

An overview of the drivers of performance in nonbreeding Nearctic–Neotropical migratory songbirds

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ABSTRACT

Developing conservation and recovery strategies for Nearctic–Neotropical migratory songbirds requires key research because population-limiting factors remain unknown for many species. In particular, the stationary nonbreeding period (sometimes referred to as overwintering) encompasses 6–8 months of the full annual cycle. We conducted a systematic review to assess what is known about the factors that influence individual-level performance (i.e., fitness proxies or indicators of self-maintenance) of Nearctic–Neotropical migratory songbirds during the stationary nonbreeding period. We focused on the metrics of apparent survival, persistence, and body condition (mass-related) indices. We found that 51 of 125 migratory Passeriformes species' performance has been studied in 57 studies during the nonbreeding period. However, most species appear in only one study; thus, knowledge is skewed toward 3 species appearing in ≥ 10 studies. Body condition indices were the most studied group of metrics and apparent survival was the least studied. Habitat type, food availability, and precipitation were studied much more than other drivers, such as disease and predation. The most studied driver of nonbreeding performance was habitat type. Evidence was found among these studies that suggest that natural habitat types, wetter habitats or precipitation, and high availability of food may positively influence body condition, apparent survival, and persistence. Significant knowledge gaps remain that, if filled, could inform conservation strategies, especially for 59.2% of Passeriformes that are Nearctic–Neotropical migratory species and for areas of the nonbreeding range.

Keywords: landbirds, long-distance migrants, migration ecology, Nearctic–Neotropical migration, Passeriformes

How to Cite

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LAY SUMMARY

- Research is needed in all phases of the full annual cycle to conserve migratory songbirds. The nonbreeding periods (stationary nonbreeding or overwintering, and migration) are less studied than other phases despite being a significant portion of a migrant's full annual cycle and frequently implicated as the critical phase.
- We conducted a systematic review to summarize research on what influences migratory songbirds' condition and survival (collectively called performance) during the nonbreeding (excluding pre-breeding and post-breeding migrations) period.
- Our systematic review has provided insight into how environmental drivers may influence performance but revealed that almost half of all Nearctic–Neotropical songbirds lack a study on performance during the nonbreeding phase. There is an opportunity to understand better the roles of disease, predation, climate and landscapes' change on performance to link it to full annual cycle population dynamics.

Una visión general de los factores que influyen sobre el desempeño de las aves Passeriformes neártico-neotropicales durante el período no reproductivo

RESUMEN

Las estrategias de conservación de las aves Passeriformes migratorias neártico-neotropicales requieren de investigaciones puntuales, ya que para varias especies aún se desconocen los factores que limitan a sus poblaciones. En particular, el período estacionario, no reproductivo (conocido como de invernada o invernación) abarca de seis a ocho meses del ciclo anual completo. Llevamos a cabo una revisión bibliográfica, sistemática, para resumir el conocimiento sobre los factores que influyen en el desempeño a nivel individual (indicadores de aptitud biológica o de auto mantenimiento) de las aves Passeriformes, migratorias neárticas-neotropicales, durante el período no reproductivo. Nos centramos en las medidas de supervivencia aparente, permanencia e índices de condición corporal relacionados con la masa. Encontramos que el desempeño de 51 de 125 especies Passeriformes migratorias se evaluó en 57 estudios durante el periodo no reproductivo. Sin embargo, la mayoría de las especies sólo aparecen en un estudio, por lo que el conocimiento está sesgado hacia tres especies que aparecen en 10 o más estudios. Los índices de condición corporal fueron el grupo de medidas más estudiado y la supervivencia aparente el menos estudiado. El tipo de cobertura

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vegetal, la disponibilidad de alimento y precipitación se estudiaron mucho más que otros factores como las enfermedades y la depredación. El factor más estudiado del desempeño no reproductivo fue la cobertura vegetal. Entre algunos de estos estudios se sugiere que los tipos de cobertura vegetal nativos, los hábitats más húmedos o las precipitaciones y la alta disponibilidad de alimento pueden influir positivamente en la condición corporal, la supervivencia aparente y la permanencia. Aún existen vacíos de información importantes que, de comprenderse, podrían informar las estrategias de conservación, especialmente para el 59.2% de Passeriformes que son especies migratorias neártico-neotropicales y para las zonas del área no-reproductiva que requieren más estudio.

Palabras clave: Aves terrestres, Aves migratorias de larga distancia, Ecología de Migración, Passeriformes

INTRODUCTION

There are ~250 Nearctic–Neotropical migratory land birds that are long-distance travelers, conducting spectacular journeys to and from their breeding areas annually (Newton 2007). Of these, 125 species belong to the Order Passeriformes and are considered Nearctic–Neotropical migratory songbirds (Partners in Flight 2021). From the 1990s until recent years (~2010s), one motivator for research is the population declines reported for many species (Finch 1991, Rosenberg et al. 2019). The steepest declines of bird populations for the avifauna breeding in North America were reported among Passerine families such as Passerellidae (New World Sparrows), Parulidae (New World Wood Warblers), and Icteridae (New World Blackbirds) with high proportions (67–87%) of species in these families in decline (Rosenberg et al. 2019). To understand and counter these declines, the species' Full Annual Cycle (hereafter “annual cycle”) must be studied (Rosenberg et al. 2016).

The annual cycle of migratory birds can be divided into 4 phases or periods: 2 migratory periods, pre-breeding and post-breeding migration; and 2 stationary periods, breeding and nonbreeding. Throughout this work, we use the term “nonbreeding” to refer to the stationary nonbreeding period, although we note that nonbreeding can be used to refer to the 2 migration periods as well as the stationary nonbreeding period (Albert and Siegel 2023). We also note that the use of the term “stationary” as a qualifier can be misleading since many species move long distances during this phase (Rappole et al. 1989, Ruiz-Gutierrez et al. 2016, Knight et al. 2019). In other work, the stationary nonbreeding period is often referred to as “winter” or “overwintering,” but these terms comprise a temperate zone bias, because it is not winter in the tropical nonbreeding ranges during the months when the birds are present (Albert and Siegel 2023).

Nearctic–Neotropical migratory songbirds experience threats in multiple phases of their annual cycle as well as carry-over effects, where processes in one phase can influence the next (Harrison et al. 2011). Major threats to songbird populations include climate change (Robinson et al. 2009), habitat loss and degradation, collisions, predation by outdoor cats (Rosenberg et al. 2016), and pesticides (Eng et al. 2019). For many migratory songbird species, we lack basic knowledge of some stages of their annual cycle, hindering our ability to develop effective conservation strategies or our capacity to fit informative, full annual cycle population models (Hostetler et al. 2015, Taylor and Stutchbury 2016). One period within the annual cycle that is particularly lacking in research is the nonbreeding period (Marra et al. 2015a).

The nonbreeding phase for migratory songbirds can last for 6–8 months of the annual cycle (Albert et al. 2020) and has been identified as a population-limiting phase for some species (Rappole and McDonald 1994, Sherry and Holmes 1996, Taylor and Stutchbury 2016). Studies conducted in the nonbreeding phase have shown how carry-over effects may

affect pre-breeding migration success when individuals cannot obtain sufficient resources to prepare adequately for the journey (Rushing et al. 2017), sometimes leading to lower reproductive success due to later arrival or arrival in poorer condition on the breeding grounds (Norris et al. 2004, Rockwell et al. 2012). Nonbreeding studies that have used community-level indicators such as species richness and diversity have provided insight into habitat preferences, habitat use, and ranges, and have been used to identify conservation areas of the nonbreeding grounds where high concentrations of migratory songbirds are found (LaSorte et al. 2017, Wilson et al. 2019). Additionally, nonbreeding studies using population-level indicators such as abundance and density have provided insight into species-level habitat use and informed conservation (Bennett et al. 2018, Céspedes and Bayly 2019, Céspedes Arias et al. 2022). However, community and population-level indicators can be too broad in resolution or may not associate habitat use with an organism's fitness (Van Horne 1983, Garshelis 2000), and evaluating nonbreeding performance at the individual level is important to understand how birds maintain energy reserves for survival and success during the subsequent migratory phase (Bennett 1980). In particular, the interpretation of habitat quality solely based on density or abundance is not straightforward because these metrics depend on whether behaviors of territoriality are present or if habitats have similar qualities (Fretwell and Lucas 1970). Density may be decoupled from habitat quality under a hypothesis like the ideal free distribution, where if habitats have similar qualities, then low or high densities can signal high-performing individuals (Fretwell and Lucas 1970). Under the ideal dominant distribution, several patterns could occur depending on the quality of habitats and the territorial behavior of individuals; for example, density may be low in low-quality habitats if successful competitors secure the available high-quality habitats (Fretwell and Lucas 1970). Still, under other mechanisms of population regulation, such as site-dependence, abundance can be higher when there is a mixture of high-quality and poor-quality territories within an area (Rodenhouse et al. 1997). Therefore, to understand declines and population limitation, we need to supplement and synthesize knowledge gained from community and population-level metrics with the evaluation of drivers of variation in individual-level performance. The opposite is also recommended, for performance to be complemented by density metrics. This approach enables the use of multiple measures to assess habitat quality (Albert et al. 2020).

