

**POPULATION DECLINE IN AN AVIAN AERIAL INSECTIVORE
(*TACHYCINETA BICOLOR*) LINKED TO CLIMATE CHANGE**

By
Amelia Robin Cox

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Abstract

Avian aerial insectivores, a taxonomically diverse guild of birds, are facing dire population declines. The primary commonality among these birds is that they forage on flying insects, suggesting that diet has exposed these birds to environmental challenges that cause their decline, but it has been unclear how. For most aerial insectivores the demographic data necessary to isolate the cause of decline are lacking. However, using data from a tree swallow (*Tachycineta bicolor*) population that has been continuously monitored from 1975-2017, I investigated demographic and environmental causes of population decline. In my first chapter, I conducted a life stage simulation to determine which demographic transitions had the most influence on population growth rates, finding that juvenile and adult survival overwinter fledging success had the potential to influence population growth. In my second chapter, I found that both juvenile survival and fledging success declined concurrently with the overall population decline. Poor fledging success was associated with increased predation and rainy, cold weather during nestling development. When raining or cold, the flying insects nestlings rely on are inactive, likely causing temporary food shortages. Low juvenile survival overwinter was linked to poor weather conditions during the post-fledging period and perhaps to conditions on the wintering grounds. Finally, in my third chapter I show that the body mass of older nestlings that are approaching fledging has declined over time. In 2017, nestlings were lighter for their age after rainy weather, suggesting that increasingly poor growth could be explained by more spring rain. As a consequence of climate change, rainfall during nestling development had increased 9.3 ± 0.3 mm/decade, explaining poor nestling growth, fledging success, and potentially juvenile survival. Overall, my findings show that declining nestling and juvenile survival may be driven by increasingly rainy weather, which may in turn cause decline in this tree swallow population and

avian aerial insectivores more generally. Therefore, I suggest that tree swallows and other avian aerial insectivores be added to the growing list of species threatened by climate change.

Co-authorship

This thesis conforms to the publication format as outlined in the Department of Biology Guide to Graduate Studies, with consolidated Acknowledgements and Literature Cited sections.

Manuscripts resulting from the thesis are outlined below:

Chapter 2

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List of Abbreviations

AAI: avian aerial insectivore

AICc: Akaike information criterion, corrected for small sample size

ASY: after-second-year, referring to a bird two years of age or older

ENSO: El Niño Southern Oscillation index

GLM: general linearized model

LMM: linear mixed model

PIT: passive integrated transponder

RFID: radio frequency identification

SY: second-year, referring to a one-year-old bird

Chapter 1: General introduction

With an estimated 21-52% of the world's biodiversity at risk of extinction, we may currently be experiencing Earth's sixth mass extinction event (Barnosky *et al.* 2011; Dirzo *et al.* 2014). Biodiversity loss is a serious issue. First, biodiversity is intrinsically valuable, displaying the fantastic array of possibilities that evolution has generated over the millennia (Leopold 1949; McCauley 2006). Second, we enjoy spending time in nature, and doing so is good for our health and wellbeing (reviewed in Hartig *et al.* 2014). Finally, biodiversity is important to ecosystem stability and function. Ecosystems with high biodiversity produce more goods and recycle more waste than ecosystems with low biodiversity, and these benefits only increase with time (Reich *et al.* 2012). Biodiverse ecosystems are more stable, and less prone to cascading extinctions because they have many different connections between species (e.g., species A eats species B, C, and D, not just species B) (Dunne *et al.* 2002). Thus, biodiversity loss threatens ecosystem function and ecosystem stability, as well as our personal wellbeing.

Regional biodiversity loss starts with the loss of a single species. Across a region, not all habitat is suitable for any one species, resulting in collections of smaller populations distributed across patches of suitable habitat, which are connected by dispersal of individuals between populations, forming locally inter-connected metapopulations (reviewed in Hanski 1997). Within a population, four demographic processes influence population size: birth, death, immigration, and emigration. In high-quality habitats, birth rates often surpass death rates, so there may be more offspring than there are available territories, forcing young individuals to emigrate elsewhere. These populations with net outflux of individuals are often referred to as source populations. In contrast, in lower quality habitat patches, there may be lower birth rates and/or higher death rates, forming sink populations. For a sink population to persist over time, it must

be sustained by immigrants from other populations (Brawn & Robinson 1996). Determining whether a population is a source or a sink can be difficult but is crucial to understanding how a single population fits into the surrounding metapopulation (Brawn & Robinson 1996). If overall patch quality declines, source populations may not be able to sustain sink populations or may become sink populations themselves.

Across the world, broad-scale environmental change is influencing population dynamics of numerous species. Habitat loss, typically caused by increasing human land use and development, is the single largest threat facing species at risk worldwide (Sala *et al.* 2000), affecting at least an estimated 33% of all threatened species (Gurevitch & Padilla 2004). As we develop large swaths of land, patches of suitable habitat get ever smaller and farther apart causing overall biodiversity loss and preventing ecosystems from functioning effectively (Fischer & Lindenmayer 2007; Haddad *et al.* 2015). For long-lived species in particular, extinction and biodiversity loss can occur many years after the initial habitat loss (Tilman *et al.* 1994; Krauss *et al.* 2010; Haddad *et al.* 2015). We will likely reap the consequences of our habitat destruction for decades to come, regardless of current conservation efforts.

Another way we are influencing populations around the world is through climate change. Climate change is expected to have the largest impact on arctic, alpine, and boreal habitats, and to influence other habitat types to a lesser degree (Sala *et al.* 2000), but tropical species may also be strongly impacted as they generally have relatively narrow ranges of thermal tolerance (Deutsch *et al.* 2008). Worldwide, species are responding to climate change by shifting their ranges poleward by an average of 0.61km yearly to track suitable habitat (Sala *et al.* 2000; Parmesan & Yohe 2003). However, many species are not able to shift their range because of ecological constraints (e.g., species with limited dispersal abilities, or species already at high

latitudes or elevations). In fact, species are predicted to lose an average of 21-26% of their ranges by 2050 (Jetz *et al.* 2007). Additionally, many species are responding to climate change by breeding earlier as spring temperatures warm (Dunn & Winkler 1999; Sala *et al.* 2000).

Unfortunately, breeding earlier is not advantageous if prey species have not shifted to the same degree, causing mismatches between offspring demand for food and peak food availability.

Mismatches are common because there is substantial variation in the magnitude of different species' phenological responses to climate change (reviewed in Walther *et al.* 2002), which can cause interacting species to become temporally disconnected. Food availability mismatches caused by climate change have been demonstrated in a number of species and linked to population declines (e.g., Gaston *et al.* 2009, McKinnon *et al.* 2012, Visser *et al.* 2012). As the global climate continues to change, its effects on species loss will become ever more apparent.

Avian aerial insectivore decline

One taxonomic group facing strong threats of extinction is birds (Butchart *et al.* 2004; Barnosky *et al.* 2011). In fact, current bird extinction rates have already exceeded the prehistoric extinction rates estimated during the previous five mass extinctions (Barnosky *et al.* 2011), making birds of particular concern for conservation efforts. Because birds are incredibly diverse and experience an equally diverse array of threats, finding one conservation strategy to address declines across all birds is an impossible task.

Among birds, aerial insectivores, a guild of birds that forage on flying insects, are declining particularly quickly (Nebel *et al.* 2010; Inger *et al.* 2015). Avian aerial insectivores are a taxonomically diverse group, including swifts, nightjars, swallows, and flycatchers and encompassing more than thirty species in North America alone. Despite their distant phylogenetic relations, avian aerial insectivores as a group have been in marked decline since the

1980s, and exhibit particularly strong declines in northeastern North America (Nebel *et al.* 2010, Smith *et al.* 2015, but see Michel *et al.* 2016).

Alternative hypotheses to explain aerial insectivore population decline

The taxonomic diversity of avian aerial insectivores suggests that something about their shared feeding strategy makes them susceptible to large-scale environmental challenges (Nebel *et al.* 2010). A wide array of hypotheses has been proposed to explain population declines in this guild of birds, but a few have become prominent in the literature and are supported by some empirical evidence. Testing these non-exclusive hypotheses, which I describe below, is the focus of this thesis.

H1: Aerial insectivore declines are caused by impacts of land use on insect abundance.

Many avian aerial insectivores forage in large open spaces, many of which are disappearing or being degraded. Low-intensity agricultural fields are increasingly being converted to high-intensity agriculture, allowed to regenerate to forest, or urbanized, none of which provide suitable habitat for aerial insectivores (reviewed in Rey Benayas 2007). Increasing forest cover likely limits aerial insectivores' line of sight and foraging efficiently, consequently preventing them from inhabiting reforested areas (Purves 2015). Aerial insectivores are uncommon in urbanized areas, suggesting that insect food or other important resources are unavailable in urban areas and these areas are avoided (English *et al.* 2017). Insect availability in agricultural areas depends largely on what type of farming activity is taking place on the landscape, with cattle pasture and hedgerows between crops exhibiting the highest insect abundances (Moller 2001; Evans *et al.* 2007; Gruebler *et al.* 2007; Rioux Paquette *et al.* 2013). As agricultural land use has shifted away from low-intensity cattle farming towards high-intensity cropland, birds that forage or breed in grasslands have declined substantially (Murphy

& Moore 2003). While these grassland species are not exclusively aerial insectivores, one common avian aerial insectivore, the barn swallow (*Hirundo rustica*), is consistently more abundant in years following high insect abundance when agriculture is less intense (i.e., more cattle pasture, less total agricultural land, less pesticide and fertilizer use) (Moller 2001; Benton *et al.* 2002; Evans *et al.* 2007). Shifting land use patterns may affect aerial insectivores on both the breeding and overwintering grounds. Overall, the shift away from small-scale farms has lowered insect abundance and may be contributing to declines in avian aerial insectivore populations.

H2: Aerial insectivore declines are caused by global climate change and its impacts on insect abundance and availability.

Global climate change may challenge avian aerial insectivores by reducing food availability. Climate change affects temperature, wind, and precipitation patterns, all of which correlate with avian aerial insectivore population sizes (Irons *et al.* 2017; McArthur *et al.* 2017; Weegman *et al.* 2017). In northeastern North America where declines are strongest, climate change is predicted to cause increased precipitation and more variable temperatures with both more heat waves and cold snaps (Kunkel *et al.* 2013). Insect prey decrease with decreasing temperature (Cucco & Malacarne 1996; Gruebler *et al.* 2007), likely because the ectothermic insects are less active in the short-term and grow and reproduce less over the long-term. Notably, many aerial insectivores almost exclusively forage on the wing; that is, they forage while flying, catching insects that are also flying, so even in the absence of decreases in overall insect abundance, periods of inclement weather (windy, rainy, cold) can effectively reduce food availability to zero for these specialized foragers. Cold snaps may reduce adults' ability to feed nestlings, or even cause nest abandonment if adults prioritize their own survival over their

nestlings' (McCarty & Winkler 1999a; Winkler *et al.* 2013; Ouyang *et al.* 2015). Similarly, poor foraging success overwinter could hinder adult survival.

