1994). Ecological and evolutionary inferences from morphology: An ecological perspective. In Ecological Morphology: Integrative Organismal Biology (P. Wainwright, and S. Reilly, Editors). The University of Chicago Press. Chicago, IL, USA. pp. 13–41.
Ricklefs, R. E., and D. Schluter (Editors) (1993). Species Diversity in Ecological Communities: Historical and Geographical Perspectives. The University of Chicago Press, Chicago, IL, USA.
Robinson, S., J. Fitzpatrick, and J. Terborgh (1995). Distribution and habitat use of Neotropical migrant landbirds in the Amazon Basin and Andes. Bird Conservation International 5:305–323.
Rockwell, S. M., C. I. Bocetti, and P. P. Marra (2012). Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's Warbler (*Setophaga kirtlandii*). The Auk 129:744–752.
Rockwell, S. M., Wunderle, J. M., Sillett, T. S., Bocetti, C. I., Ewert, D. N., Currie, J. D. White, and P. P. Marra (2017). Seasonal survival estimation for a long-distance migratory bird and the influence of winter precipitation. Oecologia 183:715–726.
Rodríguez-Eraso, N., D. Armenteras-Pascual, and J. Retana-Alumbreros (2013). Land use and land cover change in the Colombian Andes: Dynamics and future scenarios. Journal of Land Use Science 8:154–174.
Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra (2019). Decline of the North American avifauna. Science 366:120–124.
Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, et al. (2016). Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States. Partners in Flight Science Committee. https://partnersinflight.org/resources/the-plan/.

Ruegg, K. C., E. A. Anderson, R. J. Harrigan, K. L. Paxton, J. Kelly, F. Moore, and T. B. Smith (2016). Genetic assignment with isotopes and habitat suitability (gaiah), a migratory bird case study. Methods in Ecology and Evolution 8:1241–1252.

Ruegg, K. C., E. C. Anderson, K. L. Paxton, V. Apkenas, S. Lao, R. B. Siegel, D. F. DeSante, F. Moore, and T. B. Smith (2014). Mapping migration in a songbird using high-resolution genetic markers. Molecular Ecology 23:5726–5739.

Ruegg, K. C., R. J. Harrigan, J. F. Saracco, T. B. Smith, and C. M. Taylor (2020). A genoscape-network model for conservation prioritization in a migratory bird. Conservation Biology. In press. doi: 10.1111/cobi.13536.

Ruiz-Gutierrez, V., W. L. Kendall, J. F. Saracco, and G. C. White (2016). Overwintering strategies of migratory birds: A novel approach for estimating seasonal movement patterns of residents and transients. The Journal of Applied Ecology 53:1035–1045.

Ruiz-Sánchez, A., K. Renton, and R. Rueda-Hernández (2017). Winter habitat disturbance influences density and territory size of a Neotropical migratory warbler. Journal of Ornithology 158:63–73.

Runge, C. A., J. E. M. Watson, S. H. M. Butchart, J. O. Hanson, H. P. Possingham, and R. A. Fuller (2015). Protected areas and global conservation of migratory birds. Science 350:1255–1258.

Runge, M. C., and P. P. Marra (2005). Modeling seasonal interactions in the population dynamics of migratory birds. In Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Editors). Smithsonian Institution Press, Washington, D.C., USA. pp. 275–289.

Rushing, C. S., T. B. Ryder, and P. P. Marra (2016). Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. Proceedings of the Royal Society B 283:1823.

Ryder, T. B., J. W. Fox, and P. P. Marra (2011). Estimating migratory connectivity of Gray Catbirds (*Dumetella carolinensis*) using geolocator and mark–recapture data. The Auk 128:448–453.

Saino, N., T. Szép, M. Romano, D. Rubolini, F. Spina, and A. P. Møller (2004). Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. Ecology Letters 7:21–25.

Saracco, J. F., D. F. DeSante, M. P. Nott, and D. R. Kaschube (2009). Using the MAPS and MoSI Programs to monitor landbirds and inform conservation. In Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics (T. D. Rich, C. D. Thompson, D. Demarest, and C. Arizmendi, Editors). University of Texas-Pan American Press, TX, USA. pp. 651–658.

Schroth, G., and C. A. Harvey (2007). Biodiversity conservation in cocoa production landscapes: An overview. Biodiversity Conservation 16:2237–2244.

Sechrist, J. D., E. H. Paxton, D. D. Ahlers, R. H. Doster, and V. M. Ryan (2012). One year of migration data for a Western Yellow-billed Cuckoo. Western Birds 43:2–11.

Şekercioğlu, Ç. H., P. R. Ehrglich, G. C. Daily, D. Aygen, D. Goehring, and R. F. Sandí. (2002). Disappearance of insectivorous birds from tropical forest fragments. Proceedings of the National Academy of Sciences USA 99:263–267.