Individual-level performance can be a proxy for fitness and an indicator of habitat quality and requires collecting data at the individual's level, even though these metrics can subsequently be summarized at the study site level. We focused specifically on the performance metrics of body condition (any metric that relates to mass), apparent survival, and persistence. Body condition indices are used in ecological studies as a metric to interpret an individual's energy reserves (Peig and Green 2009). Body condition indices incorporate

body mass alone or as a function of an organism's structural size and have been shown to correlate to fitness-related traits such as survival or nest success (Labocha and Hayes 2012). Caveats of using body condition as an indicator of better performance are that the estimated body condition must reflect the response to the predicted driver rather than a trade-off (e.g., lighter birds might better avoid predation) or a lagged response in bird condition to past environmental conditions (Johnson 2007). Nonbreeding survival is a demographic metric intrinsically tied to understanding population declines and in the absence of breeding, it may be considered a proxy for fitness (Bennett 1980, Sherry and Holmes 1995). Measuring survival is challenging, so metrics such as apparent survival and persistence probability are used to approximate true survival. Apparent survival estimates the probability that an individual is alive within a study period and area (Kéry and Schaub 2012) but is termed “apparent” since mortality cannot be disentangled from permanent emigration (Schaub and Royle 2014). Persistence, on the other hand, refers to the probability of individuals remaining in a study area or rates at which individuals move away from an area (i.e., transience; Ruiz-Gutierrez et al. 2016, Bailey and King 2019). Studies can measure site or species level persistence by marking a group of individuals and quantifying the percentage of marked individuals that remain at the end of a study period (Strong and Sherry 2000, Wunderle and Latta 2000). We focused on persistence estimated with individual detection or recapture histories, which makes the metric more aligned with apparent survival, where both can be used as proxies of actual survival—the demographic metric intrinsically tied to understanding population declines (Bennett 1980, Sherry and Holmes 1995).

Our review will add value to prior reviews that also focused on the nonbreeding phase and highlighted how this phase is understudied. Faaborg et al. (2010) conducted a synthesis to identify knowledge gaps necessary to effectively conserve migratory landbirds, and concluded that while there was enough research to start conservation efforts, much more was needed to successfully protect declining species. The knowledge gaps identified by Faaborg et al. (2010) included the need for more studies in Central America and South America, comparable to those conducted in the Caribbean, in order to understand how different types of habitats contribute to vital rates in the nonbreeding range. Another gap was migratory connectivity. These gaps were considered important to understand the contribution of the nonbreeding period to population limitation of declining species (Holmes 2007, Faaborg et al. 2010). In Colombia, researchers distilled the studies conducted on migration ecology at the country level and proposed a pathway to increase ecological knowledge for the conservation of migratory species. The pathway consists of delineating the species' distribution, identifying focal species by region, and identifying areas to monitor population size, followed by studies to determine the quality of habitats through parameters such as performance (Gómez et al. 2011).

Ten years later, Albert et al. (2020) highlighted that there is still a need to expand migratory connectivity studies to determine where populations are most limited and identify the responsible factors. This review also identified a need to expand knowledge on how intraspecific habitat use (i.e., behavioral transience, use of multiple nonbreeding regions) contributes to a population's status, how interspecific competition contributes

to population limitation and how diverse crops can serve as quality habitats for birds (Albert et al. 2020). These articles draw attention to knowledge gaps in basic ecology, habitat use, and natural history during the nonbreeding period for several migratory species (Faaborg et al. 2010, Gómez et al. 2011, Albert et al. 2020). It is necessary to fill these gaps to better understand how a changing climate will affect migratory songbird populations (Albert et al. 2020). In this work, our specific objectives were to (1) catalog the drivers, species, and geographic areas studied to influence the performance of nonbreeding, Nearctic–Neotropical, migratory songbirds; and (2) provide an overview of the findings, highlighting knowledge gaps to guide future research avenues.

REVIEW METHODOLOGY

We based our systematic review methodology on the guidelines and steps laid out by Foo et al. (2021). Our question was: What drives the performance of Nearctic–Neotropical migratory songbirds in the nonbreeding period? Based on the PECO (Population, Exposure, Comparator, Outcome) framework delineated by Haddaway et al. (2016), we parsed our question into components from which we listed search terms and prepared search strings. We determined that to keep the search broad enough, we would focus on the Population and Outcome components of the research question and did not select search terms for the Exposure and Comparator. In this systematic review, the population or study system was Nearctic–Neotropical migratory songbirds (Order Passeriformes) and the outcome was performance considering the metrics of body condition (any mass-related index or mass), nonbreeding persistence and apparent survival (daily, monthly, or seasonal). From this point forward, “persistence” and “apparent survival” refer to metrics within the nonbreeding period.

We conducted a naive search (Supplementary Material Table 1) in Web of Science Zoological Records and Web of Science Core Collections and then, using the R package *litsearchr*, built a comprehensive search string (Grames et al. 2019) where the naive search outputs were used to identify terms or keywords (Supplementary Material Table 1). We primarily searched in 4 databases: Web of Science Core Collection, Web of Science Zoological Records, SciELO, and EBSCOHost Open Dissertations. Searches were conducted in English in 3 databases and Spanish in the SciELO database. We also conducted searches in 9 Neotropical peer-reviewed journals (Supplementary Material Table 1). We simplified the search string for the Spanish sources because the comprehensive string yielded no results (Supplementary Material Table 1). All searches were conducted using the “Topic” field option, which searches the title, abstract, and author keywords. The search results from all databases were saved into a spreadsheet (Microsoft Excel) where we de-duplicated studies. The final search was conducted in January 2024.

We evaluated the title and abstract of each study against an abstract decision tree to determine if the study was relevant (Supplementary Material Figure 1). Any study for which there was ambiguity over a criterion was considered a “maybe” for inclusion and was evaluated in the full-text screening process. The full-text screening process consisted of assessing the entire text of the article, including title, abstract, introduction, methods, results, and conclusions against a full-text decision

tree (Supplementary Material Figure 1). We supplemented the search with a forward and backward search in the Web of Science Core Collection and the first 10 pages of Google Scholar, for 7 relevant papers with many citations that focused on different species and regions of the Neotropics (Sherry and Holmes 1996, Marra and Holmes 2001, Johnson et al. 2006, Bakermans et al. 2009, Smith et al. 2010, Chandler and King 2011, Bailey and King 2019). An abstract screening and full-text screening process were conducted for these, as well as for other ancillary reports or articles identified that had not appeared in our main search. Once we identified the studies to be included, we extracted general information on the study region, species and key findings on what influenced body condition, persistence or apparent survival. Finally, we grouped and summarized findings based on the predictor variables, which we will refer to as drivers of performance, and identified knowledge gaps for future research.