H3: Aerial insectivore declines are caused by global climate change induced mismatches between the timing of high-quality food availability and peak nutritional demand by nestlings.

Nestlings may be particularly sensitive to climate change because of mismatch between demand and supply of insects. For one avian aerial insectivore, the tree swallow (*Tachycineta bicolor*), egg-laying shifted five days earlier from 1959 to 1991 (Dunn & Winkler 1999). Some evidence suggests that insect abundance increases over the course of the breeding season, which has been interpreted as evidence that mismatches between insect abundance and offspring nutritional demand are unlikely in these populations (Dunn *et al.* 2011). However, nestling growth increases more with higher quality food with more fatty acids than simply with more food overall (Twining *et al.* 2016). Aquatic insects contain more high-quality fatty acids than do terrestrial insects (Twining *et al.* 2016). Aquatic insects peak in abundance earlier than terrestrial insects (Nakano & Murakami 2001), and, in some populations, do exhibit mismatch with nestling demand for high-quality food (Twining *et al.* 2016). Therefore, climate change may influence avian aerial insectivore population dynamics by creating a mismatch between nestling demand and the emergence of high-quality food.

Tree swallows as a model species

Although the factors described above might be affecting all avian aerial insectivores, for most species we lack the long-term, detailed data to be able to evaluate even the basic demographic processes responsible for population decline. Tree swallows are an ideal model species for studying avian aerial insectivore decline. Naturally nesting in cavities excavated by other species, tree swallows take readily to artificial nest boxes, making them easy to study

(Robertson *et al.* 1992; Jones 2003). Accordingly, researchers across North America have studied box-nesting populations since the mid-1960s, collecting a wealth of data along the way (Jones 2003; Shutler *et al.* 2012). Like other avian aerial insectivores, tree swallows show more severe population decline in northeastern North America (Nebel *et al.* 2010, Shutler *et al.* 2012, Smith *et al.* 2015, Michel *et al.* 2016). Additionally, tree swallow population declines began in the 1980s, which is congruent with patterns of decline in other species (Nebel *et al.* 2010, Shutler *et al.* 2012, Smith *et al.* 2015, but see Michel *et al.* 2016). Because tree swallows exhibit similar spatial and temporal trends in population declines as other avian aerial insectivores, tree swallows are a suitable model organism to study avian aerial insectivore decline.

Tree swallows are an avian aerial insectivore from the family Hirundinidae. They eat aerial insects, predominantly and preferentially 3-5mm Diptera, although they also eat large amounts of Hemiptera and Odonata (Quinney & Ankney 1985; McCarty & Winkler 1999a). Tree swallows primarily rely on insects foraged during the breeding season to produce eggs (Winkler & Allen 1995; Nooker *et al.* 2005; Ardia *et al.* 2006), incubate, and provision nestlings (Winkler & Allen 1995; Nooker *et al.* 2005). Although they eat almost exclusively aerial insects during the breeding season, during winter, in times of insect shortage, tree swallows will supplement their diet with lipid-rich fruits and vegetation (Robertson *et al.* 1992; Piland & Winkler 2015).

Tree swallows migrate south to the southern U.S. and Mexico, and overwinter roosting in flocks of hundreds of thousands of birds in coastal habitat along the Gulf of Mexico (Robertson *et al.* 1992; Winkler 2006). Migrating and wintering birds often roost in agricultural habitat, most notably sugar cane fields (Robertson *et al.* 1992). First-time breeders usually return to breed within 10km of their natal population (Winkler *et al.* 2005). Adults typically also return within 10km from their previous breeding sites (Winkler *et al.* 2004) but have been observed

dispersing farther following unsuccessful breeding (Winkler *et al.* 2004, Lagrange *et al.* 2017, but see Shutler and Clark 2003).

Tree swallows are one of only two North American species that display delayed plumage maturation in females, but not males: one-year-old females have brown body feathers in their plumage, and two-year-old or older females have full adult, iridescent blue-green plumage (Hussell 1983). The delayed plumage maturation in females has allowed comparison of one-year-old females with older females, revealing that older females breed earlier in the season and have higher reproductive success (Stutchbury & Robertson 1988; Bentz & Siefferman 2013). One-year-old females are also subordinate and less likely to occupy a territory if territories are limiting, resulting in “floater” populations of young females (Stutchbury & Robertson 1985, 1987). Territories can often be limiting as tree swallows are secondary cavity nesters, relying on cavities excavated by other species in dead trees in beaver ponds and other open spaces (Rendell & Robertson 1989).

Thesis objectives

The overarching aim of this thesis is to determine why tree swallows, and avian aerial insectivores more generally, are declining. To address this aim, I analyzed long-term data (1975-2017) from a box-nesting population of tree swallows at the Queen’s University Biological Station. Each year, an average of 168 boxes (range 77-264) were monitored. Researchers have tracked nesting success in each box, measuring when egg laying starts, the total clutch size, when incubation starts, when and how many eggs hatch, and when and how many nestlings survive to leave the nest (i.e., fledge). Additionally, nestlings and adults were measured for body size and body mass and banded with uniquely-numbered Canadian Wildlife Service leg bands, allowing individuals to be tracked across years. In total, from 1975-2017, 5,506 nests, 18,366 nestlings,

and 6,355 unique adults have been monitored. As the purpose of this data collection was originally to answer fundamental biological questions, many nests were experimentally manipulated. While experimentation may have influenced population dynamics in our nest-boxes, it is not the cause of regional decline, so I have focused my analyses on unmanipulated nests. The intensive and long-term nature of our data (spanning both before and during population declines) gives us an unprecedented opportunity to investigate why tree swallow populations are declining.

In chapter 2, I assess the relative importance of each of the demographic transitions between life stages (egg, nestling, fledgling, one-year-old, two+-year-old) to population growth rate using a life stage simulation analysis. For instance, does a small change in hatch rate create a larger change in population growth than a small change in adult overwinter survival? Answers to questions like this tell us which demographic transitions have the greatest impact on population growth. Such an analysis can inform conservation efforts, as efforts will be most effective when focused on these influential transitions. Similarly, environmental threats have bigger impacts on population size when they affect one of these important transitions.

Building on chapter 2, in chapter 3, I asked whether the demographic transitions that I determined to be most important to population growth, overwinter survival and fledging success, have changed concurrently with the overall population decline. Specifically, I tested whether overwintering and migratory habitat loss, local weather post-fledging and/or global climate indices explain trends in survival overwinter and whether local weather patterns explain trends in nestling fledging success.

Given the importance of nestling growth in determining fledging success and juvenile survival (Tinbergen & Boerlijst 1990; Michaud & Leonard 2000; Cleasby *et al.* 2010; Maness &

Anderson 2013), in chapter 4, I asked whether nestling body mass close to fledging has changed over time. Using detailed growth curves and parental provisioning data collected during the 2017 breeding season, I also investigated the effect of local weather conditions (temperature, precipitation, and wind speed) and parental effort on nestling growth. Finally, I assessed whether weather conditions during nestling development have deteriorated over the study period.

Ultimately, my research suggests that climate change, particularly increasing spring rainfall, may be responsible for tree swallow population declines by decreasing fledging success and juvenile survival. Understanding the role of climate change in these declines is crucial for acknowledging both which conservation management strategies are likely to be most effective and the unfortunate reality that, without stemming climate change, these strategies are likely to only be stop-gap measures.

**Chapter 2: Demographic drivers of local population decline
in Tree Swallows (*Tachycineta bicolor*)**

Amelia R. Cox, Raleigh J. Robertson, Bradley C. Fedy, Wallace B. Rendell, and Frances Bonier

In press in *The Condor*

Abstract

Bird species around the world are threatened with extinction. In North America, avian aerial insectivores are experiencing particularly severe population declines. To conserve these species, we need to know which life stages have the largest influence on population growth. Unfortunately, for most avian aerial insectivores, and most organisms, the detailed demographic data required to identify the most influential vital rates are not available. We monitored a box-nesting population of Tree Swallows (*Tachycineta bicolor*) from 1975 to 2017. From this long-term dataset, we derived estimates of nine vital rates: clutch size, reproductive attempts, and overwinter return for two age classes of adult females, and nestling hatch, fledge, and juvenile recruitment rates. We conducted a life-stage simulation analysis on this population based on a three-stage, female-based population projection matrix to determine which of these vital rates had the greatest influence on overall population growth rate. We determined each vital rate's sensitivity (i.e., the effect of a small change in each vital rate on population growth), elasticity (i.e., the effect of a proportional change in each vital rate on population growth), and ability to explain variation in population growth rate. Juvenile recruitment, female return for both age categories, and fledging success determine population growth because they have high sensitivity, elasticity, and explained large amounts of variation in population growth rate. Contrary to expectations, the number of nesting attempts, clutch size, and hatch rate have little impact on

population growth rate. To stem Tree Swallow decline, and potentially the declines we see across the aerial insectivores, fledging success or overwinter survival must increase.

Introduction

Across the globe, numerous species are threatened with extinction, and more are experiencing population decline (reviewed in Dirzo *et al.* 2014). Currently, birds are going extinct especially quickly, with extinction rates that are faster than during the previous five mass extinctions (Barnosky *et al.* 2011). To effectively manage at-risk species, we need to know which life stages have the largest impacts on population growth, and target management to protect those life stages.

In Europe and North America, populations of avian aerial insectivores are declining particularly quickly (Nebel *et al.* 2010; Inger *et al.* 2015). Avian aerial insectivores are a group of phylogenetically diverse birds that includes swifts, nightjars, swallows, and flycatchers (Sibley & Monroe 1990). The defining feature of this group is that they forage on flying insects. These birds have been experiencing population declines across North America since the 1980s with marked declines in the northeast (Nebel *et al.* 2010, Shutler *et al.* 2012, Smith *et al.* 2015, but see Michel *et al.* 2016). The spatial and temporal congruence of these declines across species suggests that something about these birds' common feeding strategy puts them at risk (Nebel *et al.* 2010). Aerial insectivore declines may be influenced by intensification of industrial agriculture and/or changing climate throughout the annual cycle, both of which might affect food availability, although there are other possibilities such as bioaccumulation of toxins or disease (e.g., Dunn and Winkler 1999, McCarty and Winkler 1999, Benton *et al.* 2002, Brasso and Cristol 2008, Ghilain and Belisle 2008, Niebuhr *et al.* 2016, Weegman *et al.* 2017). Given these concerns, it is imperative we understand the mechanisms underlying the declines. However, prior

to examining specific mechanisms, we must first identify the most important life stages for determining population growth, as environmental impacts could vary throughout the lifecycle.

