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The Plight of Migrant Birds Wintering in the Caribbean: Rainfall Effects in the Annual Cycle

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Abstract: Here, we summarize results of migrant bird research in the Caribbean as part of a 75th Anniversary Symposium on research of the United States Department of Agriculture Forest Service, International Institute of Tropical Forestry (IITF). The fate of migratory birds has been a concern stimulating research over the past 40 years in response to population declines documented in long-term studies including those of the IITF and collaborators in Puerto Rico's Guánica dry forest. Various studies indicate that in addition to forest loss or fragmentation, some migrant declines may be due to rainfall variation, the consequences of which may carry over from one stage of a migrant's annual cycle to another. For example, the Guánica studies indicate that rainfall extremes on either the temperate breeding or tropical wintering grounds affect migrant abundance and survival differently depending on the species. In contrast, IITF's collaborative studies of the migrant Kirtland's Warbler (*Setophaga kirtlandii*) in the Bahamas found that late winter droughts affect its annual survival and breeding success in Michigan. We review these IITF migrant studies and relate them to other studies, which have improved our understanding of migrant ecology of relevance to conservation. Particularly important is the advent of the full annual cycle (FAC) approach. The FAC will facilitate future identification and mitigation of limiting factors contributing to migrant population declines, which for some species, may be exacerbated by global climate change.

Keywords: annual cycle; carry over effects; climate change; Guánica; Nearctic-Neotropical

1. Introduction

Since the 50th anniversary of the International Institute of Tropical Forestry (IITF), the institute's wildlife program has increased its research on migrant birds in the Caribbean basin in response to evidence that migrant populations were decreasing in an effort to better understand their winter ecology to help guide conservation efforts. The expansion of IITF's migrant studies coincided with a substantial increase in migrant research by others working on both the breeding and wintering grounds as well as during the migration period (reviewed in Greenberg and Marra [1]). By studying all stages of the migrant annual cycle—breeding, nonbreeding, and migratory stages—in many cases it is now possible to identify when and where in the annual cycle populations are limited or the stage in which mortality is highest. Our migrant studies have taken advantage of recent technological and conceptual advances to better understand how events throughout a migrant's annual cycle are interrelated and how multiple limiting factors affect wintering migrant populations in the Caribbean. Continued population declines of migrants in North America [2] and Puerto Rico [3] provide the impetus for our research. In this essay, we summarize some results of our studies, particularly on the effects of rainfall on different stages of the annual cycle of migrants that winter in the Caribbean. We use a historical approach to relate our avian migrant research over the past 25 years with the advancements in understanding of migrant biology of relevance to their conservation.

1.1. Historical Background

The fate of migratory birds has been a focus of concern stimulating research and conservation over the past 40 years. This concern was due to population declines in migrant birds, which breed in North America and overwinter in the tropics (i.e., Nearctic-Neotropical migrants). Some of this early apprehension arose from long-term population studies in small parks and woodlots of eastern United States, which indicated major declines of forest-dwelling birds, most of which overwinter in the Neotropics [4,5]. Not only was evidence accumulating for migrant declines in the North American breeding grounds, but evidence also came from the tropical wintering grounds where declines were detected in long-term monitoring studies of winter resident migrants in Puerto Rico [6,7]. These migrant declines were also consistent with the impressions of population declines held by local ornithologists, bird watchers, and conservation stewards on various Caribbean islands [8]. Additional analyses suggested that the migrant declines covered major regions of the continent [9,10]. These declines were not just reducing avian abundance and diversity in eastern forests of the U.S. and Canada, where migrants frequently comprise 65%–85% of the breeding birds [11], but these declines were expected to diminish ecosystem services, such as insect pest control and seed dispersal [12]. Concerns arising from these studies provided support for the initiation of the Neotropical Migratory Bird Conservation Program, currently known as Partners in Flight.