RESULTS

Characteristics of Studies on Nonbreeding Songbird Performance

Our search yielded 304 scientific studies, 57 of which evaluated the performance metrics of body condition, nonbreeding persistence, and apparent survival (Supplementary Material Figure 2, Table 2). These 57 studies evaluated 51 Nearctic–Neotropical migratory bird species (mean per study = 2.90 species, SD = 5.83 species). The 51 species represent 40.8% of the 125 Neotropical migratory Passeriformes. Three species were the most studied (Figure 1), each with at least 10 or more studies: *Setophaga ruticilla* (American Redstart), *Parkesia noveboracensis* (Northern Waterthrush), and *Hylocichla mustelina* (Wood Thrush). Wetlands, coastal, and anthropogenic habitats were the most studied in 17 countries (Figure 2). Jamaica had the most studies, and there are several Neotropical countries within South America and the Caribbean for which we did not find any studies on nonbreeding songbird performance (Figure 2). Body condition was the most frequently evaluated metric among the 57 studies (84.2%), followed by nonbreeding apparent survival (26.3%), and persistence (8.8%). Performance metrics were measured in diverse ways (Table 1) and each study focused on 1–3 of the performance metrics we evaluated (mode = 1 performance metric, mean = 1.23, SD = 0.54) and studies were conducted within 1–14 field seasons (mean = 4.16, SD = 3.10). The main drivers of performance studied were habitat type, climate, and food availability; the least studied were disease and predation (Figure 3).

Studied Drivers of Performance

We identified 10 categories of drivers of performance; 3 were environmental drivers that shape habitats: habitat type (i.e., vegetation attributes), food availability, and climate; 5 may be considered processes: space-use strategies, density-dependence, predation, competition and disease; 2 were demographic factors: age and sex (Figure 3). All of these drivers are inextricably linked.

Habitat type

Forty-two of 57 studies (73.7%) studied performance within a natural or anthropogenic habitat by comparing metrics among habitat types or elevations and by evaluating vegetation struc-

ture or landscape characteristics in relation to performance. We use natural habitat to refer to native vegetation or native cover type that is not managed for anthropogenic activities.

Natural habitat types

Thirty-two studies of 57 (56.1%) occurred in natural habitats such as arid lands, coastal habitats, forests, and wetlands. Twenty-six studies showed that the natural habitat type and/or its wetness conditions influenced the performance of 32 songbird species (Table 2). The findings indicated that dry habitat conditions negatively influenced songbird performance, whereas performance was higher or did not decline when individuals inhabited natural habitats, wetter habitats, habitats with high primary productivity, or vertical structural complexity (e.g., pine forests over thorn scrub; Holmes et al. 1989, Marra et al. 1998, Marra and Holberton 1998, Marra and Holmes 2001, Strong and Sherry 2001, Latta and Faaborg 2002, Reitsma et al. 2002, Studds and Marra 2005, Johnson et al. 2006, Studds and Marra 2007, Saracco et al. 2008, Smith et al. 2010, Angelier et al. 2011, Smith et al. 2011, Saracco et al. 2012, Townsend et al. 2012a, Wunderle et al. 2014, McKinnon et al. 2015, Akresh et al. 2019, Bulluck et al. 2019, González et al. 2020, 2021, Stanley et al. 2021, Oliveira 2022, Oliveira et al. 2022, Rodríguez Vásquez 2023). Twenty-four studies showed this pattern based on body condition indices, 4 studies on apparent survival, and 3 studies on persistence. For *S. ruticilla*, multiple lines of evidence demonstrate the value of wetter and natural nonbreeding habitats. In mangrove habitat, the body condition baseline was higher, or body condition loss was less marked throughout the nonbreeding period compared to other habitats (Marra and Holberton 1998, Marra et al. 1998, Marra and Holmes 2001, Johnson et al. 2006, Studds and Marra 2007). Apparent survival was higher in mangroves than in dry limestone (Johnson et al. 2006), and an experiment in which individuals were upgraded from the “poor” second-growth scrub to the “optimal” mangrove habitat showed that the upgraded individuals maintained their body condition (Studds and Marra 2005). Wetter habitats were also correlated with higher body condition in *H. mustelina* studied in Belize and in *S. discolor* (Prairie Warblers) in The Bahamas, and persistence in moist habitats was reported to be 13.2% higher than in dry habitats for *Protonotaria citrea* (Prothonotary Warblers) in Panama (Akresh et al. 2019, Bulluck et al. 2019, Stanley et al. 2021).

Nine studies found that performance in 11 species was comparable among natural habitat types or remained constant within natural habitat types such as broad-leaved forests, successional stages of dry forests, and wetland types (Table 2; Lefebvre et al. 1992, Wunderle 1995, Conway et al. 1995, Warkentin and Hernandez 1996, Roberts 2007, Calvert et al. 2010, Ruiz-Sánchez et al. 2017, Latta et al. 2018, Bulluck et al. 2019)—6 studies based these findings on body condition indices, and 4 on apparent survival. Furthermore, 3 of these studies showed that performance was different for age and sex groups (Wunderle 1995, Warkentin and Hernandez 1996, Calvert et al. 2010), and we expand on the influence of age and sex in a section below.

Anthropogenic habitat types, landscape metrics, and vegetation structure

Thirteen of 57 studies (22.8%) compared performance in relatively natural to anthropogenically modified habitats or

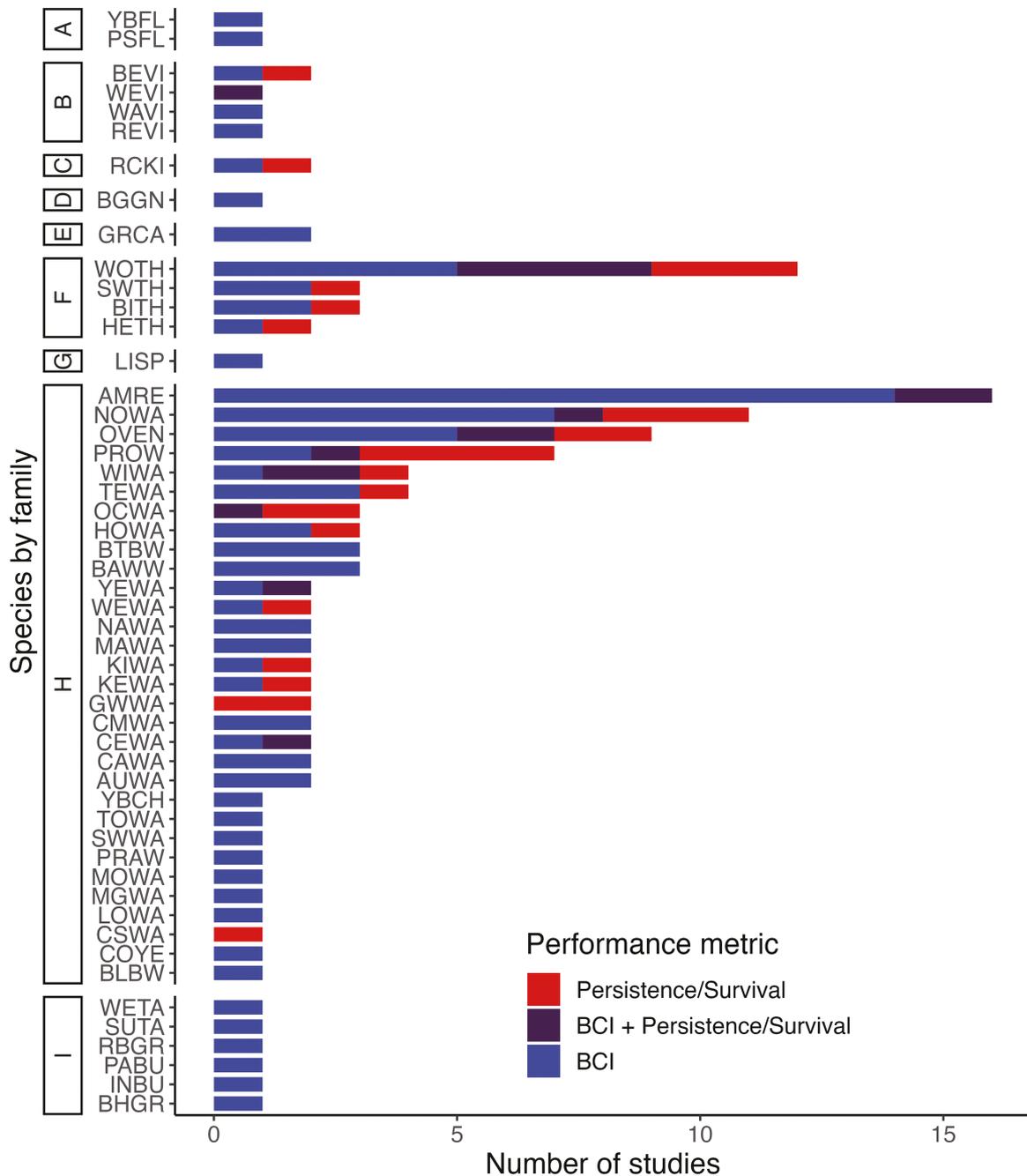


FIGURE 1. Nearctic–Neotropical migratory songbirds (Passeriformes) for which performance has been studied during the nonbreeding period. Families: A = Tyrannidae, B = Vireonidae, C = Regulidae, D = Polioptilidae, E = Mimidae, F = Turdidae, G = Passerellidae, H = Parulidae, I = Cardinalidae. Full english names for the alpha codes can be found by [Pyle and DeSante \(2022\)](#).

studied performance within anthropogenic habitats. The anthropogenic habitats studied included urban habitats, coffee farms, citrus orchards, and other croplands (i.e., tomato, sorghum production and oil palm). The studies were skewed toward shade coffee, with 8 of 13 evaluating this habitat type as a predictor and 2 of 13 evaluating vegetation structure or landscape features in coffee-producing regions.