Stage-structured population projection models allow us to determine which life-stage specific survival and fertility rates (i.e., vital rates) have the greatest influence on population growth. Assessing model sensitivity allows us to estimate each vital rates' relative effect on population growth rate (Caswell 2001; Morris & Doak 2002). Ecologists have applied sensitivity analyses to many threatened populations with success. For instance, sensitivity analysis suggested that management of threatened bighorn sheep (*Ovis canadensis*) populations should focus on predator control to improve adult survival (Johnson *et al.* 2010) and, in fact, translocated populations flourished in areas without mountain lion (*Puma concolor*) predation (Rominger *et al.* 2004).

One of the challenges to performing a life-stage simulation is the requirement for detailed vital rates data across many years and environmental conditions. With few exceptions (e.g., Brown *et al.* 2013), long-term data available on avian aerial insectivores is limited to abundance counts and cannot be used for such an analysis. Tree Swallows (*Tachycineta bicolor*) are one species for which we have extensive long-term data estimating vital rates across many years. Tree Swallows are secondary cavity nesters, naturally nesting in cavities excavated by other species, and preferentially nesting in artificial nest boxes when available (Rendell & Robertson 1989). Tree Swallows may provide insight into the threats facing the rest of their foraging guild because they show the same spatial and temporal patterns of population decline as many other avian aerial insectivores (Nebel *et al.* 2010, Shutler *et al.* 2012, Smith *et al.* 2015, but see Michel *et al.* 2016). Analysis of many box-nesting populations across their range shows that Tree

Swallows are declining in the Northeast, but not in the western or southeastern portion of their range (Shutler *et al.* 2012).

Like most avian aerial insectivores, Tree Swallows live relatively short lives, with an average lifespan of 2.7 years (Butler 1988). Population growth rates in short-lived birds with larger clutch sizes are typically driven by fecundity (i.e., number of nests per year, clutch size) (Saether & Bakke 2000), suggesting that in Tree Swallows vital rates surrounding breeding success might be important drivers of population dynamics. Additionally, nesting attempts for Tree Swallows and other cavity-nesting birds may be limited by the number of available natural cavities (Wiebe 2011), further suggesting that nest success and fecundity might be strong predictors of population growth in Tree Swallows. Although avian aerial insectivores are not exclusively cavity-nesting, many species are either cavity-nesting (e.g., Purple Martin (*Progne subis*), Great Crested Flycatcher (*Myiarchus crinitus*)) or nest-site specialists who may also experience nest-site limitation (e.g., Cliff Swallow (*Petrochelidon pyrrhonota*), Bank Swallow (*Riparia riparia*), Chimney Swift (*Chaetura pelagica*)). Additionally, cavity nesters like Tree Swallows may have lower predation rates and correspondingly higher fledging success than open cup avian aerial insectivores (Alerstam & Högstedt 1981), particularly in nest box systems where predator guards protect the nests. Safer nests and consistently high fledging success would suggest that fledge rates might have less impact on population growth rates in Tree Swallows than in open cup nesting avian aerial insectivores.

Here, we use long-term monitoring data from a box-nesting population of Tree Swallows at the Queen's University Biological Station in southeastern Ontario, Canada, to perform a life-stage simulation analysis and identify vital rates with relatively large impacts on Tree Swallow population growth rate. We monitored survival and breeding success from 1975 to 2017, a time

before and during marked declines (Shutler *et al.* 2012), and spanning a wide range of environmental conditions, allowing us to estimate natural variation in vital rates. From these data, we estimate nine different vital rates: clutch size, reproductive attempts, and overwinter return rates for two age classes of adult females, and hatch, fledge, and juvenile recruitment rates. Conducting a vital rates analysis on these data allowed us to assess the relative importance of these nine vital rates in determining the growth rate of this population. From this analysis, we make suggestions as to causes of avian aerial insectivore declines that warrant further attention and which management strategies could be most effective going forward.

Methods

Study system

We used data from a box-nesting population at the Queen's University Biological Station in Chaffey's Lock, ON (44.5212°N, 76.3854°W), from 1975 to 2017. Nest boxes were placed in grids in large open areas and along roadsides. The grids mimicked the distribution of natural cavities (Robertson & Rendell 1990).

Starting between late April and early May, each spring, we monitored nest boxes regularly to track the outcome of each nesting attempt. We recorded clutch size, the number of nestlings that hatched, and the number of nestlings that fledged. We banded all nestlings with a uniquely-numbered Canadian Wildlife Service band. Throughout the breeding season, we caught adult tree swallows, identifying returning birds via their band number and banding new immigrants. Adults were sexed according to the presence of a cloacal protuberance (male) or brood patch (female). Females, but not males, in this species, show delayed plumage maturation, allowing us to estimate the age of females as one-year-old (second year, SY) or older (after second year, ASY) (Hussell 1983). Because female capture records were more complete and

females could be aged more precisely, we calculated female-based vital rates. As a socially monogamous species requiring biparental care (Robertson *et al.* 1992), Tree Swallow population dynamics are unlikely to be influenced by sex-specific differences (Caswell 2001). From 1975-2017, we monitored 5,506 nests and 3,740 unique females.

Estimating vital rates

We estimated mean annual averages for each of the vital rates relating to fecundity. We estimated mean annual clutch size for SY and ASY females as the total number of eggs laid across all nests in the population for a given year divided by the total number of nests with eggs in the same year. Although Tree Swallows in our population are single-brooded, if her first nest fails early in the year, a female may attempt a second nest. We calculated the yearly average number of nests per female as the total number of nests of known female parentage divided by the total number of known parental females for SY and ASY females separately. Similarly, we calculated yearly hatch rates as the number of nestlings that hatched divided by the total number of eggs in the entire population and fledge rates as the total number of nestlings that fledged divided by the total hatched.

We conducted a Cormack-Jolly-Seber analysis in MARK (White & Burnham 1999) using the interface RMark (Laake 2013) to estimate adult female apparent survival and capture probabilities. Note that apparent survival encompasses both death and permanent emigration, as they are indistinguishable in our dataset. We modeled five scenarios to explain adult survival rates. Survival could: be constant across years, randomly vary between years, differ between younger and older birds, vary between years with one age class consistently surviving better, or vary between years with the effect of age differing between years. We modeled capture probabilities as either remaining constant or varying between discrete years as we might expect if

capture effort differed among years. We assessed model fit by plotting residual and fitted values and considered any model with a variance inflation factor of less than three adequate following White and Burnham (1999). All adult female return estimates used in subsequent analyses come from model averages of all models, weighted by AICc.

We used a separate Cormack-Jolly-Seber analysis in RMark to estimate juvenile recruitment rates. This analysis is separate from our analysis of adult female return because nestling sex is unknown and therefore capture histories of nestlings were not included in the analysis of female adults. To properly estimate juvenile recruitment, we included capture histories of all birds of both sexes. We modeled variation in survival probabilities with the same factors as described above for adult survival, but age categories were set to fledgling, SY, or ASY. Like our adult analysis, capture probabilities could remain constant, or vary by year, but here we also included variation by age, or age and year combined. We included age effects on capture because SY females are subordinate to ASY females (Coady & Dawson 2013), and might have lower ability to acquire a nest box which is the preferred nesting habitat (Stutchbury & Robertson 1985; Robertson & Rendell 1990). All recruitment estimates used in subsequent analyses come from the model with the lowest AICc score. No other models had delta AICc less than 2.

We calculated distribution parameters for clutch size, the average number of re-nests, hatch rate, fledge rate, recruitment rate, SY female return, and ASY female return. We described clutch size by a stretched beta distribution, and the average number of re-nests with a beta distribution, where the average number of re-nests + 1 equals the average number of nests per female in the breeding population. We described all other rates using beta distributions. Note that the variance for these distributions includes both sampling variance and environmental variance

for all rates except survival rates, which include only environmental variance (White *et al.* 2002). All nest boxes were surveyed each year so sampling variance was low.

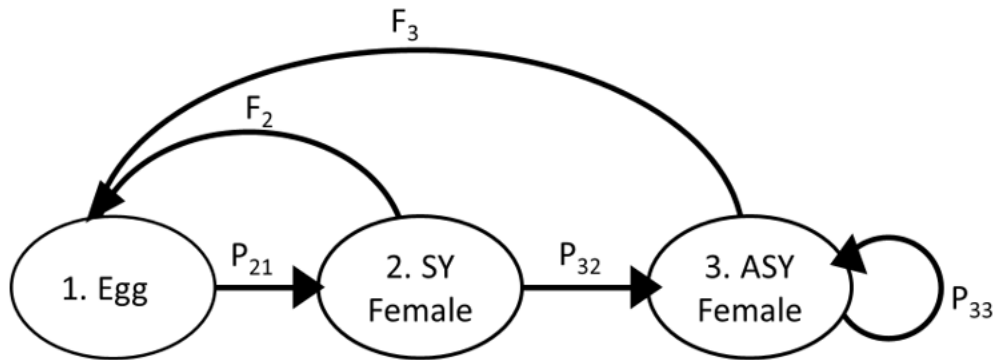


Figure 2.1: Three-stage Tree Swallow life cycle diagram. Note that the transition from egg to SY female (P_{21}) includes three vital rates (hatch rate, fledge rate, and recruitment rate), and the transition from SY female and ASY female to egg (F_2 and F_3) both include two vital rates (number of nests and clutch size). The transition from SY female to ASY female (P_{32}) is the vital rate SY female return. Likewise, the transition from ASY female back to ASY female (P_{33}) is the vital rate ASY female return.

Matrix model

We developed a three-stage female-based demographic model for the Tree Swallow lifecycle, in which eggs transition to SY females, which transition to ASY females (Figure 2.1).

This lifecycle diagram can also be depicted as a population projection matrix:

$$\begin{bmatrix} 0 & F_2 & F_3 \\ P_{21} & 0 & 0 \\ 0 & P_{32} & P_{33} \end{bmatrix}$$

From parameterized vital rates, we randomly drew 10,000 sets of vital rates from their distributions (Figure 2.2; Table A1). We then combined these vital rates into matrix elements (SY female fertility [F_2], ASY female fertility [F_3], nestling survival [P_{21}], SY female survival [P_{32}], and ASY female survival [P_{33}]). For example, nestling survival is estimated as the product of hatch rate, fledge rate, and recruitment. From the matrix elements, we parameterized 10,000 population projection matrices.