At the time of the institute’s 50th anniversary in 1989, the two most commonly cited causes for migrant bird population declines were attributed to deforestation and fragmentation on the temperate breeding grounds and deforestation on the subtropical and tropical wintering grounds. Breeding-ground forest loss and fragmentation were implicated in declines because fragmentation increased the relative amount of edge habitat through which edge-dwelling predators and brood parasites (i.e., cowbirds) obtained access to nests of forest interior species, most of which are Nearctic-Neotropical migrants [5,13,14]. Evidence for tropical deforestation as a driver of migrant declines came from analyses of population trends in long-term Breeding Bird Surveys conducted throughout the continental U.S. by Robbins et al. [15]. Their analyses indicated that 75% of the breeding migrant bird species that wintered in tropical forests declined between 1978 and 1987, a period of rapid deforestation in the Neotropics. In contrast, during the same period migrant species wintering in tropical scrub habitats showed no declines, nor were consistent patterns found in short-distance migrants and resident temperate zone species. The Robbins et al. [15] analyses were expanded and subsequently verified by Askins et al. [4]. Thus, by the time of IITF’s 50th anniversary in 1989, the major factors or stresses hypothesized to cause migrant population declines were viewed as either occurring on the breeding or the wintering grounds, with most declines in the recent past attributed primarily to the negative consequences of breeding ground forest loss and fragmentation [5]. It was recognized, however, that identifying the factor or factors contributing to migrant declines was challenging given their complex life cycle, which often involves several habitats distributed across large spatial scales and ignorance of where specific populations bred, migrated, or overwintered [16].

Improvements in our understanding of the migrant annual cycle are attributable to recent technological advances. For example, increased computational power has facilitated use of more sophisticated statistical and population models to estimate migrant survival at different stages of the annual cycle, and refinements in stable isotope usage and modeling enable remotely sensed determination of habitat use and distribution [17]. In addition, improvements in battery and memory storage have facilitated miniaturization of devices that allow studies of habitat use and distribution of small birds at both the scale of a home range during sedentary periods (with radio transmitters) [18], as well as tracking long-distance movements of birds (with light-sensitive geolocators [19]) during migration and the full annual cycle (henceforth, FAC).

Not only have recent technological advances aided identification of when and where in the annual cycle mortality is greatest for some species, but the FAC focus has enabled biologists to determine how events in one stage of the annual cycle can affect a migrant in some other stage(s). This was nicely illustrated in the pioneering work of Marra et al. [20] who demonstrated a relationship between the quality of a tropical habitat (i.e., food rich vs. food poor) occupied by a migrant during the winter and its subsequent reproductive success on its North American breeding grounds. Studying male American Redstarts (*Setophaga ruticilla*) wintering in Jamaica on high quality habitat (i.e., insect-rich, mangrove forest) and nearby poor quality habitat (i.e., insect-poor, dry second-growth scrub), Marra and his team discovered that males in high-quality winter habitat had better body condition and departed earlier on spring migration and subsequently arrived earlier on the temperate breeding grounds than males that occupied poorer quality habitat. Therefore, males arriving early on the breeding grounds were coming from high quality moist winter habitat as ascertained by stable isotopes, and had high reproductive success. In contrast, males arriving later on the breeding grounds came from low quality winter habitats and had low reproductive success. This contribution, subsequently substantiated by others [21–25], indicates that events occurring during one stage of a migrant's annual cycle can "carry over" to other stages of the annual cycle. We now recognize that wintering ground habitat quality, often governed by moisture availability, can affect migrant reproductive success on the breeding grounds, but also that conditions on the breeding ground can carry over to affect overwinter survival.