Five shade coffee studies found evidence that this habitat was not detrimental to the performance of 7 species ([Table 2](#); [Bakermans et al. 2009](#), [Chandler and King 2011](#), [Colorado and Rodewald 2017](#), [González et al. 2020, 2021](#)). Within shade coffee, 5 species of songbirds showed the ability to in-

crease body condition and 4 species saw no change throughout the nonbreeding period ([Bakermans et al. 2009](#), [Colorado and Rodewald 2017](#)). Body condition was found to be comparable in shade coffee and native forests for species such as *Catharus ustulatus* (Swainson’s Thrush) and *Cardellina canadensis* (Canada Warbler) in Colombia ([González et al. 2020, 2021](#)), while apparent survival was comparable among natural and the coffee agroforestry systems in Costa Rica for *Vermivora chrysoptera* (Golden-winged Warbler) ([Chandler and King 2011](#)). On the other hand, 2 studies that evaluated shade coffee in Jamaica found that *Seiurus aurocapilla* (Ovenbird) and *Setophaga ruticilla* held higher mean body

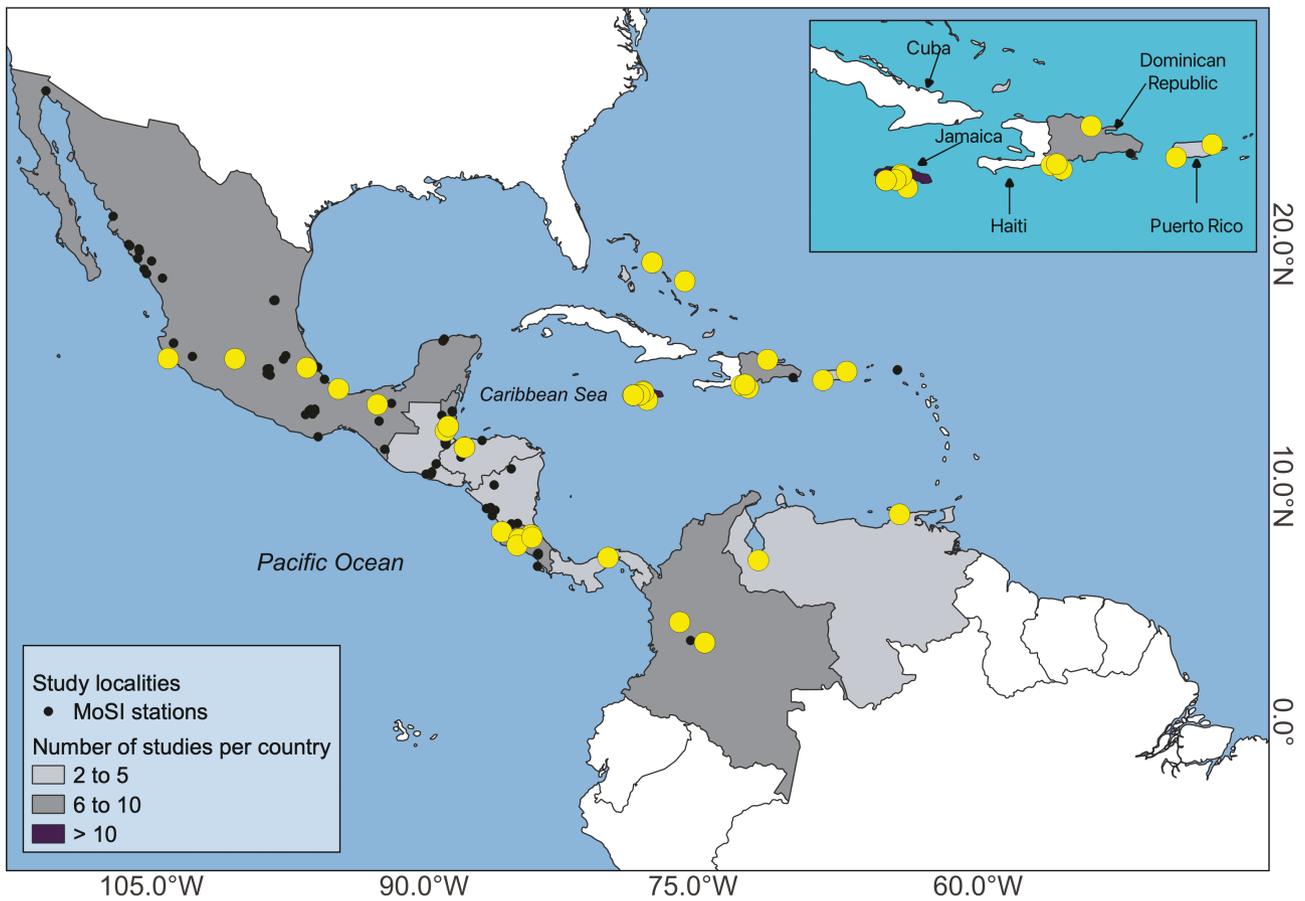


FIGURE 2. Distribution (decimal degrees WGS84) of studies (larger, yellow dots) on nonbreeding performance of Nearctic–Neotropical migratory songbirds. Inset depicts the Caribbean region to magnify the locality with most studies, Jamaica.

TABLE 1. Measurements used to quantify body condition, apparent survival and persistence for non-breeding migratory songbirds. Performance metrics were grouped by the method in which the metric was estimated.

| Performance metric | Number of studies | Description |
|--------------------------------------|-------------------|---|
| Body condition | 17 | Residuals of mass regressed against body size. Studies could use a principal component analysis (PCA) axis that used morphometrics as the size measurement, wing chord or tarsus length measurements. |
| | 4 | Quotient resulting from mass divided by wing chord. |
| | 5 | Quotient change or grams change divided by studied months total. These measurements show the difference between two time periods within the nonbreeding period |
| | 5 | Grams obtained from the Scaled Mass Index as proposed by Peig and Green (2009) . |
| | 7 | Body mass minus predicted body mass, obtained from a regression of body mass as a function of tarsus length and wings length. Can be presented as a percentage. |
| | 4 | Mass corrected for body size (i.e., obtained with PCA of morphometrics or wing chord) and as a function of time of day. The output value is in grams and not residuals. |
| | 6 | Mass |
| Nonbreeding survival and persistence | 14 | Probability of apparent survival or persistence measured for the duration of the nonbreeding study (e.g., 5 months) or estimated monthly. |
| | 5 | Rate of daily survival, transience (the opposite of persistence) or persistence |
| | 1 | Percentage of individuals found dead from total marked. |

condition in shade coffee compared to the natural habitat of scrub; but in these studies, body condition also decreased across habitats over time suggesting that habitat type is not the only driver of performance ([Strong and Sherry 2000](#), [Johnson et al. 2006](#)). Shade coffee was not beneficial in all

studies. One study in Colombia showed that the body condition of *Vireo olivaceus* (Red-eyed Vireo) did not improve over the nonbreeding period in shade coffee, and another study in Honduras showed that survival rates of *H. mustelina* that selected heavily shaded coffee farms were lower than those

