REVIEW

Evidence for multiple drivers of aerial insectivore declines in North America

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ABSTRACT

Aerial insectivores (birds that forage on aerial insects) have experienced significant population declines in North America. Numerous hypotheses have been proposed for these declines, but current evidence suggests multiple factors could be operating in combination during their annual migratory cycles between breeding and nonbreeding areas. Potential drivers include decreased prey abundance, direct or indirect impacts of environmental contaminants, habitat loss, phenological changes due to warming climate, and conditions on migratory stopover or wintering grounds. While no single threat appears to be the cause of aerial insectivore declines, existing evidence suggests that several of these factors could be contributing to the declines at different times in the annual lifecycle. Breeding productivity for most of these species does not appear to be limited by overall prey abundance, contaminants, or habitat loss, which suggests that similar issues on nonbreeding grounds or carryover effects could play important roles. However, a better understanding of the importance of prey quality throughout the lifecycle is critically needed. Based on current evidence, we propose that changes in availability of high-quality prey, with variability across breeding and nonbreeding grounds, reduce various combinations of fledging success, post-fledging survival, and nonbreeding season body condition of aerial insectivores, resulting in species and geographic differences in population trends. We encourage others to use this hypothesis as a starting point to test specific mechanisms by which availability of high-quality prey influences demographic parameters. We suggest that future research focus on defining prey quality, monitoring insect abundance in conjunction with birds, comparing demographic models across local populations experiencing different population growth rates, and using tracking technology to document important migratory and nonbreeding areas. Considerable research progress already has been made, but additional research is needed to better understand the complex web of potential causes driving aerial insectivore declines.

Keywords: aerial insectivores, carryover effects, contaminants, population declines, prey quality

Evidencia de causas múltiples en las disminuciones de insectívoros aéreos en América del Norte

RESUMEN

Los insectívoros aéreos (aves que se alimentan de insectos aéreos) han experimentado disminuciones poblacionales significativas en América del Norte. Numerosas hipótesis han sido propuestas para estas disminuciones, pero la evidencia actual sugiere que múltiples factores podrían estar actuando en combinación durante sus ciclos migratorios anuales entras las áreas reproductivas y no reproductivas. Las causas potenciales incluyen una menor abundancia de presas, impactos directos o indirectos de contaminantes ambientales, pérdida de hábitat, cambios fenológicos debido al calentamiento climático y las condiciones en los sitios de parada migratoria o de invernada. Mientras que ninguna de estas amenazas parece ser la causa única de las disminuciones de los insectívoros aéreos, la evidencia existente sugiere que varios de estos factores podrían estar contribuyendo a las disminuciones en diferentes momentos en el ciclo de vida anual. La productividad reproductiva para la mayoría de estas especies no parece estar limitada por la abundancia global de presas, los contaminantes o la pérdida de hábitat, lo que sugiere que aspectos similares en las áreas no reproductivas o efectos de arrastre podrían tener roles importantes. Sin embargo, se necesita con urgencia un mejor entendimiento de la importancia de la calidad de las presas a lo largo del ciclo de vida. Basados en la evidencia actual, proponemos que los cambios en la disponibilidad de presas de alta calidad, con variabilidad a través de las áreas reproductivas y no reproductivas, reduce varias combinaciones del éxito de emplumamiento, la supervivencia post-emplumamiento y la condición corporal de la estación no reproductiva de los insectívoros aéreos, dando como resultado diferencias geográficas y entre especies en las tendencias poblacionales. Alentamos a otros a usar esta hipótesis como un punto de partida para evaluar los mecanismos específicos mediante los cuales la disponibilidad de presas de alta calidad influye sobre los parámetros demográficos. Sugerimos que las investigaciones futuras se enfoquen en definir la calidad de presas, monitorear la abundancia de insectos en conjunto con las aves, comparar modelos demográficos a través de poblaciones locales que experimenten diferentes tasas de crecimiento poblacional, y usar tecnología de seguimiento

para registrar las áreas de importancia migratoria y no reproductiva. Ya se ha alcanzado un progreso importante en las investigaciones, pero se necesitan estudios adicionales para comprender mejor la compleja red de causas potenciales que determinan las disminuciones de los insectívoros aéreos.

Palabras clave: calidad de presas, contaminantes, disminuciones poblacionales, efectos de arrastre, insectívoros aéreos

INTRODUCTION

Migratory aerial insectivores are experiencing significant population declines in North America. This diverse guild of birds that consume insects in flight includes swallows, swifts, nightjars, and flycatchers. Bird survey data such as the North American Breeding Bird Survey (BBS), which has been tracking bird abundance and population trends since 1966, have revealed either regional or widespread declines in many of these species (Blancher et al. 2009, Sauer et al. 2017; Appendix Table 1). The majority of declines appear to have started in the 1980s (Nebel et al. 2010, Smith et al. 2015). In the 2012 North American Bird Conservation Initiative's (NABCI) report, "The State of Canada's Birds," aerial insectivores were declining at greater rates than any other bird group and potentially since before the 1980s (NABCI Canada 2012). While many of the species in this guild are still relatively abundant, their steep rates of decline have prompted concern in assessments and management plans, such as the Partners in Flight Landbird Conservation Plan (Rosenberg et al. 2016), the NABCI "State of the Birds 2014" summary report (NABCI 2014), and numerous State Wildlife Action Plans (Appendix Table 1).

Population declines of aerial insectivores appear to vary by species and region (Shutler et al. 2012, Michel et al. 2015, Smith et al. 2015). Nebel et al. (2010) found that aerial insectivores were more likely to be declining than other passerines, with the greatest probability of aerial insectivore declines in northeastern North America. They also found that long-distance migrants were declining more than short-distance migrants. There are also regional patterns of decline within species, such as Vaux's Swifts (*Chaetura vauxi*) declining in their northern range but increasing in their southern range (Pomfret et al. 2014), and nest box occupancy of Tree Swallows (*Tachycineta bicolor*) generally decreasing in the east but increasing in the west, although variations exist among local populations (Shutler et al. 2012). Furthermore, according to BBS population data, flycatchers as a group appear to be faring better than swifts, swallows, and nightjars (Sauer et al. 2017; Appendix Table 1). For the purposes of this review, published study results need to be interpreted within the context of variation in regional and species-specific trends, but we examine all evidence available to inform our final conclusions.

Multiple hypotheses have been posed as to why these birds are declining, including decreases in prey, habitat loss, phenological changes due to warming climate, and degraded wintering ground conditions. Many of these potential drivers are interconnected, and evidence supporting each one exists to some extent. In this review, we examine and synthesize the current evidence supporting each of the potential drivers for aerial insectivore declines and suggest priority research needs for filling key knowledge gaps.

REVIEW OF POTENTIAL CAUSES OF DECLINES

Declines in Aerial Insects

Because aerial insectivores vary considerably in other life history characteristics, one leading hypothesis is that guild-wide declines may be related to their communal prey base of flying insects. Globally, an estimated 41% of insect species are currently in decline (Sánchez-Bayo and Wyckhuys 2019), and invertebrate populations in general have shown an estimated 45% decline over 40 yr, with Lepidoptera abundance declining by an estimated 35% and up to 67% of assessed Orthoptera and 90% of assessed Hymenoptera species being considered vulnerable (Collen et al. 2012, Dirzo et al. 2014). Increasing concern over consequences of pollinator loss has pushed this issue into the spotlight (Potts et al. 2010, Collen et al. 2012). In Britain, two-thirds of moth species declined over 35 yr (Conrad et al. 2006) and three-quarters of nonmigratory butterfly species declined over 30 yr (Warren et al. 2001). Britain and the Netherlands lost ~30% of both their bee and hoverfly species present before 1980 (Biesmeijer et al. 2006), and Germany lost nearly 40% of butterfly species over 2 centuries (Habel et al. 2016). A study of 63 protected areas in Germany estimated a 76% decline in overall biomass of flying insects over a 27-yr period (Hallmann et al. 2017). However, a 30-yr study of aerial insect biomass in southern Britain found a significant decline in only 1 of 4 study areas, although it was unclear whether similar declines might have happened prior to the study at the remaining 3 study sites (Shortall et al. 2009). Although there are less data available in North America, the trends appear similar. Bee species in the United States have shown loss of species richness, abundance, and geographic range (Grixti et al. 2009, Cameron et al. 2011), and declines in moth species have been reported in the northeastern United States (Wagner 2012, Young et al. 2017). Proposed causes of declines in both insect abundance and richness include agricultural intensification,

habitat loss, pesticides, decreased resource diversity, extreme weather events, and warming climate (Potts et al. 2010, Ewald et al. 2015, Sánchez-Bayo and Wyckhuys 2019).