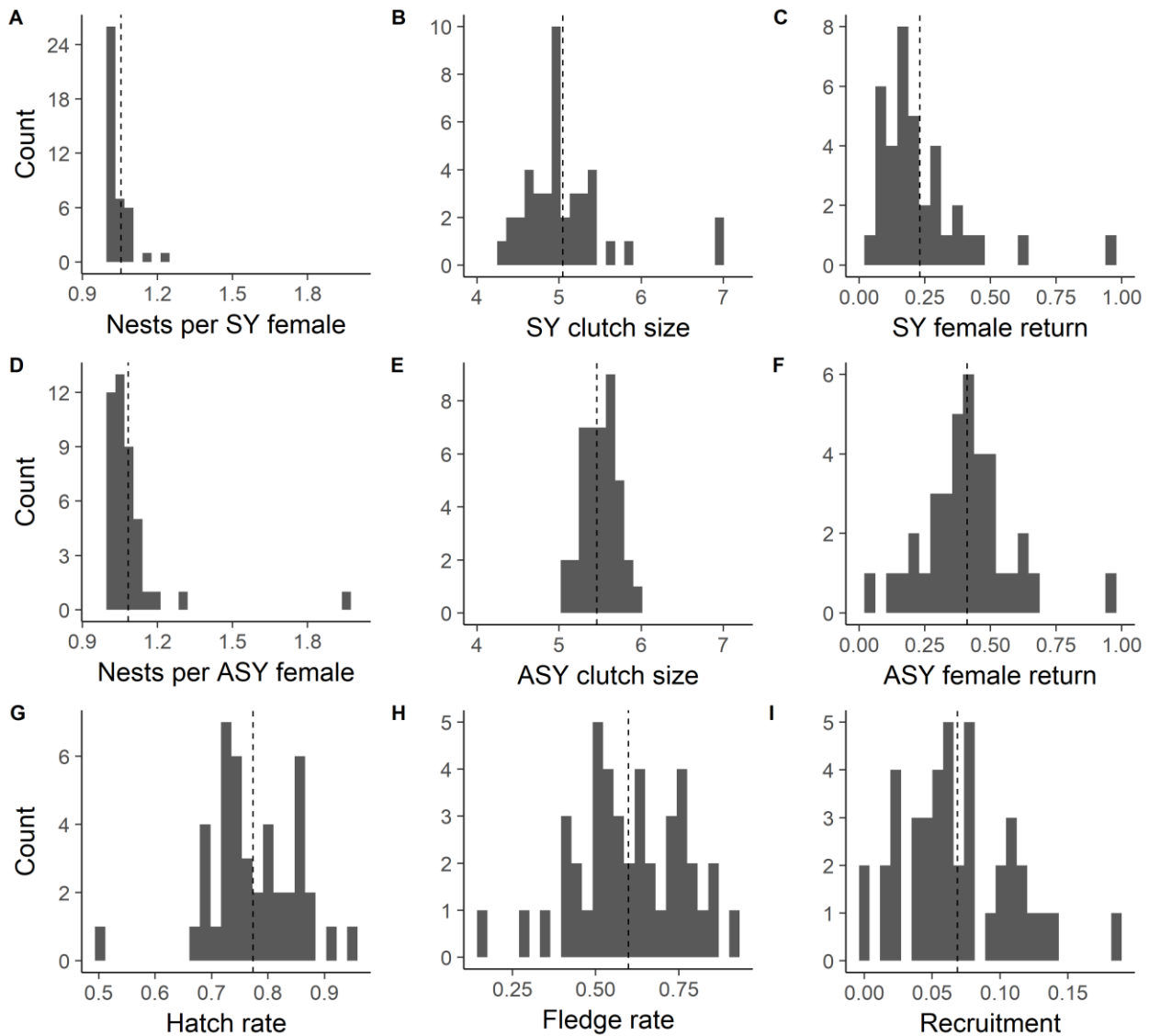


Figure 2.2: Histograms displaying the distributions of annual means for all nine vital rates for Tree Swallows from 1975-2017. Dashed lines represent the overall mean of each vital rate.

Determining relative importance

We analyzed the simulated data using three different metrics: sensitivity, elasticity, and the proportion of variation in population growth rate explained by variation in each vital rate. Sensitivity is a direct measure of how much population growth rate changes in response to a small change in each vital rate, here specifically estimating how much population growth rate

changes when we increase all vital rates by 0.01. We calculated sensitivity values for the individual vital rates in each simulated matrix. Sensitivity values calculated in each iteration varied considerably so we also ranked vital rates by sensitivity to determine which vital rates were most likely to be the most sensitive.

Sensitivity assumes that a small, feasible change in one vital rate is equally small and feasible for all other vital rates, which may not be the case if some vital rates are measured on different scales (e.g., comparing low survival common in many animals during their first year of life to high fertility). One solution is to calculate elasticity and the proportion of variation in population growth rate explained by variation in each vital rate, in addition to sensitivity. Elasticity measures how much population growth rate changes due to a proportional change in each vital rate. Mathematically, elasticities are equivalent between vital rates that are multiplied together to form one matrix element. Therefore, we calculated elasticity values for the five matrix elements (SY female fertility, ASY female fertility, nestling survival, SY female survival, and ASY female survival) in each simulated matrix using the “vitalsens” command in the popbio package (Stubben & Milligan 2007). We then ranked matrix elements by elasticity to determine the most elastic matrix element in each iteration. Additionally, we determined the proportion of variation in population growth rate explained by variation in each vital rate by calculating the coefficient of determination (R^2) for the regression of population growth rate on each vital rate, corresponding to a univariate, pairwise correlation between each vital rate and population growth rate.

Correlations among vital rates

When positive, correlations between vital rates increase variability in annual population growth rate and, when negative, correlations can have a stabilizing effect (Morris & Doak 2002).

Correlated vital rates are common if one environmental condition influences multiple vital rates. For instance, juveniles, SY females, and ASY females might overwinter in the same location, so harsh weather in the overwintering grounds could reduce survival for all three age categories. We conducted the sensitivity analysis with and without the inclusion of the correlation structure indicated by our data following the procedure outlined by Morris and Doak (2002). All analyses were conducted in R version 3.4.3 (2017-11-30) (R Core Team 2016).

Results

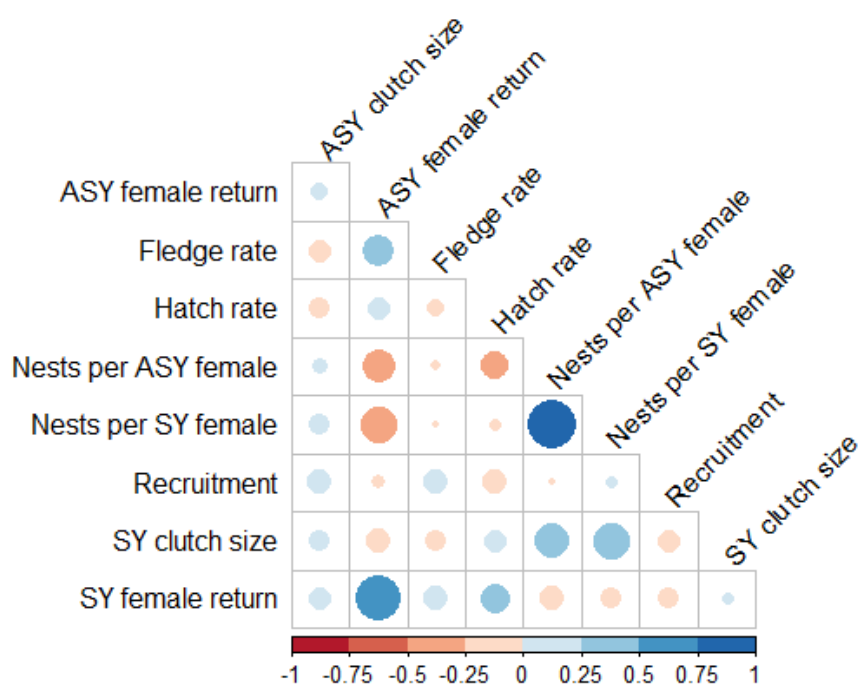


Figure 2.3: Correlation structure of annual vital rates for a box-nesting population of Tree Swallows. Dark blue indicates a Pearson correlation coefficient of 1, while dark red indicates a Pearson correlation coefficient of -1 with correlations of intermediate strength in intermediate colors. Larger circles indicate stronger correlations.

Vital rates and correlations between vital rates

As expected, several of the vital rates correlated with each other (Figure 2.3). Female return varied annually, and SY females had lower return rates than ASY females but the

magnitude of this difference varied between years (Table A2). Juvenile recruitment also varied annually and was considerably lower than female return regardless of female age (Table A3).

Population growth rate

Mean asymptotic population growth rate for all 10,000 simulated population matrices was 0.59 ± 0.17 (mean \pm SD) when no correlations between the vital rates were included.

Including correlations did not change the mean population growth rate (0.59 ± 0.17). This growth rate is well below replacement levels (population growth rate = 1).

Sensitivity analysis

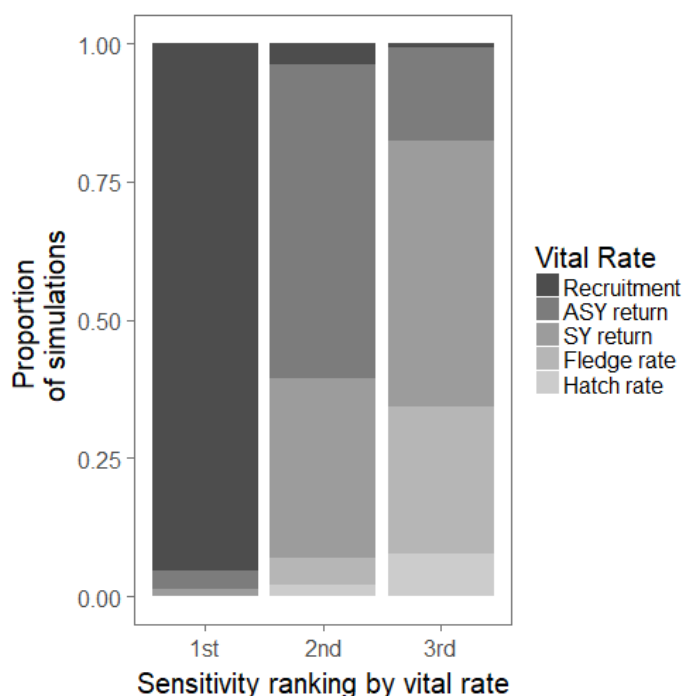


Figure 2.4 Proportion of analysis iterations where each vital rate ranked 1st through 3rd most sensitive (i.e., greatest influence of a small change in the vital rate on population growth). Juvenile recruitment had the highest sensitivity ranking in 95.5% of the simulations. ASY female return (55.5%) usually ranked second in sensitivity, but SY female return (33.9%) and other vital rates also ranked second some of the time. Usually, SY female return (47.4%) ranked third in sensitivity but other candidates were fledging rate (27.2%), ASY female return (17.1%), and other rates (8.3%).