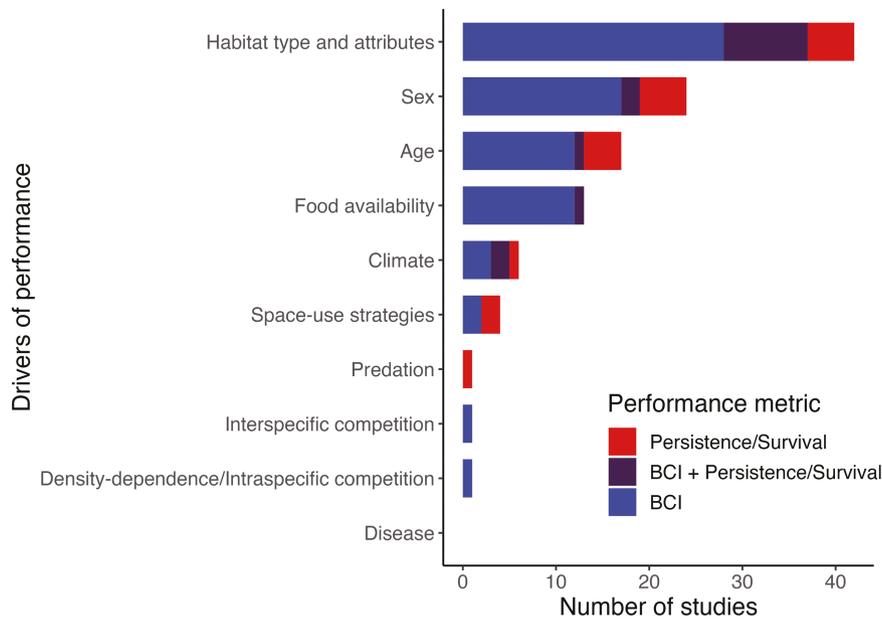


FIGURE 3. Studied drivers of nonbreeding performance in Nearctic–Neotropical migratory songbirds. Persistence = individual level nonbreeding persistence. BCI = body condition index. Survival = apparent survival or survival rate measured within the nonbreeding phase.

that spent more time in the forest (Colorado and Rodewald 2017, Bailey and King 2019).

Most studies focused on evaluating shade coffee using the habitat type as a predictor, but vegetation structure features and landscape context were considered in 4 studies (Table 2). Vegetation structure can influence habitat selection and use, consequently, performance (Cody 1981). Bailey and King (2019) found that the basal area of medium-sized trees correlated negatively with the likelihood of transience and the survival rate of *H. mustelina* individuals within farms in Honduras. Ritterson et al. (2021) found that taller canopy heights negatively influenced the apparent survival of *V. chrysoptera* in Costa Rica. In contrast, Chandler and King (2011) found no relationship between vegetation structure and apparent survival for *V. chrysoptera* in Costa Rica. Another study that focused on landscape metrics and body condition and apparent survival in Honduras found that *C. pusilla* (Wilson’s Warbler) body condition increased with shade coffee farm area in a landscape of ~20 ha. However, apparent survival increased with forests with high edge density in these landscapes (Rodríguez Vásquez 2023). With so few studies evaluating these relationships between vegetation structure or landscape context and performance, we perceive this as an important research gap (Box 1). Landscape- and site-level studies may complement each other—where site-level knowledge could help guide farm or forest management, and landscape-level knowledge informs on the quantity and distribution of natural habitat optimal for sustaining performance.

Only 3 out of the 13 studies in anthropogenic habitats focused on variables that were not in the scope of coffee farming and they were all conducted in Mexico. One of these studies found that *Setophaga petechia* (Yellow Warbler) had a higher monthly apparent survival in riparian forests and agricultural habitats (sorghum, chili peppers) compared to scrub-mangrove, while birds in riparian habitat had a higher size adjusted mass (Valdez-Juarez et al. 2019). In an urban

habitat, another study found that scaled mass was comparable between green and urban spaces for *S. coronata* (Yellow-rumped Warbler) and *Leiothlypis ruficapilla* (Nashville Warbler) (Pacheco-Muñoz et al. 2022). Finally, a study found that *S. ruticilla* and *Dumetella carolinensis* (Gray Catbird) showed higher body condition in native forests than in oil palm farms, but *S. magnolia* (Magnolia Warbler) showed the opposite response (Oliveira et al. 2022).

Elevation as a proxy for habitat type

Habitats vary by elevation because climatic conditions and topography influence floristic composition and structure (Holdridge 1967). Three studies used elevation as a predictor variable and the results were inconsistent across species or country. In Honduras, a study on *H. mustelina* found an interaction between elevation and heavily shaded coffee farms where survival rates increased with elevation. Still, when heavily shaded coffee farms were present at high elevations, these had a negative influence on performance (Bailey and King 2019). In Costa Rica, elevation did not influence the apparent survival of *V. chrysoptera* (Chandler and King 2011). Finally, a study conducted across 14 countries and 5 nonbreeding seasons found that elevation positively influenced the nonbreeding body condition for 9 species, negatively influenced 4 species, and had no influence for 22 species (Table 2; Saracco et al. 2008). For the species for which apparent survival was evaluated, none of the 6 species of songbirds were influenced by elevation (Saracco et al. 2008).

Food availability

Food is a resource that can limit populations during the nonbreeding period and can correlate with habitat quality, performance, or movement of individuals (Sherry et al. 2005). We found 13 studies of 57 (22.8%) where food availability was studied in relation to persistence and body condition but not nonbreeding survival (Figure 3). Food availability was usually evaluated indirectly by measuring food availability in

TABLE 2. Summary of habitat type drivers and their influence on Nearctic-Neotropical migratory songbirds

| Evidence of influence of a habitat type driver on species performance | References |
|--|--|
| Evidence for negative influence of dry habitat or drying conditions, evidence for positive influence of natural and wet habitat types | |
| <i>Hylocichla mustelina</i> | Holmes et al. (1989), Marra and Holberton (1998), Marra et al. (1998), |
| <i>Setophaga ruticilla</i> | Marra and Holmes (2001), Strong and Sherry (2001), Latta and |
| <i>Setophaga caerulea</i> | Faaborg (2002), Reitsma et al. (2002), Studds and Marra (2005), |
| <i>Setophaga tigrina</i> | Johnson et al. (2006), Studds and Marra (2007), Saracco et al. |
| <i>Dumetella carolinensis</i> | (2008), Smith et al. (2010, 2011), Angelier et al. (2011), Saracco et al. |
| <i>Setophaga discolor</i> | (2012), Townsend et al. (2012a), Wunderle et al. (2014), McKinnon |
| <i>Protonotaria citrea</i> | et al. (2015), Akresh et al. (2019), Bulluck et al. (2019), Stanley et al. |
| <i>Setophaga kirtlandii</i> | (2021), González et al. (2020, 2021), Oliveira 2022, Oliveira et al. |
| <i>Catharus bicknelli</i> | (2022), Rodríguez Vásquez (2023) |
| <i>Catharus ustulatus</i> | |
| <i>Parkesia noveboracensis</i> | |
| <i>Setophaga citrina</i> | |
| <i>Limothlypis swainsonii</i> | |
| <i>Cardellina pusilla</i> | |
| <i>Vireo bellii</i> | |
| <i>Helmitheros vermivorum</i> | |
| <i>Leiothlypis celata</i> | |
| <i>Passerina cyanea</i> | |
| <i>Setophaga petechia</i> | |
| <i>Poliophtila caerulea</i> | |
| <i>Vireo griseus</i> | |
| <i>Empidonax flaviventris</i> | |
| <i>Empidonax difficilis</i> | |
| <i>Corthylio calendula</i> | |
| <i>Leiothlypis ruficapilla</i> | |
| <i>Setophaga magnolia</i> | |
| <i>Setophaga coronata</i> | |
| <i>Setophaga townsendi</i> | |
| <i>Geothlypis tolmiei</i> | |
| <i>Geothlypis trichas</i> | |
| <i>Piranga ludoviciana</i> | |
| <i>Cardellina canadensis</i> | |
| Evidence for comparable performance in different natural habitat types (e.g. successions of forest) or for not changing significantly within a natural habitat type | |
| <i>Protonotaria citrea</i> | Lefebvre et al. (1992), Wunderle (1995), Conway et al. (1995), |
| <i>Parkesia noveboracensis</i> | Warkentin and Hernandez (1996), Roberts (2007), Calvert et al. |
| <i>Hylocichla mustelina</i> | (2010), Ruiz-Sánchez et al. (2017), Latta et al. (2018), Bulluck et al. |
| <i>Cardellina pusilla</i> | (2019) |
| <i>Geothlypis formosa</i> | |
| <i>Setophaga citrina</i> | |
| <i>Seiurus aurocapilla</i> | |
| <i>Setophaga caerulea</i> | |
| <i>Setophaga ruticilla</i> | |
| <i>Mniotilta varia</i> | |
| <i>Setophaga tigrina</i> | |
| Examples of shade coffee farm showing comparability to forest or no significant effect on performance | |
| <i>Parkesia noveboracensis</i> | Bakermans et al. (2009), Chandler and King (2011), Colorado and |
| <i>Geothlypis philadelphia</i> | Rodewald (2017), González et al. (2020, 2021) |
| <i>Vermivora chrysoptera</i> | |
| <i>Setophaga cerulea</i> | |
| <i>Setophaga fusca</i> | |
| <i>Cardellina canadensis</i> | |
| <i>Catharus ustulatus</i> | |