One potential driver for decreases in insect populations, and potentially aerial insectivores, is agricultural changes, such as agricultural intensification and pesticide use. Agricultural intensification over the last several decades has led to changes in crop production practices in order to increase agricultural output, including increased and new agrochemical use, improved drainage, loss of natural habitats such as hedgerows and wetlands, earlier planting and harvesting, and shifts from hay to silage (Chamberlain et al. 2000, Donald et al. 2001, Tilman et al. 2002, Tscharntke et al. 2005, Meehan et al. 2011, Meehan and Gratton 2016). Declines in abundance of (non-aerial) insectivorous birds—often called grassland or farmland birds—have been correlated with agricultural intensification in the United States (Murphy 2003), the UK (Chamberlain et al. 2000, Donald et al. 2001, Benton et al. 2002), and across Europe (Reif 2013), supporting the idea that agricultural changes can affect birds through decreases in food quality or quantity. Some aerial insectivores, such as swallows, often use agricultural landscapes for foraging habitat as well. Studies on Tree Swallows along gradients of agricultural intensity in Quebec, Canada, revealed that agricultural intensification increased interspecific nest site competition with House Sparrows (*Passer domesticus*) and reduced reproductive success and late-season prey abundance, but was not related to observed declines in population or body mass (Rioux Paquette et al. 2013, 2014; Bellavance et al. 2018). While agricultural intensification was not related to Tree Swallow diet in Saskatchewan, Canada, mass and condition were greater in grassland habitat compared to cropland (Michelson et al. 2018). Grassland and pasture sites were correlated with higher prey and Barn Swallow (*Hirundo rustica*) abundance in the UK (Evans et al. 2007), as well as higher return rates and decreased foraging time for Tree Swallows in Saskatchewan, when compared to agricultural or crop sites (Stanton et al. 2016, 2017). Due at least partly to higher flying insect abundance and larger insect prey on farms where animals are bred, livestock farming was the best predictor of breeding Barn Swallows in Italy (Ambrosini et al. 2002a, 2002b) and Poland (Orlowski and Karg 2013). However, while the presence of livestock may potentially be a buffer to population declines, swallow declines were greatest in areas that were more intensively cultivated (Ambrosini et al. 2012). While these studies suggest that agricultural intensity may negatively affect food availability for species such as swallows, the effects of agricultural practices on breeding success, body condition, or survival appear to be more complex and require further investigation.

Increased pesticide use, a component of agricultural intensification, is also suspected to be altering or reducing food availability for insectivorous birds. Examining historical guano deposits from Chimney Swift (*Chaetura pelagica*) and Vaux's Swift roost sites has revealed shifts in diet over the years, corresponding in the Chimney Swift samples with a steep rise in DDT metabolites, potentially indicating large-scale historical changes in insect populations due to pesticides (Nocera et al. 2012, Pomfret et al. 2014). Reduced insect abundance due to pesticide use has been correlated with diminished reproductive success and foraging intensity in grassland bird species in the UK and Common House-Martins (*Delichon urbicum*) in southern France (Poulin et al. 2010). In Gray Partridge (*Perdix perdix*), decreases in prey abundance due to pesticides were directly linked to reduced chick survival and population declines (Rands 1985, Morris et al. 2005, Mineau and Palmer 2013).

Neonicotinoid pesticides in particular have been implicated in the global declines of insect populations, especially pollinator species (Whitehorn et al. 2012, Gilburn et al. 2015, Woodcock et al. 2016). Insects in the order Diptera are not only one of the most common and nutritionally important items in the diets of swallows (McCarty and Winkler 1999, Beck et al. 2013, Twining et al. 2016, 2018), but were also among species of aquatic insects (along with other aerial insect groups such as Ephemeroptera and Trichoptera) most sensitive to acute and chronic toxicity of neonicotinoids (Morrissey et al. 2015). Furthermore, >74% of surface water studies from 9 countries reporting maximum and average neonicotinoid concentrations were above the thresholds recommended for avoiding both short-term and long-term impacts to aquatic invertebrate communities (ranging from impacts on growth and emergence to lethal effects), indicating the potential for broad-scale impacts to important prey taxa for aerial insectivores (Morrissey et al. 2015). Neonicotinoid use in the Netherlands was correlated with declines of insectivorous bird species, including Barn Swallows, after their introduction in the mid-1990s (Hallmann et al. 2014). The American Bird Conservancy has suggested that the toxicity of neonicotinoids may require further assessment, and the possibility of broad aquatic contamination from neonicotinoids means that the effects of these insecticides should be examined on a much larger scale—watershed or regional—than at the farm level (Mineau and Palmer 2013). However, the widespread use of neonicotinoids started in early 1990s, well after the probable initiation of aerial insectivore declines. Thus, while neonicotinoids are potentially exacerbating these species' population declines through decreased food availability, it is unlikely that their use initiated the observed population declines.

Studies correlating insect declines or contamination from insecticides on the breeding ground with breeding and productivity of aerial insectivores are lacking, although

this does not eliminate the possibility that changes in diet quality might have negative effects or the potential for significant carryover effects beyond the breeding season. Twining et al. (2016) found in a controlled laboratory study that diet quality, specifically related to levels of highly unsaturated omega-3 fatty acid in prey, improved Tree Swallow nestling performance more than food quantity, suggesting that abundance of high-quality aquatic insects with more of these fatty acids than terrestrial insects could be a better predictor of breeding success than overall insect abundance. Using field data, they further demonstrated a positive association between aquatic insect biomass and reproductive success (Twining et al. 2018). Neither nestling survival nor mass were related to total insect abundance in 3 species of swallows experiencing steep declines at 3 study sites in New Brunswick, Canada, providing further evidence that total insect abundance alone might not affect breeding success (Imlay et al. 2017). If findings for other locations and other species are similar, such results would suggest that changes in the availability of high-quality prey could be more important for aerial insectivore populations than overall insect abundance. Such changes could result from population declines of those insects providing key nutrients, due to increasing mismatches in availability of those key insects and aerial insectivore breeding phenology with changing climate (as suggested by Twining et al. 2018) or nonlethal impacts of pesticides on aquatic insect growth and emergence (Morrissey et al. 2015). English et al. (2018) found a 1.4–2.8% decline in δ^{15}N values of Eastern Whip-poor-will (*Antrostomus vociferous)* tissues over the last 130 yr, suggesting that this species is decreasing its trophic position, adding further evidence that prey quality could be declining. Additional data on dietary requirements or how reduced prey quality impacts other species of aerial insectivores, as well as direct evidence that reduced prey quality is associated with population change, are needed to understand what role changes in prey quality are playing in overall declines of aerial insectivores.