1.2. The Caribbean as a Wintering Site

The Caribbean is important for Nearctic-Neotropical migrants because many winter near the continental U.S., where migrants constitute half or more of all terrestrial birds present during the winter in parts of Mexico, the Bahamas, Hispaniola, Cuba, Jamaica, Puerto Rico, and the Virgin Islands [12,26]. Although early analyses suggested that migrant abundance in the islands decreased with distance from North America and increased with island size [27], subsequent analyses found that the distance/size relationship with abundance held only when migrants in the same habitat type were compared among islands [26]. Controlling for habitat type in the latter analyses was required because different habitats on the same island can vary substantially in migrant abundance and species richness. Of the estimated 44 terrestrial migrants that winter in the Caribbean (52% in family Parulidae), small gleaning insectivores are disproportionately overrepresented in contrast to hawking, aerial, and large gleaning insectivores and frugivores and granivores, which are rare or absent [28]. Two migrant species winter exclusively in the Caribbean and have populations considered threatened or endangered (Kirtland's Warbler, *Setophaga kirtlandii*; Bicknell's Thrush *Catharus bicknelli*). Presumed extinct, the Bachman's Warbler (*Vermivora bachmanii*) wintered primarily in Cuba but has not been observed since the early 1970s [29]. Habitat loss, either clearing for agricultural crops on its breeding grounds in the Southeastern U.S. and/or conversion of its winter habitat for sugar cane in Cuba, are suspected to have contributed to its disappearance [29,30].

Forested habitats in the Caribbean have been viewed as precarious given the small land areas and high human population densities on many islands resulting in substantial forest loss and degradation [31–33]. However, much of this forest loss has occurred in the past, and on some islands, the proportion of forest cover has increased in recent years as people abandon agriculture and migrate to towns and cities [34–37]. Although forest cover has increased with abandonment of agriculture on these islands, development and urbanization have increased mostly in the lowlands where habitats continue to face increased development pressures [37,38]. On abandoned lands, some of the regenerating second-growth forests have a mix of native and alien tree species and given this mixture, have been designated as novel forests [39,40]. Although the suitability of novel forests to provide habitat for wintering migrants requires more study, evidence suggests that suitability is related to the specific dominant alien tree species in the forest. For example, a study by Beltrán and Wunderle [41] found that some alien tree species with an abundance of insects were favored foraging sites for some insectivorous birds, including migrants, whereas other alien tree species, some with few insects, were avoided by insectivores. Even cultivated lands with a shade overstory, such as shade coffee plantations, can provide winter habitat for some migrants [26,42], which can be equivalent to natural forest in terms of overwinter site fidelity and annual return [43]. The trend in the Caribbean, however, is to eliminate the shade overstory to permit open grown sun coffee, which is less suitable for many wintering migrants. Thus, the availability of forest or forest-like habitats for migrants wintering in the Caribbean is in flux, suggesting that on some islands availability of winter habitats for migrants may be increasing relative to 50 years ago.

2. Institute Migrant Studies

2.1. Rainfall Effects in the Long-Term Studies of the Winter-Resident Bird Community in the Guánica Dry Forest in Puerto Rico

A long-term bird monitoring program, based on a mist-netting session for three consecutive days each January, was established in the Guánica Commonwealth Forest, a United Nations Biosphere Reserve, in southwestern Puerto Rico. Initiated in 1972, the ongoing, annual netting session has been conducted every January (except in 1977 and 1979) for 45 years in one of the last remaining tracts of nearly pristine subtropical dry forest in the Caribbean (site and methods described in [6,7]). The Guánica migrant bird community is comprised of two diverse sets of seasonal residents [44]: (1) winter residents that are fully integrated into the Guánica forest bird community and consisting of mostly territorial species (e.g., Black-and-white Warbler *Mniotilta varia*, American Redstart and Ovenbird *Seiurus aurocapilla*); and (2) opportunistic species whose numbers vary greatly from year to year and show little site fidelity (Cape May Warbler, *Setophaga tigrina*; Northern Parula, *S. americana*; and Prairie Warbler, *S. discolor*, among others). The Guánica constant-effort mist-netting program has documented dramatic declines in several species of year-round resident birds as well as the dominant set of winter resident migrants (henceforth, "winter residents"), as evidenced by capture rates that are now ~33% of the capture rates recorded 20 years ago [3]. Population estimates for the three most commonly captured winter residents (American Redstart, Black-and-white Warbler, Ovenbird) have declined markedly, and other formerly common migrant species are rarely captured. Despite these dramatic declines in captures of winter residents, annual survival rates of the three most common species have remained constant [3,17], suggesting that declines in migrant captures are driven by declining recruitment into the Guánica forest.