The results of our sensitivity analysis differed slightly between the life-stage simulations that did and did not include the correlations between vital rates. Therefore, we present the results from the correlated life-stage simulation (Table A4), as this simulation better reflects the biological and environmental constraints on this population. Results from the uncorrelated life-stage simulation analysis are presented in the supplemental material (Figure A1; Table A5).

In 95.5% of the simulations, juvenile recruitment had the highest sensitivity ranking (Figure 2.4). However, the sensitivity of juvenile recruitment varied substantially (2.25 ± 0.88 , mean \pm SD). The identity of the vital rate with the second highest ranking varied even more among simulations. ASY female return (0.50 ± 0.24) ranked second in sensitivity in 55.5% of simulations, but SY female return (33.9%, 0.44 ± 0.31), fledging (5.3%, 0.24 ± 0.12), and other vital rates (5.3%) all ranked as second most sensitive some of the time (Figure 2.4). Usually, SY female return (47.5%) ranked third in sensitivity but fledging (27.2%), ASY female return (17.1%), and hatching (7.5%, 0.19 ± 0.11) all also ranked third in some simulations (Figure 2.4).

Elasticity analysis

Of the five matrix elements in the elasticity analysis (SY female fertility, ASY female fertility, nestling survival, SY female return, and ASY female return), ASY female return was the most elastic matrix element (and vital rate) 60.3% of the time (0.39 ± 0.25), while nestling survival (0.25 ± 0.12) was the most elastic matrix element the other 39.7% of the time.

Coefficients of determination

ASY female return, SY female return, fledge rate, and recruitment explained the highest proportion of variation in overall population growth rate ($R^2=0.50, 0.37, 0.31, \text{ and } 0.24$ respectively; Table A4).

Discussion

Avian aerial insectivores are in decline across North America (Nebel *et al.* 2010; Smith *et al.* 2015; Michel *et al.* 2016), but it has been unclear which aspects of the life-cycle are the most important drivers of these declines. To address this gap in knowledge, we conducted a life-stage simulation analysis to determine relative sensitivity, elasticity, and proportion of variation in population growth rate explained by each vital rate using long-term demographic data from a population of tree swallows, a model avian aerial insectivore.

Contrary to our prediction that fecundity-based vital rates would be most influential for the short-lived tree swallow, clutch size, hatch rate, and nesting attempts did not strongly influence population growth rate. As a cavity-nesting species, we had predicted that Tree Swallow fledging rate would be high and therefore not limit population growth. However, juvenile recruitment, return rates of both SY and ASY females, and fledging rate were the most sensitive, elastic, and predictive vital rates. Our results are in contrast to findings from studies of other short-lived songbirds for which measures of fecundity (particularly clutch size and nesting attempts) are more important drivers of population dynamics (e.g., Saether and Bakke 2000). Therefore, we suggest that changes to one or more of these important vital rates (fledging success or survival of any age class) are most likely causing population declines in tree swallows, and avian aerial insectivores more generally.

A similar study of another Tree Swallow population found that breeding success did not influence population dynamics (Taylor *et al.* in press). Located on a maritime island and relying solely on artificial nestling sites, this population is a sink with population dynamics driven almost entirely by immigration from the mainland and adult survival (Taylor *et al.* in press). While we did not directly estimate immigration rates, given that our study population has

persisted for over 40 years (albeit declining since 1991) with simulated population growth rates averaging at 0.59 ± 0.17 (mean \pm SD), our population also relied on new immigrants. Across years, an average of $63.1 \pm 16.6\%$ of all females captured per year are unbanded new breeders. However, Tree Swallows are highly philopatric, typically returning within 10km of their natal and previous breeding sites (Winkler *et al.* 2004, 2005; Lagrange *et al.* 2014), so new immigrants to this site likely originate from the natural habitat surrounding our study site and, as such, experience a similar environment and are subject to similar demographics as birds nesting in the nest boxes. In contrast, new immigrants to the isolated island population in Maine, which lacks natural cavities, likely originate from the mainland and experience different environmental conditions and population dynamics (Taylor *et al.* in press). Therefore, we point to a high importance of immigration for maintaining an island sink population, while in our mainland population we found that juvenile recruitment and fledging success were more influential, suggesting a stronger impact of local breeding success.

The bulk of juvenile mortality occurs on the breeding ground post-fledging (Naef-Daenzer *et al.* 2001; Gruebler *et al.* 2014). Tree Swallow nestlings fledge at least a month before migration and spend the intervening time on the breeding ground improving their flying skills and learning to forage independently (Robertson *et al.* 1992). In Great Tits (*Parus major*) and Coal Tits (*Periparus ater*), mortality from predation and starvation during this post-fledging period accounts for the bulk of mortality in the first year (Naef-Daenzer *et al.* 2001), indicating that conditions on the breeding ground may substantially influence recruitment success. Where juvenile recruitment has been explored, nestlings that fledge in better condition consistently survive this period of post-fledging mortality better (Tinbergen & Boerlijst 1990; Naef-Daenzer *et al.* 2001; Monros *et al.* 2002; Greño *et al.* 2008), possibly because high-quality nestlings are

better able to escape predators and have fat reserves to buffer them through periods of low foraging success.

Larger, higher-quality nestlings are consistently more likely to fledge and subsequently recruit in Tree Swallows (e.g., Michaud and Leonard 2000) and other species (e.g., Tinbergen and Boerlijst 1990, Maness and Anderson 2013). As expected, Tree Swallow nestlings grow slower and fledge at lower weights when fed a low-quality or low-quantity diet (Twining *et al.* 2016). Although the cause is still unknown, aerial insect abundance has declined substantially since at least the 1970s across Europe (Benton *et al.* 2002; Shortall *et al.* 2009; Hallmann *et al.* 2017) and likely North America as well, although long-term insect records are sparse (Cameron *et al.* 2011; English *et al.* 2018). Declining insect abundance likely reduces food availability for developing nestlings. Additionally, because some aerial insectivores nearly exclusively forage for flying insects on the wing, when temperatures drop or it rains, flying insects can effectively disappear, explaining poor nestling growth and high rates of nest failure in Tree Swallows during cold and rainy weather (McCarty & Winkler 1999b; Winkler *et al.* 2013; Ouyang *et al.* 2015). Therefore, increasingly poor weather conditions and/or declining insect availability may decrease both fledging success and juvenile recruitment by decreasing nestling growth rates.

Although variation in adult survival overwinter likely contributes to variation in yearly population growth rate, it might be less likely to drive population decline in Tree Swallows. Adult survival is linked to habitat quality and weather conditions on the overwintering grounds in many migratory species (e.g., Sillett *et al.* 2000, Schaub *et al.* 2005). Most mortality occurs during migration rather than when birds are stationary on the overwintering or breeding grounds (Sillett & Holmes 2002; Klaassen *et al.* 2014) suggesting that habitat quality along the migratory corridor may also influence variation in overwinter survival. Tree Swallows migrate to the

southern U.S., Mexico, and Central America, roosting in flocks of hundreds of thousands of birds along the Gulf of Mexico (Robertson *et al.* 1992; Winkler 2006). Swallows from the northeastern portion of the range, likely including the birds from this population, overwinter in Florida and the Caribbean (Knight *et al.* in press). However, other populations which are not experiencing declines share migratory corridors and overwintering grounds (Knight *et al.* in press). If conditions on the overwintering grounds were exclusively responsible for population declines, then all populations overwintering together likely would be exhibiting similar declines. Additionally, across their range, adult Tree Swallow survival varies substantially across years and is not consistently predicted by broad-scale climate factors or overwintering grounds (Clark *et al.* in press). Although SY and ASY female survival was not distinguished in previous work, the survival rates in other populations appear similar to those of this study population (Clark *et al.* in press). Taken together, these factors suggest that changes in overwintering habitat are unlikely to drive population decline in Tree Swallows through direct effects on adult survival, even though adult survival has the potential to strongly impact annual variation in population growth rates. Changes on the overwintering ground may still influence other vital rates if birds that return to the breeding ground are in poorer condition, thus hindering breeding success.

This study is based on demographics from a single breeding population and it is possible that the relative importance of different vital rates in influencing population growth varies across locations. For example, in places with consistently more insects, nestlings tend to allocate more energy toward increasing their body reserves than they do when there is less food available (Ardia 2006). If nestlings always fledge with more fat reserves, there may be less variation in juvenile recruitment, making recruitment less of a driver of annual population growth. Alternatively, at more northern latitudes the breeding season is shorter, potentially forcing birds

to begin migration sooner with less time to recuperate body condition post-breeding (adults) and learn to forage independently (juveniles). Additionally, while Tree Swallows are single-brooded (Robertson *et al.* 1992), shorter seasonality at northern latitudes may prevent a second female from using the same nesting site in cavity-limited populations.

Although we do not yet understand fully why avian aerial insectivores are declining, our results highlight fledging success and overwinter survival as vital rates that determine whether Tree Swallow populations decline, remain stable, or grow. To understand these declines, we need to pinpoint which of these important vital rates has declined and determine what environmental factors are driving this change. Regardless, even without fully understanding why aerial insectivores are declining, if management policies are enacted to improve overwinter survival or fledging success, aerial insectivore populations should respond positively.

**Chapter 3: Long-term study of an avian aerial insectivore (*Tachycineta bicolor*)
points to climate change as a driver of decline**

Amelia R. Cox, Raleigh J. Robertson, Wallace B. Rendell, and Frances Bonier

Abstract

Population decline and the threat of extinction are realities currently facing many birds. Avian aerial insectivores, birds that forage on flying insects, are declining particularly quickly but the detailed demographic data necessary to identify causes of population decline are often lacking. Using data from a box-nesting population of tree swallows (*Tachycineta bicolor*) that has been monitored for 43 years (1975-2017), we identified reduced fledging success and juvenile survival overwinter as probable causes of population decline. Poor fledging success was associated with increased predation and poor weather conditions during early nestling development. Low juvenile survival overwinter was linked to poor weather conditions during the post-fledging period and may also be linked to conditions on the wintering grounds. Our results suggest tree swallows, and perhaps other avian aerial insectivores, should be added to the growing list of species challenged by climate change.