Contamination

In addition to reducing food availability, pesticides and other environmental contaminants may affect insectivorous birds directly, such as through contamination of food sources. Contaminants can bioaccumulate in insects exposed to pesticides or polluted aquatic systems, and these contaminants can be transported up the food web to insectivorous birds. Many aerial insectivores have a diverse food base, and thus are vulnerable to contaminants from both terrestrial and aquatic systems (Alberts et al. 2013, Rowse et al. 2014). Higher concentrations of contaminants such as selenium and mercury have been found in aquatic insects compared to terrestrial insects, and riparian swallows with greater

proportions of aquatic insects in their diet consequently showed more exposure (Alberts et al. 2013). Detectable levels of phyto-pharmaceutic compounds (such as neonicotinoids) were reported in roughly 30% of Tree Swallow boluses sampled along an agricultural gradient in Canada (Haroune et al. 2015). Species such as Purple Martin (*Progne subis*) consume twice as much insect biomass on their breeding grounds than elsewhere throughout their range, so the risks of biomagnification on the breeding grounds are high (Kelly et al. 2013).

There have been notable cases of bird mortality due to consuming insects contaminated with agrochemicals (Goldstein et al. 1999). In the United States, higher correlation was found between grassland bird species decline and lethal risk from insecticide use than with herbicide use or agricultural intensification (Mineau and Whiteside 2013). Neonicotinoids such as imidacloprid have shown moderate to high toxicity to the few bird species assessed (Gibbons et al. 2015). However, exposure to pesticides may also have significant sublethal effects on birds and other vertebrates, such as diminished growth, immune response, development, and reproductive success (Lopez-Antia et al. 2013, 2015; Gibbons et al. 2015), as well as impairing migratory orientation of birds (Eng et al. 2017). A variety of pollutants have been shown to cause reproductive effects in birds, including organophosphate pesticides, petroleum hydrocarbons, heavy metals, herbicides, fungicides, and, perhaps most infamously, organochlorine pesticides such as DDT and its analogs (Fry 1995). Acadian Flycatchers (*Empidonax virescens*) suffered reduced reproductive success at trace levels of mercury that were lower than previously described thresholds, most likely due to the prevalence and mobility of mercury in aquatic systems (Rowse et al. 2014). Presently, global use of neonicotinoids has resulted in widespread contamination of agricultural soils, freshwater resources, wetlands, and coastal marine systems, with huge knowledge gaps in sublethal effects (other than in bees) and long-term toxicity on nontarget organisms (Van der Sluijs et al. 2015). More data are needed on the effects of contaminants on the full life cycle of aerial insectivore birds, including the potential for sublethal and carryover effects.

Breeding Habitat Loss

Population declines of many bird species, including aerial insectivores, have been attributed to habitat loss (Robbins et al. 1989, Herkert 1994, Grüebler et al. 2010). Species with more specific habitat requirements may be more vulnerable to habitat loss, such as Eastern Whip-poor-wills (Purves 2015). Whip-poor-will abundance in Ontario was related to both habitat and food supply, and the early successional habitat in which they are

often found has been in decline in northeastern North America due to a lack of natural disturbance allowing for forest succession (Askins 2001, English et al. 2017b). Declines of several species of flycatchers also might be driven by breeding habitat loss, including Eastern Kingbird (*Tyrannus tyrannus*; human development and forest succession; Murphy and Pyle 2018), Willow Flycatcher (*Empidonax traillii*; destruction and degradation of shrubby riparian habitats; Remsen 1978, Serena 1982), Least Flycatcher (*Empidonax minimus*; loss of contiguous forest patches and suitable forest structure; Dellasala and Rabe 1987, Holmes and Sherry 2001), and Olive-sided Flycatcher (*Contopus cooperi*; lower nest success in harvested forests compared to post-fire forests; Robertson and Hutto 2007). However, not only do most species in the aerial insectivore guild use a variety of habitats, but the population trends vary by species and region (Shutler et al. 2012, Michel et al. 2015, Smith et al. 2015). Consequently, it is unlikely that population declines can be attributed solely to forest or agricultural landscape changes (Blancher et al. 2009).

Loss of nesting substrate could affect breeding success of birds and is more easily examined in species that use artificial habitat such as nest boxes or chimneys. However, many studies on Tree Swallows have found decreasing nest box occupancy despite no change in the number of potential nesting sites, such as a 19% occupancy decline during a 5-yr period (Robillard et al. 2013, Rioux Paquette et al. 2014). A Tree Swallow population in New Brunswick, Canada, collapsed by 95% over a 23-yr period despite stable reproductive and survival rates and despite the surrounding habitat remaining unchanged for a 70-yr period (Shutler et al. 2012, Taylor et al. 2018). Chimney Swifts were not limited by nesting sites in Connecticut (Rubega 2013) or in Ontario, where over 75% of suitable chimneys remained unoccupied from 2009 to 2011 (Fitzgerald et al. 2014). Such studies suggest that many of these species are not limited by nesting substrate. In contrast, the provision of housing for Purple Martins has benefitted or even recovered local populations, although it is unclear whether these effects extend to populations at higher scales (Brown and Taroff 2013). Anecdotally, Barn Swallows might be negatively impacted by the loss of old wooden barns as nesting habitat in northeastern North America (Connecticut Audubon 2013); Barn Swallow distribution and colony size was positively correlated with presence of older barns in Italy (Ambrosini et al. 2002b). With a few exceptions (e.g., whip-poor-wills, some flycatchers), breeding habitat loss or loss of suitable nesting structures does not appear to be a significant threat for aerial insectivores, although we also need a better understanding of what constitutes good foraging habitat for these species.

Climate Change

Climate change has resulted in a number of impacts to bird species, including both distributional shifts in species' ranges and phenological changes, such as earlier migration arrival and nesting (Parmesan and Yohe 2003). Flycatchers in Europe have advanced their laying date but not arrival date over the last 20 yr in response to increasing spring temperatures (Both and Vissar 2001, Both et al. 2004); consequently, population declines have been attributed to a mismatch in timing of breeding with peak food abundance (Both et al. 2006). Tree Swallows studied at 5 sites across Canada and the northern United States advanced their mean laying date by 9 days over about 60 yr (Dunn et al. 2011) and in southern Quebec advanced their laying date by 4.2 days over a 10-yr period (Bourret et al. 2015). Other studies have found mixed results on the relationship between breeding dates and peak food abundance or biomass (Dunn et al. 2011, Rioux Paquette et al. 2013, 2014; Twining et al. 2018). Tree Swallow adult survival in Saskatchewan and fledging success in New York were driven more by local rather than continental weather conditions (Winkler et al. 2013, Weegman et al. 2017). Barn, Tree, and Cliff (*Petrochelidon pyrrhonota*) swallows in New Brunswick and Nova Scotia, Canada, advanced their breeding by 8–10 days over ~60 yr. While these populations have experienced improved or stable reproductive success, Bank Swallows (*Riparia riparia*), which have not advanced their breeding significantly, showed much lower success at all stages of breeding (Imlay et al. 2018). Despite this last example, the current evidence that climate change is having a significant effect on aerial insectivore population declines through phenological changes is weak and does not necessarily coincide with the timing of these declines, although there does appear to be future potential for phenological and distributional changes to exacerbate stressors already affecting these species.