Rainfall, either on the breeding or wintering grounds, affects migrant abundance in the Guánica forest. Total winter resident abundance in Guánica appears to be influenced by rainfall on the breeding grounds. Declines in total winter resident captures following breeding ground droughts were followed by quick recovery in captures when breeding ground rainfall returned to normal [3,17]. Nevertheless, individual species differed in their abundance responses to various rainfall measures, as uncovered in a modeling analysis combined with knowledge of each species' breeding regions (mostly eastern U.S.) as determined with stable hydrogen-isotopes [17]. For example, variation in rainfall in Guánica, measured as total deviation (absolute value) from normal total rainfall, had a positive influence on the abundance of Black-and-white Warblers. Although this finding was unexpected, Duggers et al. [17] speculated that perhaps it resulted from density-dependent effects of permanent resident bird populations (via diffuse competition) on winter resident abundance in Guánica. Ovenbirds, in contrast, were affected by breeding ground rainfall, measured as total annual rainfall in the continental United States, which had a negative effect on their abundance in Guánica. The decline in Ovenbird captures with increased rainfall on the breeding grounds was attributed to reduced reproductive success, perhaps due to flooding of nests or chilling of chicks in this ground-nesting species [17]. The authors also suggested that increased rainfall during fledging and prior to fall migration might contribute disproportionately to juvenile mortality further diminishing the number of Ovenbirds migrating south to Guánica.

Rainfall in Guánica also affects migrant survival, although rainfall effects on survival were only weakly supported for Black-and-white Warbler or for American Redstart [17]. The strongest support for a Puerto Rican rainfall effect on apparent survival for each of these two species was the measure of Guánica rainfall in the first six months of the prior year. Apparent survival for both species declined in response to increased rainfall in the first six months of the prior year, possibly due to diffuse interspecific competition between winter and permanent residents. Previous studies demonstrated that the size of permanent resident populations was positively related to rainfall in

January–June because of dependence on early rains to end the dry season, thereby stimulating insect outbreaks and facilitating resident breeding [7,45,46]. Therefore, more rainfall in the first six months of the year results in more permanent resident insectivores, which in turn, increases competition and reduces habitat quality for the winter insectivorous residents. Further support for the role of competition from permanent resident insectivores comes from the studies of IITF cooperator, Judith Toms, who found that American Redstart abundance was reduced in areas of high density of the insectivorous, permanent resident Adelaide's Warblers (*Setophaga adelaidae*) in Guánica [47]. Given reduced habitat quality (i.e., fewer insects), migrant survival is reduced or migrants abandon Guánica for other wintering sites. In contrast, Ovenbird apparent survival was not influenced by rainfall in Guánica, but rather by summer rainfall in the southeastern U.S., to which adult survival responded positively [17].

In summary, the long-term monitoring study in Guánica has uncovered some diverse responses of migrants to various rainfall measures from the breeding and wintering grounds, depending on the species. Although the responses of the individual species to rainfall were strongest for abundance and weakest for survival, the general patterns for abundance were consistent with the best survival models for the two species with adequate data to model both response variables [17]. For instance, abundance and survival in Ovenbirds and Black-and-white Warblers appeared to be related to breeding ground and wintering ground rainfall, respectively. Although Dugger et al. [17] expected a direct relationship between rainfall, habitat quality, and migrant demography, their modeling efforts with Black-and-white Warblers suggest that rainfall positively affected abundance of permanent residents, thereby causing diffuse competition for food, resulting in a density-dependent effect on winter residents. Therefore, rainfall can affect migrant demography directly (e.g., mortality due to exposure) or indirectly (e.g., increased competition from permanent residents [47]) on either the breeding or wintering grounds, depending on the species. As Dugger et al. [17] note, testing their density-dependent hypothesis will require continued monitoring of wintering and permanent-resident populations to ascertain how those populations fluctuate together over time in the Guánica forest.