Sekercioglu, C. H. (2006). Increasing awareness of avian ecological function. Trends in Ecology & Evolution 21:464–471.

Sheehy, J., C. M. Taylor, K. S. McCann, and D. R. Norris (2010). Optimal conservation planning for migratory animals: Integrating demographic information across seasons. Conservation Letters 3:192–202.

Sherry, T. W., and R. T. Holmes (1995). Summer versus winter limitation of populations: What are the issues and what is the evidence. In Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues (T. E. Martin and D. M. Finch, Editors). Oxford University Press, New York, NY, USA. pp. 85–120.

Sherry, T. W., and R. T. Holmes (1996). Winter habitat quality, population limitation, and conservation of Neotropical–Nearctic migrant birds. Ecology 77:36–48.

Sherry, T. W., D. S. Wilson, C. S. Hunter, and R. T. Holmes (2015). Impacts of nest predators and weather on reproductive success and population limitation in a long-distance migratory bird. Journal of Avian Biology 46:559–569.

Sherry, T. W., M. D. Johnson, K. Williams, J. Kaban, C. McAvoy, A. Medori, S. Rainey, and S. Xu (2016). Dietary opportunism, resource partitioning, and consumption of coffee-berry borers by five migratory wood warblers (Parulidae) wintering in Jamaican shade coffee plantations. Journal of Field Ornithology 87:273–292.

Sherry, T. W., R. T. Holmes, P. Pyle, and M. A. Patten (2020). American Redstart *(Setophaga ruticilla)*, version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.amered.01.

Sillett, T. S., and R. T. Holmes (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Sillett, T. S., R. T. Holmes, and T. W. Sherry (2000). Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040–2042.

Skrip, M. M., N. P. Seeram, T. Yuan, H. Ma, and S. R. McWilliams (2016). Dietary antioxidants and flight exercise in female birds affect allocation of nutrients to eggs: How carry-over effects work. The Journal of Experimental Biology 219:2716–2725.

Smith, J. A. M., L.R. Reitsma, and P. P. Marra (2010). Moisture as a determinant of habitat quality for a nonbreeding Neotropical migratory songbird. Ecology 91:2874–2882.

Somveille, M., A. S. L. Rodrigues, and A. Manica (2018). Energy efficiency drives the global seasonal distribution of birds. Nature Ecology and Evolution 2:962–969.

Spiller, K. J., and R. Dettmers (2019). Evidence for multiple drivers of aerial insectivore declines in North America. The Condor: Ornithological Applications 121:1–13. https://doi.org/10.1093/condor/duz010.

Staggemeier, V. G., M. G. G. Camargo, J. A. F. Diniz-Filho, R. Freckleton, L. Jardim, and L. P. C. Morellato (2019). The circular nature of recurrent life cycle events: A test comparing tropical and temperate phenology. Journal of Ecology 108:393–404.

Stamps, J. A., V. V. Krishnan, and M. L. Reid (2005). Search costs and habitat selection by dispersers. Ecology 86:510–518.

Stanley, C. Q., M. MacPherson, K. C. Fraser, E. A. McKinnon, and B. J. Stutchbury (2012). Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. PloS One 7:e40688.

Stouffer, P. C., R. O. Bierregaard, C. Strong, and T. E. Lovejoy (2006). Long-term landscape change and bird abundance in Amazonian rainforest fragments. Conservation Biology 20:1212–1223.

Strong, A. M., and T. W. Sherry (2000). Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. Journal of Animal Ecology 69:883–895.