Nonbreeding Ground Effects

The potential causes of aerial insectivore population declines discussed so far have all been considered mostly in relation to the breeding grounds of these migratory birds; however, these factors may also still be relevant during migration and on the wintering grounds. In some breeding grounds–based studies on Tree Swallows, a lack of change in productivity or breeding season survival concurrent with the observed population declines suggests that nonbreeding effects, such as migration and wintering ground conditions, along with local population immigration–emigration dynamics, may be significant (Rioux Paquette et al. 2014, Taylor 2018). A significant decrease in female Tree Swallow body mass at breeding sites in southern Quebec was independent of breeding habitat quality, also suggesting carryover effects from nonbreeding grounds (Rioux Paquette et al. 2014). The growth rate of

a Tree Swallow population in southern Ontario appeared to be driven by a combination of fledging rate, juvenile recruitment, and return rates of adult females, suggesting importance of both breeding and nonbreeding ground effects in that population (Cox et al. 2018). Other studies failed to find any strong associations between expected wintering regions and survival rates in numerous breeding Tree Swallow populations across North America (Clark et al. 2018) and found that female Tree Swallows are also more likely to disperse after failed reproduction, which may complicate measures of adult survival and reproductive success (Lagrange et al. 2014, 2017). However, there remains an overall lack of consensus on population decline drivers on the breeding grounds of aerial insectivores. Furthermore, although most aerial insectivore species are declining, there is also variation in the spatiotemporal patterns of these declines, and the lack of synchronicity among species and regions on the breeding grounds could suggest that nonbreeding conditions are important drivers of population trends (Michel et al. 2015).

Unfortunately, comprehensive data on migratory routes and strategies or wintering ranges is lacking for many aerial insectivores. While some long-distance migrants appear to be declining more than short-distant migrants, migration patterns are often poorly described (Blancher et al. 2009, Nebel et al. 2010, Calvert et al. 2012). Eastern Whip-poor-wills exhibited sex-differential migration as well as "leap-frog" migration, where northern birds appeared to migrate farther than southern birds, potentially explaining higher declines in the northern populations (English et al. 2017a). A small number of Common Nighthawks (*Chordeiles minor*) tracked from a breeding population in Alberta, Canada, showed relatively strong migratory connectivity to wintering locations in east-central Brazil and all used relatively similar migratory routes during fall and spring migration (Ng et al. 2018). Hobson et al. (2015) found a strong east–west migratory divide for Barn Swallows in North America, with the eastern birds also exhibiting a leapfrog migration pattern and traveling farther than western birds. Such migration patterns may explain the higher declines in northeastern populations of Barn Swallows found in other studies (Michel et al. 2015), as well as the greater effect that El Niño Southern Oscillation had on survivorship of Washington populations compared to Ontario populations (Garcia-Perez et al. 2014). However, Purple Martin populations from eastern North America exhibited weak migratory connectivity, with individuals from different breeding populations sharing roost sites in the Amazon, indicating that the declining northern breeding populations likely experience conditions on the wintering grounds that are similar to those of more stable breeding populations (Fraser et al. 2012, 2017). Tree Swallows from 12 breeding sites across North America exhibited strong

connectivity between breeding and fall stopover locations, but then showed reduced connectivity at nonbreeding sites during the winter, where many individuals from different breeding populations used multiple widely spaced sites around the Gulf of Mexico (Knight et al. 2018). These results emphasize the difficulty in linking nonbreeding effects with population trends of breeding populations when many individuals are moving among several nonbreeding sites (also documented for Purple Martins by Fraser et al. 2017), but also indicate the need to develop a more detailed understanding of the scale and spatial patterns of threats to aerial insectivores across the nonbreeding grounds.

Overall, it is still unclear whether differences in rates of decline for aerial insectivores could be attributed to differences in migration routes or in wintering ground areas, or a combination of these factors. Most aerial insectivore species winter in Central or South America, and there are generally less data on potential drivers of decline in these regions, including food availability and quality, pesticide use, and habitat loss. A review of the effects of pesticide use on rice fields on birds, including information from South America, provides significant evidence of the lethal and sublethal effects that pesticide use in agricultural systems can have on birds (Parsons et al. 2010), and there are suggestions that many of the persistent organochlorine pesticides (including DDT) no longer in use in North America may still be used in South America (Fry 1995). With the likelihood that many of these pesticides are still in use in various agricultural systems throughout the western hemisphere, the potential for at least sublethal effects on some aerial insectivore species from pesticide use on the wintering grounds seems likely, but to our knowledge has yet to be demonstrated. Furthermore, the potential for carryover effects from both the breeding and wintering grounds make this topic an especially challenging one to address. Better information is needed on the migratory strategies of these birds, the areas where they winter, and the threats that they are facing on the nonbreeding grounds.

CONCLUSIONS AND FUTURE RESEARCH NEEDS

Determining what initiated declines of many aerial insectivores around the 1980s in North America is complicated by the lack of historical data on potential causal factors, especially changes in insect populations and changes in nonbreeding ground conditions. However, our review suggests that neither phenological mismatches due to climate change, nor direct mortality due to contaminants, nor direct or indirect impacts from the introduction of neonicotinoid pesticides are likely causes of those initial declines. Nonetheless, aerial insectivore species are clearly facing multiple stressors that vary by region and species across North America. Evidence suggests complex

interactions might occur between stressors at different spatial scales and during different portions of the annual lifecycle. Eastern Whip-poor-will abundance was associated with both habitat and food supply across multiple spatial scales in Canada (English et al. 2017b), and it has been suggested that both migration distance and dietary change may explain declines of Vaux's Swifts in their northern range (Pomfret et al. 2014). Cox et al. (2018) provide evidence that growth rate of a Tree Swallow population in southern Ontario is driven by a combination of breeding (fledging rate), post-breeding (juvenile recruitment), and nonbreeding (adult female return rate) effects. Although there is uncertainty regarding each of the potential threats, there is also evidence that many of them could be impacting one or more species of aerial insectivores. Another challenge is that, although population declines of aerial insectivore species are often referred to as a guild-wide phenomenon (McCracken 2008, Nebel et al. 2010), studies need to be structured by region, life history characteristics, or species (Michel et al. 2015).

We encourage continuing research on the groups of aerial insectivores that appear to be faring the worst: swallows, swifts, and nightjars. A study on change points in population trajectories of aerial insectivores found an overall group-level trend of a brief period of increase followed by a decrease starting in the mid- to late 1980s and continuing until the present. Swallows, swifts, and nightjars as a group were more consistent in the timing of the negative change point than flycatchers and exhibited less geographic variation in declines (Smith et al. 2015). BBS data appear to show smaller rates of decline for flycatchers as a group (Sauer et al. 2017; Appendix Table 1).

There are still many questions that remain unanswered about aerial insectivore declines. While a lack of conclusive evidence for breeding ground drivers for most species suggests nonbreeding ground effects are important, better information is needed on individual components of the nonbreeding period. Further research on winter distributions and migratory strategies of these species is necessary to assess the impact of nonbreeding ground conditions, including seasonal timing, length of migratory periods, significant stopover locations, and stopover duration. Importantly, there is not enough data on the dietary requirements of most of these species, including the importance of high-quality prey. While breeding habitat loss only appears to be a significant threat for certain species, such as Eastern Whip-poor-wills, we also need a better understanding of foraging habitat for aerial insectivore species.

A small but growing body of evidence suggests prey quality is important for reproductive success and body condition (Twining et al. 2016, 2018) and that diet composition of some aerial insectivores has changed over time (Nocera et al. 2012,

Pomfret et al. 2014, English et al. 2018). However, we currently lack evidence that changes in availability of high-quality prey is directly limiting population growth of aerial insectivores at any spatial scale, in part because we know little about defining prey quality. Nonetheless, we propose a general hypothesis that changes in availability of high-quality prey, with spatiotemporal variability across the breeding and nonbreeding grounds due to a complex interactions of multiple effects (e.g., broad application of pesticides, agricultural intensification and other land use changes, changes in climate), have variably impacted combinations of fledging success, post-fledging survival, and nonbreeding season body condition (including associated carryover effects) of aerial insectivores, all of which contribute to spatial, temporal, and species variation in population trends. While this hypothesis lacks many details, we believe it is consistent with most of the results reviewed in this paper. The most complete body of knowledge currently exists for Tree Swallows (e.g., Rioux Paquette et al. 2014, Twining et al. 2016, Weegman et al. 2017, Cox et al. 2018, Twining et al. 2018), and we acknowledge a heavy influence of Tree Swallow on this hypothesis. Although our hypothesis might be less appropriate for swifts and nightjars, we encourage others to use this general hypothesis as a starting point for further investigations into the mechanisms of aerial insectivore declines and to test more specific ideas regarding mechanisms by which availability of high-quality prey might impact key demographic parameters throughout the annual lifecycle.