Table 2. Continued

| Evidence of influence of a habitat type driver on species performance | References |
|--|---|
| Evidence for influence of vegetation structural or landscape composition and configuration on performance | |
| <i>Cardellina pusilla</i> | Chandler and King (2011), Bailey and King (2019), |
| <i>Hylocichla mustelina</i> | Ritterson et al. (2021), Rodríguez Vásquez (2023) |
| <i>Vermivora chrysoptera</i> | |
| Evidence for interaction between habitat type and elevation | |
| <i>Hylocichla mustelina</i> | Bailey and King (2019) |
| Evidence for a positive influence of elevation on performance | |
| <i>Seiurus aurocapilla</i> | Saracco et al. (2008) |
| <i>Parkesia noveboracensis</i> | Bailey and King (2019) |
| <i>Geothlypis formosa</i> | |
| <i>Geothlypis trichas</i> | |
| <i>Hylocichla mustelina</i> | |
| <i>Catharus guttatus</i> | |
| <i>Leiothlypis ruficapilla</i> | |
| <i>Mniotilta varia</i> | |
| <i>Setophaga citrina</i> | |
| Evidence for no influence of elevation on performance | |
| <i>Vermivora chrysoptera</i> | Saracco et al. (2008) |
| <i>Empidonax flaviventris</i> | Chandler and King (2011) |
| <i>Passerina ciris</i> | |
| <i>Piranga ludoviciana</i> | |
| <i>Empidonax difficilis</i> | |
| <i>Vireo bellii</i> | |
| <i>Vireo gilvus</i> | |
| <i>Polioptila caerulea</i> | |
| <i>Catharus ustulatus</i> | |
| <i>Dumetella carolinensis</i> | |
| <i>Melospiza lincolni</i> | |
| <i>Leiothlypis peregrina</i> | |
| <i>Setophaga petechia</i> | |
| <i>Setophaga magnolia</i> | |
| <i>Setophaga coronata</i> | |
| <i>Setophaga townsendi</i> | |
| <i>Pheucticus melanocephalus</i> | |
| <i>Protonotaria citrea</i> | |
| <i>Helmitheros vermivorum</i> | |
| <i>Geothlypis tolmiei</i> | |
| <i>Cardellina pusilla</i> | |
| <i>Icteria virens</i> | |

a habitat and quantifying the performance within the habitat. Food availability across the thirteen studies was measured as ant or arthropod biomass, ant or arthropod abundance, fruit abundance, or mean fruit trees per plot. Food consumption was only measured in 2 studies using stable nitrogen isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) to infer the consumption of arthropods or fruit (McKinnon et al. 2017, Stanley et al. 2021).

Eight studies found that wetter habitats or higher precipitation increased food availability and sustained individuals with higher body condition (Strong and Sherry 2000, Studds and Marra 2005, Brown and Sherry 2006, 2008, Smith et al. 2010, Wunderle et al. 2014, McKinnon et al. 2015, Stanley et al. 2021). Only one study evaluated the relationship between food availability and individual-level persistence and found that this metric was lower with higher food avail-

ability in wetter habitats (Stanley et al. 2021). Contrasting these findings, 3 studies found no evidence for the influence of food availability, experimental food reduction or irrigation on plants to increase arthropod biomass and body condition (Hallworth et al. 2011, Wilson et al. 2013, Cooper et al. 2015). Regarding diet, one study found no significant influence between a frugivorous and insectivorous diet on the body condition of *H. mustelina* in Belize (McKinnon et al. 2017). Still, another study found a connection between diet and sex for *Catharus bicknelli* (Bicknell's Thrush) in the Dominican Republic, where females had comparable body condition to males in the rainforest habitat, which had higher fruit availability and males had higher body condition than females in the cloud forest habitat which had higher arthropod biomass (Townsend et al. 2012a).

BOX 1. Top study opportunities for improving knowledge on Nearctic-Neotropical migratory songbird nonbreeding performance

| Knowledge gap | Scope needed and implication |
|-------------------------------|--|
| Landscape context | Working landscapes with different types of agroproduction systems. This work would improve knowledge on range-level conservation |
| Vegetation or site management | Agroforestry or other anthropogenic systems. This work could mimic breeding grounds studies that aid in quantifying management guidelines |
| Climate change | How or through which mechanisms will climate change impact performance of nonbreeding songbirds? |
| Predation | Is predation a significant contributor to mortalities of nonbreeding songbirds? How does predation or predation risk influence performance? |
| Disease | What diseases are present in migratory songbirds during the nonbreeding period? How do these influence performance? |
| Density dependence | To what degree does density dependence operate in migratory songbirds during the nonbreeding period. How can this mechanism influence performance? |

Climate

The dry season in the nonbreeding region ranges from approximately December to April (Molano and Batista 1967, Ulate 2001, León 2010, Brawn et al. 2017), with the caveat that geography across the region creates a diversity of local climates that shift the timing of the dry season (Molano and Batista 1967). Within the dry season, the countries where studies in our review were conducted, experience the lowest precipitation records in February and March, corresponding to the late nonbreeding season for migrants (Fick and Hijmans 2017). Climate and performance were studied in 6 studies where the climate predictors were mean daily precipitation (mm); precipitation recorded 30, 60, or 90 days before the measurement of body condition was collected; soil and canopy moisture derived from remote sensing images; primary productivity indices derived from remote sensing images; and stable isotope measurements that indicate moisture levels (Saracco et al. 2008, Angelier et al. 2011, Saracco et al. 2012, Wunderle et al. 2014, Akresh et al. 2019, Stanley et al. 2021). All studies found evidence for a positive correlation between a performance metric and precipitation or a negative correlation with drying.

Three studies found that mean daily precipitation and precipitation that has taken place between 30 and 90 days earlier positively correlate with the body condition of individuals (Angelier et al. 2011, Wunderle et al. 2014, Akresh et al. 2019). One study found that higher moisture levels in habitats measured by stable isotopes increase body condition and decreased persistence (Stanley et al. 2021). Two studies found that metrics such as leaf area index (LAI) and the enhanced vegetation index (EVI) at the nonbreeding range can influence body condition, persistence and apparent survival (Saracco et al. 2008, Saracco et al. 2012). Remote sensed vegetation indices such as LAI and EVI use spectral signatures to capture canopies, greenness or senescing features that vary throughout seasons (Huete et al. 2014). One of these studies evaluated data collected across 127 sites in 14 countries spanning 5 nonbreeding seasons and focused on LAI influence on body condition and apparent survival (Saracco et al. 2008) and the other extended the work by adding 4 more nonbreeding seasons and focused on EVI's influence on persistence (Saracco et al. 2012). LAI in the Neotropical range is

correlated to the seasonal shift of the dry season. When LAI declined, it negatively influenced the body condition of 13 songbird species but positively influenced the body condition of three others. LAI positively influenced apparent survival for 2 out of 6 species (Saracco et al. 2008).