2.2. Winter Rainfall Effects on Kirtland's Warblers in the Bahamas Carry Over to the Michigan Breeding Grounds

Evidence for carryover effects of wintering ground rainfall has been found in the Kirtland's Warbler (henceforth, KIWA), a species for which the breeding and wintering grounds are well known. The KIWA winters in the Bahamas archipelago and breeds primarily in Michigan [48], although small breeding colonies have been recently established in Wisconsin and Ontario [49,50]. Evidence for carryover effects from winter rainfall was first recognized by Ryel [51], who found a positive relationship between winter rainfall in the Bahamas and the number of singing males in Michigan. More recently, Rockwell et al. [24] found that after March droughts in the Bahamas, male KIWAs arrived later on the Michigan breeding grounds, where late arriving males had reduced reproductive success. Sensitivity to March rainfall declines was greater in second year males than in older males; later arrivals corresponded with lower March rainfall in the Bahamas. Although the effects of rainfall on the KIWA's food supply in the Bahamas were unknown at the time of the study by Rockwell et al. [24], previous studies elsewhere indicated drought sensitivity in arthropods [52,53] and fruits [54–56].

Studies on the Kirtland's Warbler were initiated by Wunderle and collaborators because the warbler was poorly known on its wintering grounds, despite recognition that wintering ground events could compromise breeding ground conservation efforts for this federally listed endangered species, and thus the need for wintering-ground studies was recognized [57]. Studies were initiated on the island of Eleuthera in the central Bahamas to characterize the KIWA's winter habitat [58] and to determine whether the warblers were susceptible to declines in food resources [59]. Wunderle and collaborators predicted that the KIWAs would be susceptible to food resource declines because of their use of drought-prone habitats on shallow soils on limestone substrates [58] in the dry season of October–April and especially during the driest period in March and April [60], just prior to vernal migration. Moreover, these late-winter droughts are not uncommon in the Caribbean and Middle America, where they have been found to affect migrant body condition [61], as also documented in Guánica [47]. Thus, it was predicted that rainfall or moisture conditions would influence food availability, which in turn would affect KIWA body condition, thereby setting the stage for carryover effects on reproductive success on the breeding grounds.

The study, conducted over four winters on Eleuthera [59], indicated that the warbler's food resources (fruit and arthropods) typically declined during the winter, but varied between winters and study sites. Rainfall was found to be an important driver of variation in fruit abundance, which was not surprising, given the high-water content (60%–70%) of fruits consumed by KIWAs. Despite variation in food availability, the proportion of fruits and arthropods in the KIWA diet (88% of 90 fecal samples contained both) varied little within or among winters, as expected for birds tracking food resources by moving from food-poor to food-rich sites. Supporting this resource-tracking hypothesis was the finding that when KIWAs shifted between study sites within a winter, they moved to sites with higher biomass of ripe fruit and ground arthropods, so that by late-winter, densities of the warbler were positively correlated with biomass of fruits and ground arthropods. Given changes in food abundance in space and time, the researchers expected that the KIWAs would not reside at one site for the entire winter, and indeed the warblers' overwinter site fidelity was low (an average of 43% of the KIWAs stayed on the same site from October to April), and this pattern varied with intensity of the late winter drought.

Evidence for intraspecific resource competition in the KIWAs mediated by dominance hierarchies was found in overwinter site fidelity, which differed by sex (males > females) and age class (adults > juveniles). Sex and age differences in corrected body mass (i.e., body mass scaled to body size) and fat scores were evident from midwinter through late winter, and consistent with outcomes from dominance and experience. Late-winter rains had a positive effect on corrected body mass, suggesting that in drought years the KIWAs might have inadequate body condition for early spring migration and thus arrive late on the breeding grounds, as expected from Rockwell et al.'s carryover effect studies [24].