We suggest the following topics as priority research needs for understanding aerial insectivore declines:

1. Assess the influence of different insect prey (e.g., aquatic vs. terrestrial, large vs. small) on growth and health of aerial insectivores (as has been done with Tree Swallows) to determine if there are metabolic or physiological performance differences among prey types that could help to define prey quality.

2. Monitor insect populations within and across years at the same sites where aerial insectivores are studied to link multiple components of the insect community, beyond total insect abundance or biomass, to changes in bird demographic parameters and population growth rates.

3. Develop profiles of what constitutes high-quality foraging habitat for different aerial insectivores based on prey quality and availability; compare landscape-scale availability of such habitat between breeding populations with different population growth rates.

4. Develop demographic models for multiple populations representing variation in growth rate across species' ranges to gain insights into demographic drivers of population change and associated environmental factors.

5. Utilize a variety of tracking technologies (e.g., geolocators, nanotags, pinpoint GPS) to more

precisely document migratory patterns and nonbreeding areas of importance for aerial insectivores, including migration timing and routes, locations of common stopover areas, migratory connectivity between breeding and nonbreeding populations, and overwintering areas.

6. Where overwintering areas have been identified, assess location- and habitat-specific seasonal survival rates and changes in body condition during the overwintering period.

7. Investigate carryover effects in survival and reproductive success based on indicators of body condition and health of birds during the post-fledging period and at major migratory stopover locations and overwintering areas. Assess whether availability of high-quality prey during the post-fledging, migratory, and overwintering periods have long-term effects on survival and reproduction.

8. Clarify whether lack of breeding habitat in the form of nest structures is limiting population-level reproductive success for some species (e.g., Barn Swallows).

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LITERATURE CITED

Alberts, J. M., S. M. Sullivan, and A. Kautza (2013). Riparian swallows as integrators of landscape change in a multiuse river system: Implications for aquatic-to-terrestrial transfers of contaminants. The Science of the Total Environment 463-464:42–50.

Ambrosini, R., A. M. Bolzern, L. Canova, S. Arieni, A. P. Møller, and N. Saino (2002a). The distribution and colony size of Barn Swallows in relation to agricultural land use. Journal of Applied Ecology 39:524–534.

Ambrosini, R., A. M. Bolzern, L. Canova, and N. Saino (2002b). Latency in response of Barn Swallow *Hirundo rustica* populations to changes in breeding habitat conditions. Ecology Letters 5:640–647.

Ambrosini, R., D. Rubolini, P. Trovò, G. Liberini, M. Bandini, A. Romano, B. Sicurella, C. Scandolara, M. Romano, and N. Saino (2012). Maintenance of livestock farming may buffer population decline of the Barn Swallow *Hirundo rustica*. Bird Conservation International 22:411–428.

Askins, R. A. (2001). Sustaining biological diversity in early successional communities: The challenge of managing unpopular habitats. Wildlife Society Bulletin 29:407–412.

Beck, M. L., W. A. Hopkins, and B. P. Jackson (2013). Spatial and temporal variation in the diet of Tree Swallows: Implications for trace-element exposure after habitat remediation. Archives of Environmental Contamination and Toxicology 65:575–587.

Bellavance, V., M. Bélisle, J. Savage, F. Pelletier, and D. Garant (2018). Influence of agricultural intensification on prey availability and nestling diet in Tree Swallows (*Tachycineta bicolor*). Canadian Journal of Zoology 96:1053–1065.

Benton, T. G., D. M. Bryant, L. Cole, and H. Q. Crick (2002). Linking agricultural practice to insect and bird populations: A historical study over three decades. Journal of Applied Ecology 39:673–687.

Biesmeijer, J. C., S. P. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. Peeters, A. P. Schaffers, S. G. Potts, R. Kleukers, C. D. Thomas, J. Settele, and W. E. Kuni (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313:351–354.

Blancher, P. J., R. D. Phoenix, D. S. Badzinski, M. D. Cadman, T. L. Crewe, C. M. Downes, D. Fillman, C. M. Francis, J. Hughes, D. J. T. Hussell, et al. (2009). Population trend status of Ontario's forest birds. Forestry Chronicle 85:184–201.

Both, C., and M. E. Visser (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296–298.

Both, C., A. V. Artemyev, B. Blaauw, R. J. Cowie, A. J. Dekhuijzen, T. Eeva, A. Enemar, L. Gustafsson, E. V. Ivankina, and A. Järvinen (2004). Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proceedings of the Royal Society of London: Biological Sciences 271:1657–1662.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser (2006). Climate change and population declines in a long-distance migratory bird. Nature 441:81–83.

Bourret, A., M. Bélisle, F. Pelletier, and D. Garant (2015). Multidimensional environmental influences on timing of breeding in a Tree Swallow population facing climate change. Evolutionary Applications 8:933–944.

Brown, C. R., and S. Tarof (2013). Purple Martin (*Progne subis*), version 2.0. In The Birds of North America (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.287

Calvert, A. M., S. A. Mackenzie, J. M. Flemming, P. D. Taylor, and S. J. Walde (2012). Variation in songbird migratory behavior offers clues about adaptability to environmental change. Oecologia 168:849–861.

Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold (2011). Patterns of widespread decline in North American bumble bees. Proceedings of the National Academy of Sciences USA 108:662–667.

Chamberlain, D. E., R. J. Fuller, R. Bunce, J. C. Duckworth, and M. Shrubb (2000). Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. Journal of Applied Ecology 37:771–788.

Clark, R. G., D. W. Winkler, R. D. Dawson, D. Shutler, D. J. T. Hussell, M. P. Lombardo, P. A. Thorpe, P. O. Dunn, and L. A. Whittingham (2018). Geographic variation and environmental correlates of apparent survival rates in adult Tree Swallows *Tachycineta bicolor*. Journal of Avian Biology 2018:e01659.

Collen, B., M. Böhm, R. Kemp, and J. E. M. Baillie (2012). Spineless: Status and Trends of the World's Invertebrates. Zoological Society of London, London, UK.

Connecticut Audubon (2013). Connecticut State of the Birds 2013: The Seventh Habitat and the Decline of Our Aerial Insectivores. Connecticut Audubon Society, Fairfield, CT, USA. https://www.ctaudubon.org/wp-content/uploads/2013/02/SOTB-13_Final.pdf

Conrad, K. F., M. S. Warren, R. Fox, M. S. Parsons, and I. P. Woiwod (2006). Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. Biological Conservation 132:279–291.

Cox, A. R., R. J. Robertson, B. C. Fedy, W. B. Rendell, and F. Bonier (2018). Demographic drivers of local population decline in Tree Swallows (*Tachycineta bicolor*) in Ontario, Canada. The Condor: Ornithological Applications 120:842–851.

Dellasala, D. A., and D. L. Rabe (1987). Response of Least Flycatchers (*Empidonax minimus*) to forest disturbances. Biological Conservation 41:291–299.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. Isaac, and B. Collen (2014). Defaunation in the Anthropocene. Science 345:401–406.

Donald, P. F., R. E. Green, and M. F. Heath (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society of London: Biological Sciences 268:25–29.

Dunn, P. O., D. W. Winkler, L. A. Whittingham, S. J. Hannon, and R. J. Robertson (2011). A test of the mismatch hypothesis: How is timing of reproduction related to food abundance in an aerial insectivore? Ecology 92:450–461.