Space use strategies

During the nonbreeding period, an individual can adopt a sedentary or territorial strategy instead of a transient, wanderer or floater strategy in which an individual does not remain in one site and uses a larger area to meet its energy requirements (Rappole et al. 1989). The space use strategy adopted by a nonbreeding migrant is considered to aid in exploiting resources needed for self-maintenance (Rappole et al. 1989, Sherry and Holmes 1996). Four studies out of 57 (7.0%) evaluated relationships between space-use strategies and performance. Three found evidence for performance to be higher with territorial or sedentary strategies. Rappole et al. (1989) conducted a radio telemetry study on *H. mustelina* in Mexico. They found that mortality rates were significantly higher in wanderer birds than in sedentary birds with predation as a leading cause of mortality (Rappole et al. 1989). In Belize, territorial *Seiurus aurocapilla* held higher body condition than non-territorial birds (Kresnik and Stutchbury 2014). Similarly, *Parkesia noveboracensis* individuals with more exclusive home ranges had a higher body mass than those with more overlapping home ranges (Smith et al. 2011). The three studies that found these patterns were focused on the local use of habitat by individuals. When a study evaluated persistence across the nonbreeding range, results suggested that persistence varied with latitude and not between categories of territorial and non-territorial species (Ruiz-Gutierrez et al. 2016).

Density dependence

Density dependence operates at the conspecific level and may influence individual-level songbird performance during the nonbreeding period. Through regulatory, density-dependent processes, such as conspecific competition or disease, population size impacts survival and other demographic rates (Hixon et al. 2002). Density dependence is linked to intraspecific competition, the understanding of which relies on knowledge of nonbreeding behavior and social systems among

migrants, and remains understudied (Stutchbury et al. 2005). We identified density-dependence as a knowledge gap (Box 1) because we found only 1 study out of 57 (1.8%) that directly examined the relationship between density and performance. This study found that, for *S. ruticilla* in Jamaica, body condition decreased with a higher density of conspecific individuals in mangrove habitat (considered of high quality for this species). Conversely, body condition increased with conspecific density in second-growth scrub (deemed lower quality; Marra et al. 2015b). Whether and how density dependence operates in many migratory songbird nonbreeding populations remains unknown. However, understanding if and how it operates is critical to modeling efforts (e.g., integrated population models) that evaluate how population declines are driven (Hostetler et al. 2015, Taylor and Stutchbury 2016).

Predation

Songbird predation is understudied; events during the nonbreeding period are anecdotal in several studies with predators including: avian raptors such as *Glaucidium brasilianum* (Ferruginous Pygmy Owl), *Micrastur ruficollis* (Barred Forest Falcon), and *Falco sparverius* (American Kestrel), snakes (*Boa constrictor*), and mammals such as rats and mongoose (Rappole et al. 1989, Sherry and Holmes 1996, Roberts 2007, Brown and Sherry 2008, Townsend et al. 2009, Bailey and King 2019). Only 1 of 57 studies evaluated the link between performance and predation. In the Dominican Republic, a study on *Catharus bicknelli* found that rats, an introduced predator responsible for the mortality of 5 of 53 individuals (9.4%), were more abundant in cloud forest than pine forest, both of which are habitats used by the songbird species (Townsend et al. 2009).

Interspecific competition

Competition is a mechanism that could influence performance as one outcompeting individual negatively drives a population parameter of influence of another individual (Gotelli 2008). The two main resources for which migratory birds compete during the nonbreeding period are food (mainly) and roosting sites (possibly) (Rappole 1995, Sherry et al. 2005). We identified interspecific competition as a knowledge gap (Box 1) because only 1 of 57 studies (1.8%) evaluated this driver of performance. The study found that when territories of resident *S. petechia* and *S. ruticilla* have a higher overlap, then the body condition of *S. ruticilla* adult males decreases. At the same time, the overlap does not seem to significantly impact female adults and immatures or immature males (Powell et al. 2021).

Disease

Migratory birds are susceptible to parasites (gastrointestinal, blood) (Garvin et al. 2006, Pérez-Gómez et al. 2018), viruses (Soler-Tovar and Vera 2011), and contaminants (Nemes et al. 2023) all of which could be considered under the disease umbrella as they impair the performance of individuals. We identified disease as a significant knowledge gap (Box 1) because no studies evaluated disease in relation to our studied individual performance metrics or took place during the nonbreeding region and period.

Age and Sex Influence on Performance

Findings of age and sex differential performance were mixed, suggesting that habitat selection and despotism operate in the nonbreeding period (Lynch et al. 1985, Morton et al. 1987,

Catry et al. 2005). Twenty-four out of 57 studies (42.1%) used sex and age as a factor to evaluate performance (Holmes et al. 1989, Warkentin and Hernandez 1996, Marra et al. 1998, Marra and Holmes 2001, Brown and Sherry 2006, Roberts 2007, Studds and Marra 2007, Calvert et al. 2010, Smith et al. 2010, 2011, Townsend et al. 2012a,b, Kresnik and Stutchbury 2014, Wunderle et al. 2014, McKinnon et al. 2015, Rockwell et al. 2017, Valdez-Juarez et al. 2019, Ritterson et al. 2021, González et al. 2021, Cooper et al. 2021, Stanley et al. 2021, Bulluck et al. 2019, Powell et al. 2021, Pacheco-Muñoz et al. 2022). Evidence for differential performance by age was shown in 5 studies where juveniles had lower apparent survival and/or body condition compared to their adult counterparts, with this pattern observed for *Parkesia noveboracensis* and *Vermivora chrysoptera* in Costa Rica, *Seiurus aurocapilla* in Belize, *Setophaga kirtlandii* (Kirtland's Warbler) in The Bahamas and *Catharus ustulatus* in Colombia (Calvert et al. 2010, Kresnik and Stutchbury 2014, Rockwell et al. 2017, Ritterson et al. 2021, González et al. 2021). Evidence for differential performance by sex was shown in six studies where males showed an increase in body condition over the nonbreeding period, overall higher body condition or lower body mass loss than females in *P. noveboracensis* in Puerto Rico, *S. kirtlandii* in The Bahamas, *S. petechia* in Mexico, *S. ruticilla* and *Mniotilta varia* (Black-and-White Warbler) in Jamaica, and *H. mustelina* in Belize (Holmes et al. 1989, Smith et al. 2010, Wunderle et al. 2014, Valdez-Juarez et al. 2019, Cooper et al. 2021, Stanley et al. 2021). Territoriality may explain differential performance as one study showed that male *P. noveboracensis* in Puerto Rico were more likely to be territorial, and this space-use strategy provided an opportunity to gain mass (Smith et al. 2011). Similarly adult male *S. ruticilla* in Jamaica showed mass decline with a higher interspecific overlap in territories with *S. petechia* (Powell et al. 2021). Sex differences usually indicated that males had higher values of performance metrics, but one study showed higher persistence in female *Protonotaria citrea* than males in Panama (Bulluck et al. 2019).

When studies found no differences in age or sex performance it was suggested that habitat quality is sex-specific or that access to high-quality habitat can benefit both age and sex groups. For example, *Catharus bicknelli* females showed comparable body mass to males in rainforest habitat, whereas males had higher body condition in cloud forest habitat (Townsend et al. 2012a). Two other studies showed that age and sex groups can maintain body condition in optimal habitat conditions (Marra and Holmes 2001, Studds and Marra 2007). Finally, 9 studies found no differential body condition for age and sex groups (Warkentin and Hernández 1996, Marra et al. 1998, Brown and Sherry 2006, Roberts 2007, Townsend et al. 2012b, McKinnon et al. 2017, Pacheco-Muñoz et al. 2022), nor differential sex apparent survival across sites of the same habitat type (Calvert et al. 2010), nor differential sex persistence (Stanley et al. 2021).

DISCUSSION

Overview in Context of Previous Reviews

Our overview enriches previous reviews by Faaborg et al. (2010) and Albert et al. (2020). Faaborg et al. (2010) identified the need to conduct more studies in Central and South America and measure habitat use consequences on demographic parameters. We learned from our overview that

Colombia, Mexico, Belize, and Costa Rica have contributed the most to mainland studies in the last 2 decades, with 6–10 studies on the nonbreeding performance of songbirds. The next step would be to determine why there are understudied regions (Figure 2) and if these match the distribution of passerine species that are also understudied. Furthermore, researchers can use this overview to glean the types of performance drivers that may be relevant for study. In particular, habitat type has been the most studied driver, indicating that it is a readily available driver to evaluate as a starting point. However, future work that considers some of the least studied drivers such as disease, predation, and processes like density dependence (Figure 3), would be large contributions, especially in the face of anthropogenic-induced changes (Albert et al. 2020).