The data on overwinter site fidelity and annual return of banded KIWAs (2003–2010) combined with the breeding ground site fidelity and annual return data (2006–2011) were used to estimate apparent annual, oversummer, overwinter, and migratory survival for the warbler [62]. These analyses were restricted to males, as sample sizes for females were inadequate for modeling the two mark-recapture data sets. The mean annual survival probability for male KIWAs was 0.58 ± 0.12 SE, a value consistent with annual survival estimates for other migrant warblers (reviewed in [14]). Monthly survival rates for the male KIWAs were relatively high during the stationary periods of the annual cycle (summer = 0.963 ± 0.01 SE; winter = 0.97 ± 0.01 SE) in contrast to the markedly lower monthly survival rates during the migratory period (0.886 ± 0.05 SE), which accounted for ~41% of all annual mortality of adult birds. Using a model selection framework, Rockwell et al. [62] also evaluated the influence of multiple climate variables on annual survival of the KIWA. Their analysis indicated that March rainfall in the Bahamas was the best-supported predictor of annual survival probability. Moreover, March rainfall was positively correlated with KIWA apparent annual survival in the subsequent year, indicating that the late winter rainfall effect carried over to influence an individual's survival probability in later stages of the annual cycle. Thus, the demonstration that March rainfall predicts annual survival of KIWAs corroborates theoretical and empirical evidence that migratory bird populations can be limited by weather on the wintering grounds.

Given the importance of wintering-ground rainfall to the KIWA's food resources, body condition, reproductive success, and annual survival, Wunderle et al. [59] recommended that conservation efforts for the KIWA in the Bahamas archipelago should focus on protecting the least drought-prone habitats. Habitats situated on sites with a shallow freshwater table could be especially important for providing "refugia" for the warblers during late winter droughts. These habitats have been characterized as anthropogenically-disturbed early successional sites (3–28 years post-disturbance) with an abundance of fruit [58,59].

3. Discussion and Conclusions

As studies on the Kirtland's Warblers illustrate, an increase in the length or severity of winter droughts in the Bahamas has the potential to lower the KIWA's annual survival and reduce its reproductive success, causing a two-fold negative impact on population dynamics. The sensitivity of the KIWA's population to winter droughts was evident from projection modeling, which indicated that a decrease in Bahamas March rainfall >12.4% from current mean levels could cause the size of the KIWA population to decrease due to winter droughts alone [62]. Further contributing to concerns about rainfall effects on KIWAs and other migrant birds in the Caribbean are predictions of increased occurrence of droughts under multiple climate change scenarios in the Caribbean [63]. Already, rainfall declines have been documented in Jamaica and recent studies there have found that the timing of rainfall within the dry season, not just the total amount, may be critical for setting migrant vernal departure schedules [64]. Declines in average annual rainfall have also been documented in the Bahamas in the period 1959–1990 [65]. More recently, other studies indicate that the frequency of drought and inter-annual variation in rainfall may also be increasing in the region [66,67]. As the climate changes in the Caribbean, wetter life zones may be replaced by drier life zones, as predicted for Puerto Rico based on analyses using model averaging of statistically downscaled general circulation models by IITF colleagues [68].

Increased variability in rainfall is consistent with expectations that global warming could be increasing the severity of El Niño Southern Oscillation (ENSO) events [69]. If this occurs, Sillett et al. [70] predict that the variance in demographic rates of migratory bird populations could be amplified, which could place small populations at risk of extinction. They demonstrated that demographic rates in Black-throated Blue Warblers (*Setophaga caerulescens*) on the Jamaica wintering grounds and north temperate breeding grounds varied with ENSO fluctuations. During El Niño years (dry in Jamaica), adult survival and fecundity were both lower, and during La Niña years (wet in Jamaica), both were higher. As fecundity increased, the recruitment of new individuals into winter and breeding populations also increased. The take-home message from Sillett et al. [70] is that migratory bird populations can be affected by changes in global climate patterns and that it is important for effective conservation interventions to understand how events occurring throughout a migrant's annual cycle interact to affect population size.