Introduction

An estimated 21-52% of the world's species are at risk of extinction, leaving us facing the Earth's sixth mass extinction (Barnosky *et al.* 2011; Dirzo *et al.* 2014). More than any other causes, changing land-use patterns and climate change threaten terrestrial species (Sala *et al.* 2000). Conservatively, a projected 33% of all species face extinction due to habitat loss and fragmentation following human development and agricultural practices (Gurevitch & Padilla 2004). Climate change can cause declines and extinction by shifting thermally-suitable habitat

faster than species can compensate for through dispersal (Thomas *et al.* 2004; Jetz *et al.* 2007; Bellard *et al.* 2012) and by generating mismatches between when resources are available and when they are needed (e.g., Gaston *et al.* 2009; McKinnon *et al.* 2012; Visser *et al.* 2012). Of course, neither of these stressors exist in isolation and additional challenges may compound their influence (e.g., Blaustein & Kiesecker 2002).

Bird species are disappearing particularly quickly (Butchart *et al.* 2004; Barnosky *et al.* 2011), with some groups facing especially dire futures. Avian aerial insectivores (AAIs), a diverse guild of birds that forage on flying insects, are one such group (Nebel *et al.* 2010; Inger *et al.* 2015). Despite their taxonomic diversity, AAIs as a group have been in marked decline for decades (Nebel *et al.* 2010, Shutler *et al.* 2012, Smith *et al.* 2015, Inger *et al.* 2015, but see Michel *et al.* 2016). With the exception of the flycatchers, whose declines began slightly later than other AAIs' (Michel *et al.* 2016), the spatial and temporal synchrony of decline suggests that their common feeding strategy may make AAIs vulnerable to the same challenges worldwide (Nebel *et al.* 2010). However, it is still unclear what drives population decline in AAIs.

Foraging on flying insects may leave AAIs particularly susceptible to climate change. In northeastern North America, where populations declined the most, climate change is predicted to cause more variable weather patterns, meaning both more heat waves and cold snaps (Kunkel *et al.* 2013); the same is predicted for AAIs on their overwintering grounds (La Sorte *et al.* 2018). The ectothermic insects AAIs rely on are largely inactive during rain and when temperatures are below 18.5°C (Grüebler *et al.* 2007; Winkler *et al.* 2013), suggesting that inclement weather may effectively reduce food availability to zero, even without decreasing absolute insect abundance. Furthermore, migratory birds, including most AAIs, must use cues on

their overwintering ground to determine when to return to the breeding grounds (Frederiksen *et al.* 2004). These cues may become unreliable as the climate changes, exposing nestlings to food shortages or inclement weather (e.g., Gaston *et al.* 2009, McKinnon *et al.* 2012, Visser *et al.* 2012). Indeed, migratory birds are declining particularly quickly (Jiguet *et al.* 2010; Gilroy *et al.* 2016).

Additionally, AAI's foraging habits may make them vulnerable to changing agricultural practices. Many species forage in large open agricultural spaces where insect availability depends on farming activity, with the highest insect abundance in livestock pasture and hedgerows (Møller 2001; Evans *et al.* 2007; Gruebler *et al.* 2007; Paquette *et al.* 2013). Agricultural intensification, both in the breeding and overwintering grounds, may reduce insect food availability through pesticide use, habitat simplification, and displacement of livestock (Benton *et al.* 2002; Evans *et al.* 2007; Ghilain & Belisle 2008). Additionally, many AAI's forage heavily on insects with aquatic larval stages (McCarty & Winkler 1999), which are sensitive to agricultural activities throughout the watershed (Lenat & Crawford 1994).

The long-term demographic data necessary to test whether climate change, agricultural intensification, or another factor has contributed to AAI declines are not available for most species. Fortunately, researchers across North America have used tree swallows (*Tachycineta bicolor*), a common AAI, as a model organism to address fundamental questions in biology for over 40 years (Jones 2003), leaving behind extensive long-term demographic records. Tree swallows display similar spatial and temporal trends as most other AAI's, with marked declines in recent decades, particularly in northeastern North America, making them an excellent system for studying this decline (Nebel *et al.* 2010; Shutler *et al.* 2012; Smith *et al.* 2015; but see Michel *et al.* 2016).

Here, we use 43 years of continuous long-term monitoring data from a box-nesting population of tree swallows (1975-2017) to investigate environmental causes of population decline in tree swallows. These detailed data allowed us to determine if critical demographic parameters have changed over time, coincident with the decline in population size. After documenting change in these parameters, we tested for associations between them and candidate environmental drivers of population decline. Through the long-term record, we find strong evidence of a role for changing climate, suggesting that without mitigating anthropogenic climate change we may be unable to stem tree swallow declines and, more generally, declines of AAIs worldwide.

Methods

Study species

Tree swallows breed across much of North America in secondary cavities—pre-existing holes in trees. However, they preferentially breed in artificial nest boxes when available (Rendell & Robertson 1989; Robertson & Rendell 1990; Robertson *et al.* 1992). Highly philopatric, tree swallows return year after year to breed in the same sites (Winkler *et al.* 2004, 2005; Lagrange *et al.* 2017). They forage exclusively on aerial insects during the breeding season (Winkler & Allen 1996; Nooner *et al.* 2005; Ardia *et al.* 2006). Overwinter, tree swallows migrate to the southern U.S., Mexico, and Central America, roosting in flocks of hundreds of thousands of birds, often in sugarcane fields (Robertson *et al.* 1992; Winkler 2006). Survival overwinter weakly correlates to broadscale climate indices (Clark *et al.* 2018).

Previous work has shown that dynamics of this tree swallow population are particularly sensitive to changes in survival overwinter and fledging success (Cox *et al.* in press). Fledging success appears not to have declined in four swallow species, including tree swallows (Imlay *et*

al. 2018); however, the data used in this study flanks but does not extend through the steepest population declines and would be unable to capture poor fledging success if there have been recent improvements. Similarly, juvenile or adult survival overwinter appears not to have declined since 1991 (Weegman *et al.* 2017); however, without comparing these survival rates to those from before population decline began, it is unclear whether poor survival is contributing to the decline.

Study site

From 1975-2017, we monitored a box-nesting population of tree swallows at the Queen's University Biological Station in southeastern Ontario, Canada (44.5212°N, 76.3854°W). Nest boxes were arranged in grids over open areas or along roadsides, close to wetlands and lakes for foraging. The spacing between boxes approximated their preferred distribution of natural nest sites (Robertson & Rendell 1990). Predator guards were set up to minimize predation, with limited success.

Field Methods

Boxes were visited every 1-3 days during the breeding season, from late April through July. Tree swallows lay one egg per day until incubation, so we recorded first and last egg date and the clutch size. We also monitored hatch date and the number of nestlings that hatched. Nestlings either successfully fledged (left the nest), died in the nest, or disappeared from the nest prior to the age of possible fledging (~21 days, recorded as a predation event). We recorded the date nests fledged or failed and the cause of failure.

During the breeding season, we banded adults and 12-day-old nestlings with Canadian Wildlife Service bands. We identified returning adults by band number and banded new immigrants. Adults were sexed according to the presence of a cloacal protuberance (male) or

brood patch (female). Tree swallows display delayed plumage maturation in females, but not males: one-year-old females have brown body feathers, while older females have iridescent blue-green plumage, allowing us to classify females as one-year-old or older (Hussell 1983).

Population size analysis

We used box occupancy to assess how population size changed over time. We calculated yearly box occupancy as the number of nests (excluding known renests) out of the total available boxes. When the number of available boxes varies, box occupancy is a more appropriate metric of population size than total numbers of breeding pairs (Shutler *et al.* 2012). To assess whether population size consistently declined or if there were time-periods where the population was stable or even growing, we conducted a changepoint analysis using the package ‘strucchange’, requiring a minimum 10% of observations in each segment (Zeileis *et al.* 2002, 2003). Because this breakpoint analysis was sensitive to minimum segment size, we verified our results using a likelihood approach (Appendix B1). From the breakpoint analysis, we used a linear regression to model box occupancy with fixed effects of year, time-period, and their interaction. We found three time-periods (growth (1975-1991), decline (1992-2014), and post-decline (2014-2017)) which we used throughout subsequent analyses.

Analysis of fledging success and nestling predation

After hatching, nestlings fledge, die (e.g., due to abandonment, starvation, and/or hypothermia), or are depredated. We chose to analyze fledging success independent of predation because the environment likely influences these outcomes differently. For instance, we predicted predation would increase on warmer days when snakes, the main predator in our population, are more active (Sperry *et al.* 2008), but fledging success independent of predation, should increase on warmer days when more flying insects are available (Winkler *et al.* 2013).

We analyzed changes in fledging success across years for nests where eggs hatched, excluding nests that were depredated and where experimental manipulations might have altered the nest outcome ($N_{\text{nests}}=2,830$). Fledging rate was highly bimodal, with most nestlings either fledging or dying, so we treated fledging success as binary (no nestlings fledged or at least one nestling fledged) and analyzed fledging success using a generalized linear model (GLM) with a binomial distribution and a cauchit link (Zuur *et al.* 2013). We tested for relationships with year, time-period (as identified in the changepoint analysis described above), and their interaction, on the premise that if annual variation in fledging success influenced population size, then how fledging success changed over time might depend on whether the population was declining or not.

We also analyzed associations between weather conditions and fledging success across time-periods. We counted the number of days with good weather while nestlings were 0-8 days old, the ages nestlings are most sensitive to weather (ARC unpublished data). We defined good weather conditions as not raining, with maximum temperatures above 18.5°C, because the insects nestlings rely on only fly under these conditions (Grüebler *et al.* 2007; Winkler *et al.* 2013). Weather data came from the Environment Canada Hartington Court weather station located ~30km from the study site (Environment Canada 2018). We modeled fledging success as above, using a binomial GLM with a cauchit link testing for associations between numbers of days of good weather, time-period, and their interaction to allow for the possibility that the effect of weather on fledging success varies between time-periods.

We analyzed nestling predation similarly to fledging success. Here we excluded all nests used in invasive experiments as well as all nests where the nestlings were found dead in the nest because it was unclear whether those nests would have been depredated had the nestlings

survived longer ($N_{\text{nests}}=2,392$). Almost exclusively, the entire nest was depredated at once, so we treated predation as binary. Again, we used binomial GLMs with a cauchit link to test whether the likelihood of predation 1) changed across years, and 2) was associated with the number of days temperatures were suitable for snake predation before nestlings were large enough to depart the nest prematurely in response to predation (i.e., force fledge, nestlings must be 17+ days old). Grey ratsnakes (*Pantherophis spiloides*), the most common predator at these sites, are inactive below 15°C (Landreth 1972) but their activity increases with temperature until ~20°C (P. J. Weatherhead, personal communication). Therefore, we tested whether predation was predicted by the number of days with maximum temperatures above 15°C or above 20°C during the vulnerable age window (0-16 days).

We conducted supplementary Cox-proportional hazards analyses to confirm whether mortality risk and predation risk increased through time or under different weather conditions (Appendix B2). Results were similar (Fig. B1 and B2), so we present only the binary results below.