Albert et al. (2020) highlight the importance of measuring several habitat quality indicators during the nonbreeding phase, including body condition, annual survival, density, or indicators relevant to the species ecology. We echo their recommendation and suggest that we need more studies considering apparent survival alongside body condition to better understand nonbreeding ecology. Nine studies focused on more than one of our reviewed metrics. Six of the 9 studies found that only 1 of 2 performance metrics evaluated was influenced by habitat (Roberts 2007, Saracco et al. 2008, Bakermans et al. 2009, Bailey and King 2019, Bulluck et al. 2019, Valdez-Juarez et al. 2019) whereas the other was not. Two of the 9 studies found that 2 metrics were influenced in the same way (Johnson et al. 2006, Stanley et al. 2021). However, one study found 2 performance metrics to have opposing responses to landscape drivers; Rodríguez Vásquez (2023) found that *Cardellina pusilla* body condition decreased with high forest and edge density where shade coffee area was lower within local landscapes of ~20 ha. Conversely, apparent survival increased in high forest and edge density. The opposing influences of 2 habitats that can sustain migratory songbirds suggest that species may respond differently to landscape context.

We also support Albert et al. (2020) recommendation of studying interspecific competition, density dependence, exploring other anthropogenic habitats beyond shade coffee and the need for climate change studies. We only found one study focused on performance in relation to density dependence or interspecific competition. Shade coffee was the dominant habitat type compared to palm oil, other food crops, and urban habitat type. Finally, the role of temperature, other climatic variables, or climate change scenarios was not studied as performance drivers.

Heterogeneity Across Studies

It was unsurprising to find heterogeneity across study metrics and results due to the breadth of our overview that encompasses the Order Passeriformes and the entire Neotropical region. One of the sources of heterogeneity was the diverse metrics used to gauge body condition and survival (Table 1). Future research could evaluate the extent to which metrics measurement type influences inference on what drives performance (Peig and Green 2009). We found that for every driver, there were mixed results on performance, which may be due to the conditions of the study site, species-specific ecology, or study design approaches. Faaborg et al. (2010) recommended studies of intensive quality across more nonbreeding regions,

habitats and species, but they also recognized the funding and capacity challenges. If understanding the population limitation of migratory songbirds is a goal, future studies should consider the possible sources of heterogeneity and may benefit from unified protocols. One example of the collection of demographic data in the nonbreeding range is the MoSI program, which has collected data for 21 nonbreeding seasons since 2002 using a unified protocol (DeSante et al. 2009). We found 3 studies that used MoSI data successfully (Saracco et al. 2008, Saracco et al. 2012, Ruiz-Gutierrez et al. 2016). Still, challenges can be found within programs that collect data at large scales, such as the time and capacity needed to validate and synthesize data (Albert et al. 2018).

Heterogeneity in performance response can also be due to the study area or species. Further examination would require evaluating the variation in performance across sites and species with a unified study at a larger scale, as we mentioned earlier. Alternatively, studying more than one species could contribute to expanding knowledge on the ecology of songbirds, albeit it is time, funding and capacity challenging. For example, Colorado and Rodewald (2017) measured the body condition in shade coffee farms for 8 species, finding mixed results. This type of work lays the foundation to study why some species have a positive or negative response and combines individual-level performance while informing on the status of the songbird community.

The contrasting finding to heterogeneity was the higher representation of certain species and regions within our review. *Setophaga ruticilla*, *P. noveboracensis*, *Seiurus aurocapilla*, and *H. mustelina* were the most studied species, and the first 3 species were primarily studied in the Caribbean region (i.e., Jamaica, Dominican Republic). Research on these species has been valuable in understanding the role of habitat, climate, food availability, and performance (see above sections). On the other hand, thanks to research conducted in other regions and species, we learn that migratory songbirds do not respond similarly to the performance drivers. Keeping this in mind is useful when considering the conservation of the most vulnerable species. For example, the *Dolichonyx oryzivorus* (Bobolink) is a grassland species showing accelerating rates of decline (NABCI 2022). We did not find a study that evaluated its performance during the nonbreeding phase, although there are studies on other aspects of the ecology during this phase (Renfrew et al. 2020). Other species of conservation concern, such as the ones recognized by the Species at Risk Act (SARA, 2002) in Canada, include *Setophaga cerulea* (Cerulean Warbler), *Cardellina canadensis*, *V. chrysoptera*, *H. mustelina* which were represented in our overview, but others such as the *Contopus cooperi* (Olive-sided Flycatcher), and *C. virens* (Eastern Wood-Pewee) were not.

Caveats of Overview

Our overview was written as a mix between a systematic map and narrative synthesis that catalogs what we know about nonbreeding performance of Nearctic–Neotropical migratory songbirds (Haddaway et al. 2016). Quantifying effect sizes to conduct a meta-analysis or systematic review *sensu* Higgins and Cochrane (2020) would allow for the estimation of the evidence for an intervention to a response. Because our review question was broad, we focused on documenting and synthesizing in graphic and table form, the studies that have focused on performance and where the knowledge gaps are.

In this overview, we focused on the events in 1 of 4 annual cycle phases. Within a migratory songbird's life cycle, carry-over effects are important (Harrison et al. 2011). For this reason, the need to shift away from a single-phase focus has been recommended (Calvert et al. 2009). We support the full annual cycle research paradigm and our overview contributes to it by showing the research gaps that need to be considered to make the nonbreeding studies diverse in species, region and topics to expand full annual cycle knowledge.

Conclusions

Evidence was found among these studies, suggesting that natural habitat types, wetter habitats or precipitation and high availability of food may positively influence body condition, apparent survival, and persistence for nonbreeding songbirds. While this evidence encompasses the elements of habitats (food, climate, and shelter), there was a bias toward studying habitat type as a performance driver. The use of habitat type as the main predictor may be because it is a readily categorical variable and it may be assumed that it encompasses the qualities of a habitat (e.g., shelter and food). Using habitat type is acceptable as a starting point, but we recommend studies consider other drivers of individual performance that inform what impacts population declines (Box 1).

Our overview showed knowledge gaps at the taxonomic and spatial levels. Only 51 of the 125 songbirds that spend their nonbreeding months in the Neotropical region have been evaluated and several of these species have only been considered in one study. We recommend that researchers evaluate the topic and spatial gaps for the most vulnerable species. The vulnerable species may be identified using resources such as the Species at Risk Act (SARA, 2002), the Avian Conservation Database (Partners in Flight 2021), the current State of the Birds (NABCI 2022), and state or in-country assessments for the Neotropical Region. Knowledge gaps on performance likely match those identified by species working groups that build partnerships and knowledge to propose conservation strategies. Information on songbird working groups can be found in the Partners in Flight website. After researchers select one or several species, the next step is to assess the state of knowledge within the annual cycle context. As synthesized by the "Road to Recovery's-Saving Our Shared Birds" initiative guidance document, the first gaps to fill include determining the migratory connectivity and estimating vital rates to identify the population-specific limiting factors and conservation strategies (Road to Recovery 2021). We expect the migratory connectivity information to indicate spatial regions of importance per population, potentially directing research to nonbreeding areas we identified as understudied for migratory songbird species.

For every driver studied, there were mixed results: a statistically supported positive, negative, or no influence on performance. These findings were not surprising given the broad question evaluated by the overview but highlight that songbird species conservation during nonbreeding must consider the study area, methods of gauging performance and species-specific ecology. However, to infer the impact of a driver on individual performance for migratory songbirds in general, we recommend evaluating the implications of the variety of measurements of body condition, apparent survival and persistence to be able to produce evidence synthesis documents. We also recommend future full annual cycle scope papers to

evaluate which are the best performance predictors for annual population trends.

Syntheses and reviews are valuable for learning about migration ecology and identifying next steps. We expect researchers, especially early career and students, to find this descriptive summary of the nonbreeding performance of songbirds as a guide to research opportunities. We promote similar efforts in cataloguing or synthesizing studies in systematic form to expand our question perhaps to other metrics (e.g., other physiology markers such as stress hormones, etc.) or to other taxonomic groups that undergo long-distance migrations.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Conflict of interest statement

The authors have no conflict of interest.

Author contributions

F.R. and C.T. had the original idea to conduct the review, F.R. and C.T. designed the research question, decision trees and synthesis approach, and prepared the manuscript.

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