Not only are global climate cycles expected to change in the future, but the frequency of the most powerful tropical cyclones, or hurricanes, in the North Atlantic are expected to increase with global warming [71,72]. In the Caribbean, hurricanes occur with sufficient frequency to be an integral part of the natural disturbance regime [73], and evidence to date suggests that migrant populations that have already completed migration and are residing on their nonbreeding grounds are not strongly influenced by these storms. For example, Hurricane Georges struck the Guánica forest in September 1998 and caused extensive tree limb loss and reduced canopy cover, but the effect on winter resident apparent survival estimates was weak [17]. Of the three migrant species in Guánica with adequate sample size, estimated survival of the Black-and-white Warbler showed the strongest effect of the storm, as survival estimates for the year of the storm were lower than other years. This immediate post-hurricane decrease in Black-and-white Warblers is consistent with loss of their preferred foraging substrate, as demonstrated by Wunderle et al. [74] in Jamaican coffee plantations. It is likely that these local declines were not due to mortality (e.g., hurricanes struck in September before most migrant arrival), but more likely, these warblers shifted to other less-affected sites, a common post-hurricane response in many species [74–76]. Despite Hurricane George's effect on the Guánica forest, captures of winter residents peaked three years afterwards [3], a finding consistent with rapid post-hurricane recovery of wintering migrant populations elsewhere [77–79]. Not only do the effects of wintering-ground hurricanes appear to be relatively mild for most migrant populations, but hurricanes might be beneficial for producing disturbed habitats used by species such as the Kirtland's Warbler [80] or, more generally, be associated with new vegetation growth and thus a pulse of arthropod food resources.

We now recognize that the abundance and distribution of migrant birds are limited by events occurring throughout the annual cycle [16,81] and that events happening in one stage may carry over to influence other stages [20,24,62,70]. Without knowledge of the relative importance of various limiting factors during breeding, migratory, and wintering periods on population dynamics for each species of conservation concern, it will be impossible to implement effective management actions for each of these migrant species [16]. As suggested by Sillett and Holmes [82], it is premature to argue that events on the breeding or wintering grounds or during migration are limiting migrant populations until we understand when and where in the annual cycle various events or factors might limit populations and how these factors may cause carryover effects for multiple migrant species. It is this FAC approach, coupled with continued technological breakthroughs, that will facilitate future identification and mitigation of limiting factors contributing to migrant population declines, which may be exacerbated by global climate change.

As climate change continues we expect that there will be certain migrant species, perhaps some abundant, geographically widespread (on both breeding and nonbreeding grounds), and short-distance migrants, that can adapt to climate change. Adapting to environmental change, however, depends on several conditions including adequate genetic variation (de novo and standing variation), strength and spatial patterning of selection, and requires that the pace of environmental change does not exceed the maximum rate of evolutionary change [83,84]. Nevertheless, even with these stringent conditions for the evolution of adaptation, there are examples of adaptation by migrants, such as found in the geographically widespread European Blackcaps (*Sylvia atricapilla*). Approximately fifty years ago, blackcaps began to overwinter in Ireland and the United Kingdom, where plentiful food in bird feeders and milder winters enticed blackcaps to overwinter rather than migrating to their traditional Iberian Peninsula wintering grounds [85]. Despite now wintering in two distinct wintering quarters, blackcaps return annually to nest in Germany where they pair assortatively based on their wintering areas. The birds wintering further north have a selective advantage, as they produce larger clutches and fledge more young than those wintering south in the Iberian Peninsula. Bearhop et al. [85] noted that most of the behavioral changes in the blackcaps had a genetic basis, which when combined with assortative mating could lead to sympatric speciation. Whether the declines in recruitment of winter residents in Guánica represent adaptive responses to climate change, such as a potential shift to other wintering sites, is unknown and remains to be studied. However, this hypothesis seems unlikely, at least for the declines in American Redstarts wintering in Guánica, which correspond with declines on the breeding grounds [86]. In summary, we recognize that certain species have the potential to adapt to climate or anthropogenic habitat changes, but these are species that are least likely to need conservation intervention. Therefore, the focus of our research is on those migrant species most likely to require conservation intervention. Thus, as emphasized in our essay, these conservation efforts are most likely to be effective if based on research that uses a FAC approach for identification of the factor or factors that limit population growth.

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