Analysis of overwinter survival

We calculated annual apparent survival estimates from the banding capture records using a Cormack-Jolly-Seber mark-recapture analysis in 'MARK' (White & Burnham 1999) with the 'RMark' interface (Laake 2013). Apparent survival encompasses both death and permanent emigration from the population as these states were indistinguishable. We focused our survival analyses on females because female capture rates were substantially higher than males and only females can be aged into three age-categories (fledgling, one-year-old, older). Fledglings cannot be visually sexed, but sex ratios in eggs and nestlings are equivalent (Delmore *et al.* 2008) so we assumed that half of all non-recruiting, 12-day-old nestlings were males and excluded them.

Additionally, because banding occurred prior to fledging, any banded nestling that died prior to fledging was excluded from the dataset. In total, our analysis included capture records from 17,749 birds.

We modeled five scenarios to explain adult survival rates. Survival could: be constant, randomly vary between years, differ between younger and older birds, vary between years with one age class consistently surviving better, or vary between years with the effect of age differing between years. We modeled capture probabilities as either remaining constant, being age-dependent (expected if subordinate one-year-old females were caught less often (Stutchbury & Robertson 1985)), varying between discrete years (expected if capture effort differed among years), or being both age and year dependent. The top model of apparent survival (based on AICc ranking; i.e., Akaike Information Criterion, corrected for small sample sizes) allows survival rate to differ between years with the effect of age varying between years, and capture rate to differ between years and ages. All estimates of overwinter survival come from this model (annual survival estimates: $N_{\text{juvenile}}=38$, $N_{\text{one-year-old}}=34$, $N_{\text{older}}=36$).

We determined whether juvenile survival (from fledging to the next breeding season), one-year-old female survival, and older female survival (from one breeding season to the next) declined during the time-period of population decline using separate linear regressions. Although we used untransformed survival estimates when possible, we log-transformed one-year-old female survival to meet assumptions of normality. We tested for effects of year, time-period, and their interactions. Because we used yearly survival estimates, we considered only two time-periods: population growth (1975-1991) or population decline (1992-2016). There were not enough identifiable survival estimates in the post-decline period to treat this period separately.

We tested for associations between overwinter survival and candidate environmental drivers. We focused on associations with juvenile survival because only juvenile survival had declined and was likely to have caused population decline. However, adult survival is highly influential in this population (Cox *et al.* in press) and may drive fluctuations in year to year population growth rate so is presented in the supplemental (Fig B3). We tested four environmental variables: 1) roosting habitat availability on the overwintering ground measured by sugar cane acreage (National Agricultural Statistics Service 2017) since sugar cane fields are common roost sites (Robertson *et al.* 1992), 2) extreme weather events during overwintering and migration that might reduce survival of whole roosts, as measured by the total number of hurricanes in the North Atlantic basin (Vecchi *et al.* 2011; National Oceanic and Atmospheric Administration 2018), 3) broadscale weather conditions overwinter measured by mean El Niño Southern Oscillation (ENSO) while the birds were on the overwintering ground (December to March) (Climate Prediction Center 2018) since ENSO has been linked to overwinter survival in tree swallows (Clark *et al.* 2018), and 4) weather conditions on the breeding grounds post-fledging as measured by the mean number of days with good weather 28 days post-fledging (Environment Canada 2018). Again, good weather was defined as not raining with maximum temperatures above 18.5°C because insects are only available under these conditions (Grüebler *et al.* 2007; Winkler *et al.* 2013). Juvenile tree swallows are still learning to forage independently for their first month outside the nest (Robertson *et al.* 1992), putting them at high risk of starvation in inclement weather. For each environmental variable, we used a linear regression to test for significant associations between overwinter survival and the environment, time-period, or their interaction. Then we compared the best models of overwinter survival across each

environmental variable using AICc scores, to assess the relative strength of the associations between these variables and survival (Table B1).

Analysis of trends in environmental variables

When an environmental variable was associated with fledging success or survival overwinter, we analyzed whether that environmental variable had changed over time. We used a linear regression with fixed effects of year, time-period, and their interaction. All analyses were conducted in R version 3.4.3 (2017-11-30) (R Core Team 2016).

Results

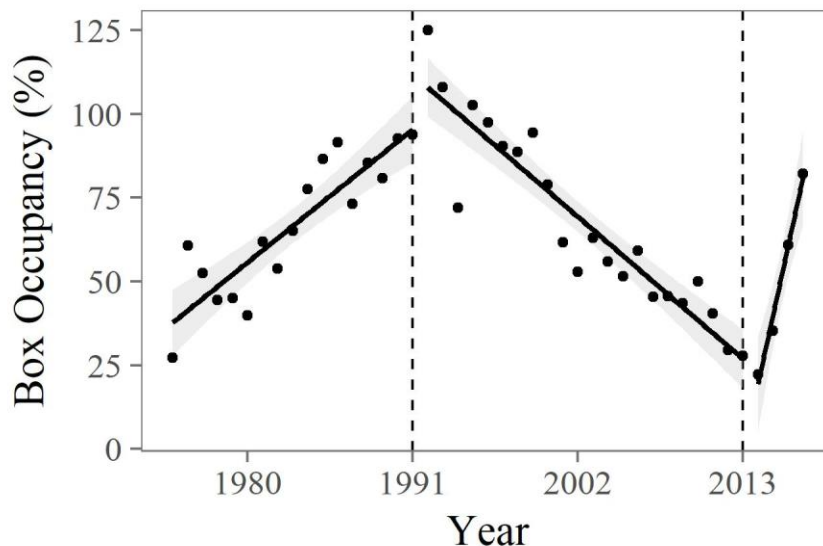


Figure 3.1: Breakpoints in population trends of box-nesting tree swallows, identified by changepoint analysis. Annual box occupancy (points; an estimate of size of the breeding population) increased from 1975 to 1991 ($3.6 \pm 0.5\%$ per year, $t=6.75$, $p<0.001$). In 1992, box occupancy began to decline steadily ($3.9 \pm 0.3\%$ per year, $t=-11.65$, $p<0.001$). Since 2013, box occupancy has been increasing ($21 \pm 4\%$ per year, $t=4.65$, $p<0.001$). Box occupancy $>100\%$ occurred in years where new breeding pairs used a nest box late in the season that had been previously occupied. Black lines represent trends in box occupancy for the three time-periods and gray shaded areas represent 95% confidence intervals. Dashed lines at 1991 and 2013 represent the boundary of each distinct time-period (growing, declining, and post-decline).

Population size

The trend in box occupancy through time changed in 1991 (95%CI: 1990-1992) and 2013 (95%CI: 2012-2014; Fig. 3.1). Box occupancy increased $3.6\pm 0.5\%$ per year from 1975 to 1991 ($t=6.75$, $p<0.001$). From 1992 to 2013, box occupancy declined $3.9\pm 0.3\%$ per year ($t=-11.65$, $p<0.001$). From 2014 to 2017, the population grew $21\pm 4\%$ per year ($t=4.65$, $p<0.001$). Therefore, we considered there to be three time-periods: growth (1975-1991), decline (1992-2014), and post-decline (2014-2017).

Fledging success

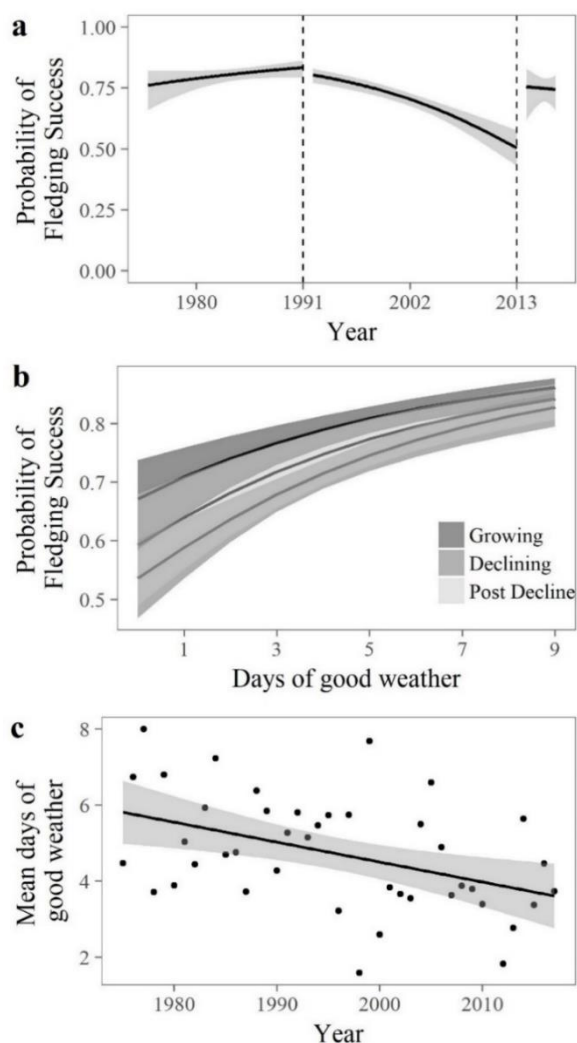


Figure 3.2: Environmental correlates of fledging success in a box-nesting population of tree swallows. a) Fledging success (excluding failures of nests due to predation) was high and stable while the population was growing and declined by half each decade during population decline ($OR=0.51\pm 0.05$ per decade, $z= -6.37$, $p<0.001$). Post-decline, fledging success has been higher,

comparable to fledging success before the decline. b) Fledging success increased when there were more days with temperatures above 18.5°C and no rain (“good weather” days) during the first eight days of nestling development (OR=1.19±0.03 per day, $z=6.23$, $p<0.001$). c) The mean number of days with good weather during early nestling development has decreased 0.52±0.17 days per decade from 1975 to 2017 (days with good weather, $F=9.49$, $p=0.004$). Solid lines represent trendlines, shaded areas represent 95% confidence intervals, and points represent annual means. For raw data, see Fig. B4.

Fledging success changed across years in different ways during the three time-periods (year * time-period, $\chi^2=15.08$, $p<0.001$; Fig. 3.2a). During the period of growth, fledging success was high and static (OR=1.5±0.4 per decade, $z=1.56$, $p=0.12$). During the period of population decline, fledging success declined to 51% of its original per decade (OR=0.51±0.05 per decade, $z=-6.37$, $p<0.001$). When the population began to grow again post-decline, fledging success was higher and comparable to fledging success during the period of growth (OR=0.4±2.6, $z=0.29$, $p=0.77$).