Eng, M. L., B. J. M. Stutchbury, and C. A. Morrissey (2017). Imidacloprid and chlorpyrifos insecticides impair migratory ability in a seed-eating songbird. Scientific Reports 7:15176.

English, P. A., D. J. Green, and J. J. Nocera (2018). Stable isotopes from museum specimens may provide evidence of long-term change in the trophic ecology of a migratory aerial insectivore. Frontiers in Ecology and Evolution 6:14.

English, P. A., A. M. Mills, M. D. Cadman, A. E. Heagy, G. J. Rand, D. J. Green, and J. J. Nocera (2017a). Tracking the migration of a nocturnal aerial insectivore in the Americas. BMC Zoology 2:5.

English, P., J. Nocera, B. Pond, and D. Green (2017b). Habitat and food supply across multiple spatial scales influence the distribution and abundance of a nocturnal aerial insectivore. Landscape Ecology 32:343–359.

Evans, K. L., J. D. Wilson, and R. B. Bradbury (2007). Effects of crop type and aerial invertebrate abundance on foraging Barn Swallows *Hirundo rustica*. Agriculture Ecosystems and Environment 122:267–273.

Ewald, J. A., C. J. Wheatley, N. J. Aebischer, S. J. Moreby, S. J. Duffield, H. Q. Crick, and M. B. Morecroft (2015). Influences of extreme weather, climate and pesticide use on invertebrates in cereal fields over 42 years. Global Change Biology 21:3931–3950.

Fitzgerald, T. M., E. van Stam, J. J. Nocera, and D. S. Badzinski (2014). Loss of nesting sites is not a primary factor limiting northern Chimney Swift populations. Population Ecology 56:507–512.

Fraser, K. C., A. Shave, A. Savage, A. Ritchie, K. Bell, J. Siegrist, J. D. Ray, K. Applegate, and M. Pearman (2017). Determining fine-scale migratory connectivity and habitat selection for a migratory songbird by using new GPS technology. Journal of Avian Biology 48:339–345.

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

Fry, D. M. (1995). Reproductive effects in birds exposed to pesticides and industrial chemicals. Environmental Health Perspectives 103(Suppl 7):165–171.

Garcia-Perez, B., K. A. Hobson, G. Albrechts, M. D. Cadman, and A. Salvadoris (2014). Influence of climate on annual survival of Barn Swallows (*Hirundo rustica*) breeding in North America. The Auk: Ornithological Advances 131:351–362.

Gibbons, D., C. Morrissey, and P. Mineau (2015). A review of the direct and indirect effects of neonicotinoids and fipronil on vertebrate wildlife. Environmental Science and Pollution Research International 22:103–118.

Gilburn, A. S., N. Bunnefeld, J. M. Wilson, M. S. Botham, T. M. Brereton, R. Fox, and D. Goulson (2015). Are neonicotinoid insecticides driving declines of widespread butterflies? PeerJ 3:e1402.

Goldstein, M., T. Lacher, B. Woodbridge, M. Bechard, S. Canavelli, M. Zaccagnini, G. Cobb, E. Scollon, R. Tribolet, and M. Hopper (1999). Monocrotophos-induced mass mortality of Swainson's Hawks in Argentina, 1995–96. Ecotoxicology 8:201–214.

Grixti, J. C., L. T. Wong, S. A. Cameron, and C. Favret (2009). Decline of bumble bees (*Bombus*) in the North American Midwest. Biological Conservation 142:75–84.

Grüebler, M. U., F. Korner-Nievergelt, and J. Von Hirschheydt (2010). The reproductive benefits of livestock farming in Barn Swallows (*Hirundo rustica*): Quality of nest site or foraging habitat? Journal of Applied Ecology 47:1340–1347.

Habel, J. C., A. Segerer, W. Ulrich, O. Torchyk, W. W. Weisser, and T. Schmitt (2016). Butterfly community shifts over two centuries. Conservation Biology 30:754–762.

Hallmann, C. A., R. P. Foppen, C. A. van Turnhout, H. de Kroon, and E. Jongejans (2014). Declines in insectivorous birds are associated with high neonicotinoid concentrations. Nature 511:341–343.

Hallmann, C. A., M. Sorg, E. Jongejans, H. Siepel, N. Hofland, H. Schwan, W. Stenmans, A. Müller, H. Sumser, T. Hörren, D. Goulson, and H. de Kroon (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12:e0185809.

Haroune, L., R. Cassoulet, M. P. Lafontaine, M. Bélisle, D. Garant, F. Pelletier, H. Cabana, and J. P. Bellenger (2015). Liquid chromatography-tandem mass spectrometry determination for multiclass pesticides from insect samples by microwave-assisted solvent extraction followed by a salt-out effect and micro-dispersion purification. Analytica Chimica Acta 891:160–170.

Herkert, J. R. (1994). The effects of habitat fragmentation on Midwestern grassland bird communities. Ecological Applications 4:461–471.

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

Holmes, R. T., and T. W. Sherry (2001). Thirty-year bird population trends in an unfragmented temperate deciduous forest: Importance of habitat change. The Auk 118:589–609.

Imlay, T. L., H. A. R. Mann, and M.L. Leonard (2017). No effect of insect abundance on nestling survival or mass for three aerial insectivores. Avian Conservation and Ecology 12:19.

Imlay, T. L., J. Mills Flemming, S. Saldanha, N. T. Wheelwright, and M. L. Leonard (2018). Breeding phenology and performance for four swallows over 57 years: Relationships with temperature and precipitation. Ecosphere 9:e02166.

Kelly, J. F., E. S. Bridge, W. F. Frick, and P. B. Chilson (2013). Ecological energetics of an abundant aerial insectivore, the Purple Martin. PLoS ONE 8:e76616.

Knight, S. M., D. W. Bradley, R. G. Clark, E. A. Gow, M. Belisle, L. L. Berzins, T. Blake, E. S. Bridge, L. Burke, R. D. Dawson, et al. (2018). Constructing and evaluating a continent-wide migratory songbird network across the annual cycle. Ecological Monographs 88:445–460.

Lagrange, P., O. Gimenez, B. Doligez, R. Pradel, D. Garant, F. Pelletier, and M. Bélisle (2017). Assessment of individual and conspecific reproductive success as determinants of breeding dispersal of female Tree Swallows: A capture–recapture approach. Ecology and Evolution 7:7334–7346.

Lagrange, P., R. Pradel, M. Bélisle, and O. Gimenez (2014). Estimating dispersal among numerous sites using capture–recapture data. Ecology 95:2316–2323.

Lopez-Antia, A., M. E. Ortiz-Santaliestra, F. Mougeot, and R. Mateo (2013). Experimental exposure of Red-legged Partridges (*Alectoris rufa*) to seeds coated with imidacloprid, thiram and difenoconazole. Ecotoxicology 22:125–138.

Lopez-Antia, A., M. E. Ortiz-Santaliestra, F. Mougeot, and R. Mateo (2015). Imidacloprid-treated seed ingestion has lethal effect on adult partridges and reduces both breeding investment and offspring immunity. Environmental Research 136:97–107.

McCarty, J. P., and D. W. Winkler (1999). Foraging ecology and diet selectivity of Tree Swallows feeding nestlings. The Condor 101:246–254.

McCracken, J. (2008). Are aerial insectivores being "bugged out"? BirdWatch Canada 42:4–7.

Meehan, T. C., and C. Gratton (2016). A landscape view of agricultural insecticide use across the conterminous US from 1997 through 2012. PLoS ONE 11: e0166724.

Meehan, T. C., B. P. Werling, D. A. Landis, and C. Gratton (2011). Agricultural landscape simplification and insecticide use in the Midwestern United States. Proceedings of the National Academy of Sciences USA 108:11500–11505.