Studds, C. E., and P. P. Marra (2005). Nonbreeding habitat occupancy and population processes: An upgrade experiment with a migratory bird. Ecology 86:2380–2385.
Studds, C. E., and P. P. Marra (2007). Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. Climate Research 35:115.
Studds, C. E., and P. P. Marra (2011). Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. Proceedings of the Royal Society of London Series B 278:3437–3443.
Sullivan, B. L., T. Phillips, A. A. Dayer, C. L. Wood, A. Farnsworth, M. J. Iliff, I. J. Davies, A. Wiggins, D. Fink, W. M. Hochachka, et al. (2017). Using open access observational data for conservation action: A case study for birds. Biological Conservation 208:5–14.
Sykes, P. W., Jr., and M. H. Clench (1998). Winter habitat of Kirtland's Warbler: An endangered Nearctic/Neotropical migrant. The Wilson Bulletin 110:244–261.
Taylor, C. M., and B. J. M. Stutchbury (2016). Effects of breeding versus winter habitat loss and fragmentation on the population dynamics of a migratory songbird. Ecological Applications 26:424–437.
Taylor, P. D., T. L. Crewe, S. A. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. M. Francis, C. G. Guglielmo, D. J. Hamilton, R. L. et al. (2017). The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12:8. https://doi.org/10.5751/ACE-00953-120108.
Toms, J. D. (2011). Non-breeding competition between migrant American Redstarts (*Setophaga ruticilla*) and resident Adelaide's Warblers (*Dendroica adelaidae*) in the Guánica Biosphere Reserve, Southwest Puerto Rico. Ph.D. Thesis, University of Missouri, Columbia, MO, USA.
U.S. Fish and Wildlife Service (2000). Neotropical Migratory Bird Conservation Act of 2000. P.L. 106–247.
Valdez-Juárez, S. O., A. Drake, K. J. Kardynal, K. A. Hobson, E. A. Krebs, and D. J. Green (2018). Use of natural and anthropogenic land cover by wintering Yellow Warblers: The influence of sex and breeding origin. The Condor: Ornithological Applications 120:427–438.
van Schaik, C. P., J. W. Terborgh, and S. J. Wright (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. Annual Review of Ecology and Systematics 24:353–377.
Vickery, P. D., P. L. Tubaro, J.M. Cardoso da Silva, B. G. Peterjohn, J. R. Herkert, and R. B. Cavalcanti (1999). Conservation of grassland birds in the Western Hemisphere. In Ecology and Conservation of Grassland Birds of the Western Hemisphere (P. D. Vickery and James R. Herkert, Editors). Studies in Avian Biology 19:2–26.
Visco, D. M., N. L. Michel, A. W. Boyle, B. J. Sigel, S. Woltmann, and T. W. Sherry (2015). Patterns and causes of understory bird declines from human-disturbed tropical forest landscapes: A case study from Central America. Biological Conservation 191:117–129.
Visser, M. E., and C. Both (2005). Shifts in phenology due to global climate change: The need for a yardstick. Proceedings of the Royal Society of London B 272:2561–2569.
Visser, M. E., and P. Gienapp (2019). Evolutionary and demographic consequences of phenological mismatches. Nature Ecology & Evolution 3:879–885.
Welton, M. J., D. L. Anderson, G. J. Colorado, P. B. Hamel, and D. Calderón-F (2012). Spring migration stopover by Cerulean Warblers in northern Middle America. Ornitológia Neotropical 23:289–305.
Wikelski, M., R. W. Kays, N. J. Kasdin, K. Thorup, J. A. Smith, and G. W. Swenson, Jr. (2007). Going wild: What a global small-animal tracking system could do for experimental biologists. Journal of Experimental Biology 210:181–186.
Wilson, S., J. F. Saracco, R. Krikun, D. T. T. Flockhart, C. Godwin, and K. R. Foster (2018). Drivers of demographic decline across the annual cycle of a threatened migratory bird. Scientific Reports 8.
Wilson, S., S. L. LaDeau, A. P. Tøttrup, and P. P. Marra (2011). Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. Ecology 92:1789–1798.
Winker, K., J. H. Rappole, and M. A. Ramos (1990). Population dynamics of the Wood Thrush in southern Veracruz, Mexico. The Condor 92:444–460.
Wolfe, J. D., and E. I. Johnson (2015). Geolocator reveals migratory and winter movements of a Prothonotary Warbler. Journal of Field Ornithology 86:238–243.
Wolfe, J. D., M. D. Johnson, and C. J. Ralph (2013). Greater mass increases annual survival of Prothonotary Warblers wintering in northeastern Costa Rica. The Condor 115:163–167.
Wolfe, J. D., M. D. Johnson, and C. J. Ralph (2014). Do birds select habitat or food resources? Nearctic–Neotropic migrants in northeastern Costa Rica. PloS One 9:e86221.
Wolfe, J. D., P. C. Stouffer, K. Mokross, L. L. Powell, and M. M. Anciães (2015). Island vs. countryside biogeography: An examination of how Amazonian birds respond to forest clearing and fragmentation. Ecosphere 6:1–14.
Wunderle, J. M. Jr. (1995). Population characteristics of Black-throated Blue Warblers wintering in three sites on Puerto Rico. The Auk 112:931–946.
Wunderle, J. M. Jr. (2017). Effects of hurricanes Irma and Maria on birds in the Fajardo Christmas bird count in northeastern Puerto Rico: A preliminary assessment. Acta Científica 31:18–33.
Wunderle, J. M. Jr., and W. J. Arendt (2017). The plight of migrant birds wintering in the Caribbean: Rainfall effects in the annual cycle. Forests 8:115.
Wunderle, J. M. Jr., P. K. Lebow, J. D. White, D. Currie, and D. N. Ewert (2014). Sex and age differences in site fidelity, food resource tracking, and body condition of wintering Kirtland's Warblers (*Setophaga kirtlandii*) in the Bahamas. Ornithological Monographs 80:1–62.