Michel, N. L., A. C. Smith, R. G. Clark, C. A. Morrissey, and K. A. Hobson (2015). Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. Ecography 39:774–786.

Michelson, C. I., R. G. Clark, and C. A. Morrissey (2018). Agricultural land cover does not affect the diet of Tree Swallows in wetland-dominated habitats. The Condor: Ornithological Applications 120:751–764.

Mineau, P., and C. Palmer (2013). The Impact of the Nation's Most Widely Used Insecticides on Birds. American Bird Conservancy, Washington, DC, USA.

Mineau, P., and M. Whiteside (2013). Pesticide acute toxicity is a better correlate of U.S. grassland bird declines than agricultural intensification. PLoS ONE 8:e57457.

Morris, A. J., J. D. Wilson, M. J. Whittingham, and R. B. Bradbury (2005). Indirect effects of pesticides on breeding Yellowhammer (*Emberiza citrinella*). Agriculture, Ecosystems and Environment 106:1–16.

Morrissey, C. A., P. Mineau, J. H. Devries, F. Sanchez-Bayo, M. Liess, M. C. Cavallaro, and K. Liber (2015). Neonicotinoid contamination of global surface waters and associated risk to aquatic invertebrates: A review. Environment International 74:291–303.

Murphy, M. T. (2003). Avian population trends within the evolving agricultural landscape of eastern and central United States. The Auk 120:20–34.

Murphy, M. T., and P. Pyle (2018). Eastern Kingbird (*Tyrannus tyrannus*), version 2.0. In The Birds of North America (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.easkin.02

Nebel, S., A. Mills, J. D. McCracken, and P. D. Taylor (2010). Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation and Ecology 5:1.

Ng, J. W., E. C. Knight, A. L. Scarpignato, A.-L. Harrison, E. M. Bayne, and P. P. Marra (2018). First full annual cycle tracking of a declining aerial insectivorous bird, the Common Nighthawk (*Chordeiles minor*), identifies migration routes, nonbreeding habitat, and breeding site fidelity. Canadian Journal of Zoology 96:869–875.

Nocera, J. J., J. M. Blais, D. V. Beresford, L. K. Finity, C. Grooms, L. E. Kimpe, K. Kyser, N. Michelutti, M. W. Reudink, and J. P. Smol (2012). Historical pesticide applications coincided with an altered diet of aerially foraging insectivorous Chimney Swifts. Proceedings of the Royal Society of London: Biological Sciences 279:3114–3120.

[NABCI] North American Bird Conservation Initiative, U.S. Committee (2014). The State of the Birds 2014 report. U.S. Department of the Interior, Washington, DC, USA. http://www.stateofthebirds.org/2014/

[NABCI Canada] North American Bird Conservation Initiative Canada (2012). The State of Canada's Birds, 2012. Environment Canada, Ottawa, ON, Canada. http://www.stateofcanadasbirds.org/

Orłowski, G., and J. Karg (2013). Partitioning the effects of livestock farming on the diet of an aerial insectivorous passerine, the Barn Swallow *Hirundo rustica*. Bird Study 60:111–123.

Parmesan, C., and G. Yohe (2003). A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Parsons, K. C., P. Mineau, and R. B. Renfrew (2010). Effects of pesticide use in rice fields on birds. Waterbirds 33(Supplement): 193–218.

Partners in Flight Science Committee (2013). Population Estimates Database, version 2013. http://pif.birdconservancy.org/PopEstimates

Pomfret, J. K., J. J. Nocera, T. K. Kyser, and M. W. Reudink (2014). Linking population declines with diet quality in Vaux's Swifts. Northwest Science 88:305–313.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin (2010). Global pollinator declines: Trends, impacts and drivers. Trends in Ecology & Evolution 25:345–353.

Poulin, B., G. Lefebvre, and L. Paz (2010). Red flag for green spray: Adverse trophic effects of *Bti* on breeding birds. Journal of Applied Ecology 47:884–889.

Purves, E. (2015). The role of breeding habitat loss in the decline of Eastern Whip-poor-will (*Antrostomus vociferus*) populations in Canada. M.Sc. thesis, Queen's University, Kingston, ON, Canada.

Rands, M. R. W. (1985). Pesticide use on cereals and the survival of Grey Partridge chicks: A field experiment. Journal of Applied Ecology 22:49–54.

Reif, J. (2013). Long-term trends in bird populations: A review of patterns and potential drivers in North America and Europe. Acta Ornithologica 48:1–16.

Remsen, J.V., Jr. (1978). Bird species of special concern in California. California Department Fish Game, Sacramento, CA, USA.

Rioux Paquette, S. R., D. Garant, F. Pelletier, and M. Bélisle (2013). Seasonal patterns in Tree Swallow prey (*Diptera*) abundance are affected by agricultural intensification. Ecological Applications 23:122–133.

Rioux Paquette, S., F. Pelletier, D. Garant, and M. Belisle (2014). Severe recent decrease of adult body mass in a declining insectivorous bird population. Proceedings of the Royal Society of London: Biological Sciences 281:20140649.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege (1989). Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Sciences 86:7658–7662.

Robertson, B. A., and R. L. Hutto (2007). Is selectively harvested forest an ecological trap for Olive-sided Flycatchers? The Condor 109:109–121.

Robillard, A., D. Garant, and M. Bélisle (2013). The swallow and the sparrow: How agricultural intensification affects abundance, nest site selection and competitive interactions. Landscape Ecology 28:201–215.

Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, et al. (2016). Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States. Partners in Flight Science Committee. https://www.partnersinflight.org/resources/the-plan/

Rowse, L. M., A. D. Rodewald, and S. M. P. Sullivan (2014). Pathways and consequences of contaminant flux to Acadian Flycatchers (*Empidonax virescens*) in urbanizing landscapes of Ohio, USA. The Science of the Total Environment 485-486:461–467.

Rubega, M. (2013). Chimney Swifts in Connecticut. In Connecticut State of the Birds 2013: The Seventh Habitat and the Decline of Our Aerial Insectivores. Connecticut Audubon Society, Fairfield, CT, USA. pp. 18–21. https://www.ctaudubon.org/wp-content/uploads/2013/02/SOTB-13_Final.pdf

Sánchez-Bayoa, F., and K. A. G. Wyckhuys (2019). Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232: 8–27.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, Jr., K. L. Pardieck, J. E. Fallon, and W. A. Link (2017). The North American Breeding Bird Survey, results and analysis 1966–2015. Version 2.07.2017. USGS Patuxent Wildlife Research Center, Laurel, MD, USA.

Serena, M. (1982). The status and distribution of the Willow Flycatcher in selected portions of the Sierra Nevada, 1982.

Wildlife Management Branch Administrative Report 82-27. California Department of Fish and Game, Sacramento, CA, USA.

Shortall, C. R., A. Moore, E. Smith, M. J. Hall, I. P. Woiwod, and R. Harrington (2009). Long-term changes in the abundance of flying insects. Insect Conservation and Diversity 2:251–260.

Shutler, D., D. J. T. Hussell, D. R. Norris, D. W. Winkler, R. J. Robertson, F. Bonier, W. B. Rendell, M. Bélisle, R. G. Clark, R. D. Dawson, et al. (2012). Spatiotemporal patterns in nest box occupancy by Tree Swallows across North America. Avian Conservation and Ecology 7:3.

Smith, A. C., M. A. Hudson, C. M. Downes, and C. M. Francis (2015). Change points in the population trends of aerial-insectivorous birds in North America: Synchronized in time across species and regions. PLoS ONE 10:e0130768.

Stanton, R., R. G. Clark, and C. A. Morrissey (2017). Intensive agriculture and insect prey availability influence oxidative status and return rates of an aerial insectivore. Ecosphere 8:e01746.

Stanton, R. L., C. A. Morrissey, and R. G. Clark (2016). Tree Swallow (*Tachycineta bicolor*) foraging responses to agricultural land use and abundance of insect prey. Canadian Journal of Zoology 94:637–642.

Taylor, L. U., B. K. Woodworth, B. K. Sandercock, and N. T. Wheelwright (2018). Demographic drivers of collapse in an island population of Tree Swallows. The Condor: Ornithological Applications 120:828–841.

Tilman, D., K. G. Cassman, P. A. Matson, R. Naylor, and S. Polasky (2002). Agricultural sustainability and intensive production practices. Nature 418:671–677.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies (2005). Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. Ecology Letters 8:857–874.

Twining, C. W., J. T. Brenna, P. Lawrence, J. R. Shipley, T. N. Tollefson, and D. W. Winkler (2016). Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. Proceedings of the National Academy of Sciences USA 113:10920–10925.

Twining, C. W., J. R. Shipley, and D. W. Winkler (2018). Aquatic insects rich in omega-3 fatty acids drive breeding success in a widespread bird. Ecology Letters 21:1812–1820.

van der Sluijs, J. P., V. Amaral-Rogers, L. P. Belzunces, M. F. Bijleveld van Lexmond, J. M. Bonmatin, M. Chagnon, C. A. Downs, L. Furlan, D. W. Gibbons, C. Giorio, et al. (2015). Conclusions of the worldwide integrated assessment on the risks of neonicotinoids and fipronil to biodiversity and ecosystem functioning. Environmental Science and Pollution Research International 22:148–154.

Wagner, D. L. (2012). Moth decline in the northeast United States. News of the Lepidopterists' Society 54:52–56.

Warren, M. S., J. K. Hill, J. A. Thomas, J. Asher, R. Fox, B. Huntley, D. B. Roy, M. G. Telfer, S. Jeffcoate, P. Harding, et al. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414:65–69.

Weegman, M. D., T. W. Arnold, R. D. Dawson, D. W. Winkler, and R. G. Clark (2017). Integrated population models reveal local weather conditions are the key drivers of population dynamics in an aerial insectivore. Oecologia 185:119–130.

Whitehorn, P. R., S. O'Connor, F. L. Wackers, and D. Goulson (2012). Neonicotinoid pesticide reduces bumble bee colony growth and queen production. Science 336:351–352.

Winkler, D. W., M. K. Luo, and E. Rakhimberdiev (2013). Temperature effects on food supply and chick mortality in Tree Swallows (*Tachycineta bicolor*). Oecologia 173:129–138.

Woodcock, B. A., N. J. Isaac, J. M. Bullock, D. B. Roy, D. G. Garthwaite, A. Crowe, and R. F. Pywell (2016). Impacts of neonicotinoid use on long-term population changes in wild bees in England. Nature Communications 7: 12459.

Young, B. E., S. Auer, M. Ormes, G. Rapacciuolo, D. Schweitzer, and N. Sears (2017). Are pollinating hawk moths declining in the northeastern United States? An analysis of collection records. PLoS ONE 12:e0185683.

APPENDIX TABLE 1. Common aerial insectivore species in the continental United States, with population estimates, trends, estimated percent total population change, and number of State Wildlife Action Plans (WAPs) in which each species is identified as a Species of Greatest Conservation Need. Population estimates taken from Partners in Flight Science Committee (2013), trend data from the North American Breeding Bird Survey (BBS; Sauer et al. 2017), and percent population change from Rosenberg et al. (2016).

Species	Global population estimate	US population estimate	Bbs population trends (1966–2015)	Percent population change (since 1970)	Number of state WAPs
Lesser Nighthawk (Chordeiles acutipennis)	11,000,000	3,000,000	0.2	15%	0
Common Nighthawk (Chordeiles minor)	16,000,000	14,000,000	−1.9*	−58%	27
Common Poorwill (Phalaenoptilus nuttallii)	2,000,000	1,800,000	−0.9	−29%	2
Chuck-will's-widow (Antrostomus carolinensis)	6,000,000	6,000,000	−2.3*	−63%	17
Eastern Whip-poor-will (Antrostomus vociferus)	2,000,000	2,000,000	−2.8*	−69%	30
Black Swift (Cypseloides niger)	190,000	13,000	−6.6*	−94%	8
Chimney Swift (Chaetura pelagica)	7,800,000	7,700,000	−2.5*	−67%	23
Vaux's Swift (Chaetura vauxi)	600,000	250,000	−1.8*	−50%	1
White-throated Swift (Aeronautes saxatalis)	1,100,000	800,000	−1.7	−48%	3
Olive-sided Flycatcher (Contopus cooperi)	1,700,000	840,000	−3.1*	−78%	22
Western Wood-Pewee (Contopus sordidulus)	9,200,000	5,400,000	−1.4*	−47%	1
Eastern Wood-Pewee (Contopus virens)	5,500,000	5,200,000	−1.4*	−44%	9
Yellow-bellied Flycatcher (Empidonax flaviventris)	12,000,000	400,000	2.3*	119%	4
Acadian Flycatcher (Empidonax virescens)	4,500,000	4,500,000	−0.3	−10%	14
Alder Flycatcher (Empidonax alnorum)	130,000,000	31,000,000	−0.9*	−37%	7
Willow Flycatcher (Empidonax traillii)	9,100,000	6,100,000	−1.5*	−46%	21
Least Flycatcher (Empidonax minimus)	36,000,000	4,300,000	−1.7*	−53%	10
Hammond's Flycatcher (Empidonax hammondii)	19,000,000	7,900,000	0.8*	33%	0
Gray Flycatcher (Empidonax wrightii)	3,000,000	3,000,000	2.4*	185%	1
Dusky Flycatcher (Empidonax oberholseri)	7,800,000	4,700,000	−0.6	−26%	1
Eastern Phoebe (Sayornis phoebe)	32,000,000	24,000,000	0.2	29%	0
Say's Phoebe (Sayornis saya)	4,000,000	3,700,000	1.1*	40%	1
Ash-throated Flycatcher (Myiarchus cinerascens)	7,400,000	5,200,000	1.1*	52%	1
Great Crested Flycatcher (Myiarchus crinitus)	6,700,000	6,100,000	0	2%	5
Cassin's Kingbird (Tyrannus vociferans)	6,000,000	2,100,000	0.2	8%	2
Western Kingbird (Tyrannus verticalis)	22,000,000	20,000,000	0.1	20%	2
Eastern Kingbird (Tyrannus tyrannus)	27,000,000	23,000,000	−1.3*	−38%	10
Scissor-tailed Flycatcher (Tyrannus forficatus)	9,500,000	8,700,000	−0.8*	−24%	3
Purple Martin (Progne subis)	7,000,000	6,000,000	−0.9*	−23%	17
Tree Swallow (Tachycineta bicolor)	17,000,000	7,600,000	−1.4*	−40%	3
Violet-green Swallow (Tachycineta thalassina)	7,000,000	4,700,000	−0.7*	−19%	1
Northern Rough-winged Swallow (Stelgidopteryx serripennis)	15,000,000	13,000,000	−0.5*	−18%	3
Bank Swallow (Riparia riparia)	19,000,000	4,000,000	−5.3*	−89%	20
Cliff Swallow (Petrochelidon pyrrhonota)	40,000,000	30,000,000	0.7*	37%	9
Cave Swallow (Petrochelidon fulva)	3,000,000	1,000,000	21.3*	>200%	1
Barn Swallow (Hirundo rustica)	120,000,000	28,000,000	−1.2*	−38%	4

*Asterisk indicates a significant long-term population trend, with the 2.5% and 97.5% percentiles of the posterior distribution of trend estimates not overlapping zero (Sauer et al. 2017).