Fledging success was predicted by weather conditions during nestling development (good days, $\chi^2=39.99$, $p<0.001$; Fig. 3.2b). When there were more days with maximum temperatures above 18.5°C and without rain during early nestling development (0-8 days old), fledging success was higher (OR=1.19±0.03 per day, $z=6.23$, $p<0.001$). The effects of weather conditions on fledging success did not differ across time-periods (good days: time-period, $\chi^2=3.46$, $p=0.18$). However, there were differences between fledging success across time-periods that could not be explained by weather conditions (time-period, $\chi^2=34.11$, $p<0.001$). Regardless of weather conditions, fledging success was 1.6 times higher when the population was growing than when the population was declining (OR=1.6±0.2, $z=3.66$, $p<0.001$).

Weather conditions on the breeding grounds for this population during early nestling development have been getting progressively worse since 1975 (year, $F=9.48$, $p=0.004$; Fig.

3.2c). The yearly mean number of good days during early nestling development has declined 0.52 ± 0.17 days per decade ($t=14.20$, $p<0.001$).

Predation

Like fledging success, predation rate also changed across years in different ways during the three time-periods (year: time-period, $\chi^2 = 26.21$, $p<0.001$; Fig. 3.3a). When the population was increasing, predation rate was very low and declining (OR= 0.03 ± 0.05 per decade, $z=-2.36$, $p=0.018$). However, when the population started to decline, predation rate increased rapidly (OR= 2.9 ± 0.8 per decade, $z=4.05$, $p<0.001$). Although predation rate is significantly increasing in the post-decline period, this trend is based on only four years of data.

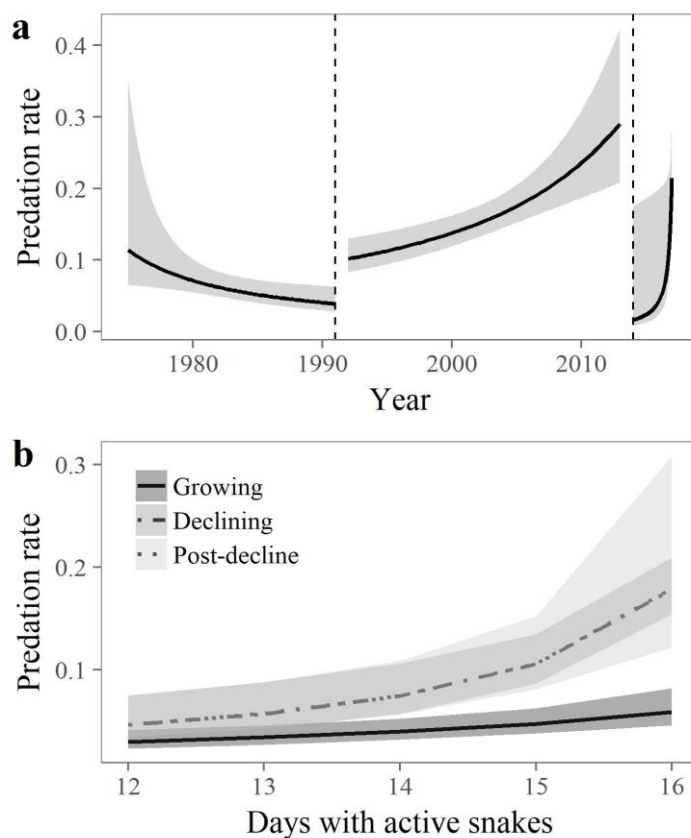


Figure 3.3: Environmental correlates of predation rate in a box-nesting population of tree swallows. Predation rate refers to the likelihood that a nest would be depredated before fledging if nestlings were not found dead in the nest from other causes. a) Until 1991, while the population was growing, predation rate was stable. From 1992 to 2013 predation increased three-

fold every decade (OR=2.9 ±0.8 per decade, $z=4.05$, $p<0.001$). Post-decline (2014 on) predation rate has been lower but increasing. b) Predation increased when there were more days with maximum temperatures above 15°C (“days with active snakes”; OR= 3.7±1.2, $\chi^2=25.09$, $p<0.001$). However, even when accounting for weather conditions, predation rates have been elevated since 1991 when the population began to decline. Lines represent trendlines with shaded areas to represent 95% confidence intervals. For plots of raw data, see Fig. B5.

Warmer weather when nestlings were vulnerable to predation (0-16 days) was associated with increased odds of predation (Fig. 3.3b). The number of days with maximum temperatures above 15°C predicted predation better than the days above 20°C ($\Delta AICc=20.14$). For every additional day with maximum temperatures above 15°C, the odds of predation increased 3.7±1.2 times (days above 15°C, $\chi^2=25.09$, $p<0.001$). However, temperatures below 15°C were rare and snakes were inactive for more than one day during nestling development for only 18.9% of nests. Along with the influence of weather, predation was also substantially lower while the population was growing compared to when the population was declining or during the post-decline period (time-period, $\chi^2=56.61$, $p<0.001$).

Survival overwinter

Adult survival did not differ depending on whether the population was growing or declining (Fig. B3). Although older female survival was highly variable (mean 41±15%), it was stable across time-periods (time-period, $F=0.007$, $p=0.93$) and there were no directional temporal trends (year, $F=0.22$, $p=0.63$). One-year-old female survival was lower and highly variable (21±16%), but stable across time-periods (time-period, $F=0.49$, $p=0.49$) and years (year, $F=1.55$, $p=0.22$).

In contrast, juvenile survival rates changed across years depending on whether the population was growing or declining (year: time-period, $F=25.07$, $p<0.001$; Fig. 3.4a). When the population was growing (1975-1991), juvenile survival was higher and increased 6.9±1.5% per

decade ($t=4.59$, $p<0.001$). However, from 1992 on when the population was declining, juvenile survival was lower and began dropping $1.7\pm 0.8\%$ per decade.

Mean ENSO during the winter months was significantly correlated with juvenile survival (ENSO, $F=6.72$, $p=0.013$; Fig. 3.4b). In years with lower ENSO values, juvenile survival was higher ($\beta=-0.14\pm 0.07$, $t=-2.06$, $p=0.046$). For reference, during El Niño events, ENSO is negative, while during La Niña events ENSO is positive. Regardless of ENSO, juvenile survival averaged $3.3\pm 1.1\%$ lower while the population was declining (time-period, $t=-2.92$, $p=0.006$). While variable, winter ENSO values have not changed significantly since 1975 (year, $F=1.12$, $p=0.29$; Fig. B6).

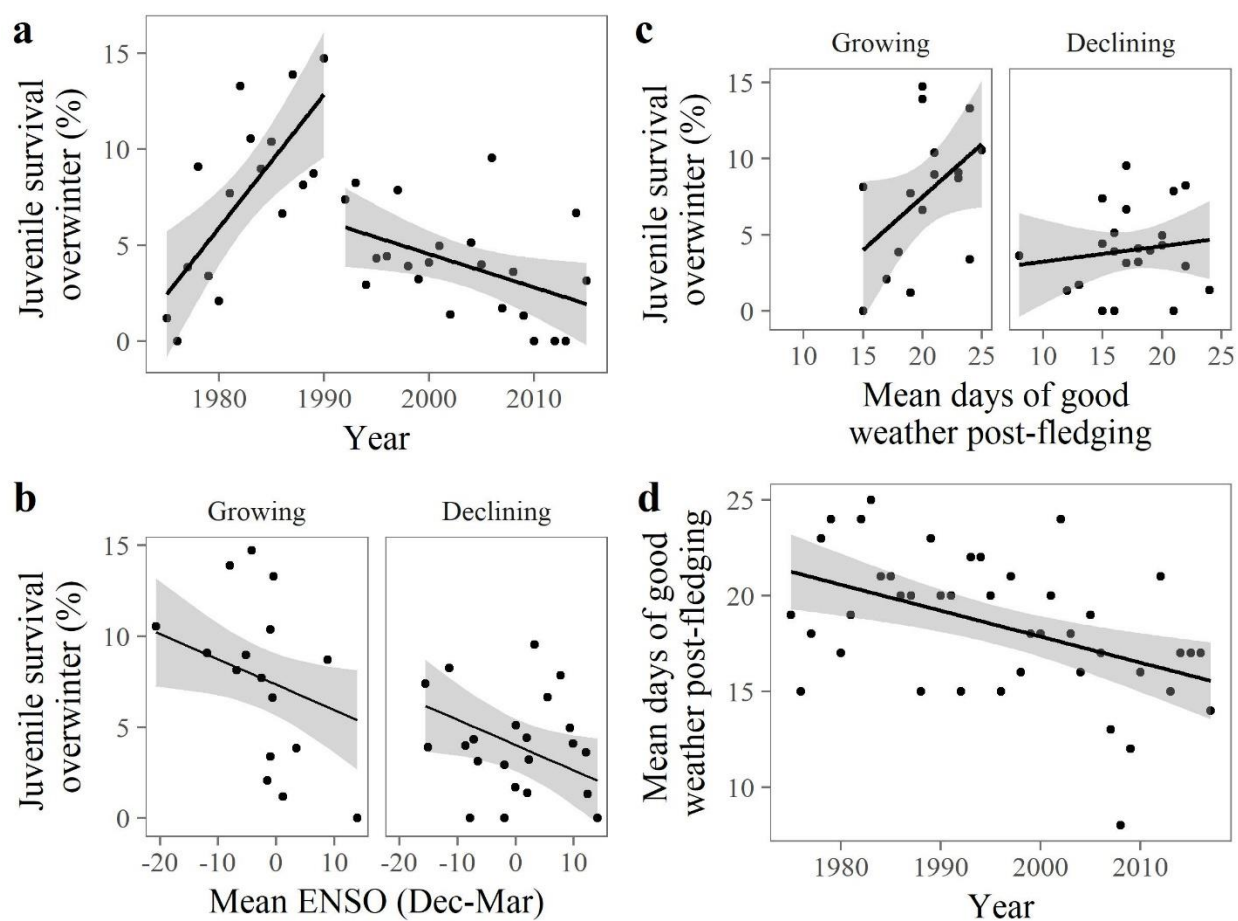


Figure 3.4: Environmental correlates of juvenile survival overwinter in a box-nesting population of tree swallows. a) Juvenile survival overwinter changed over time. While the population was

growing, juvenile survival increased $6.9 \pm 1.5\%$ per decade, but since the population started declining, juvenile survival decreased $1.7 \pm 0.8\%$ per decade. b) Juvenile survival negatively correlated with mean ENSO while the birds are on the overwintering grounds but survival was lower when the population was declining regardless of ENSO. Mean ENSO overwinter has not changed during the study period. c) While the population was growing, juvenile survival was higher when there were more good days (maximum temperature $> 18.5^\circ\text{C}$, no precipitation) in the first 28 days post-fledging. However, while the population was declining, juvenile survival was low and weather conditions post-fledging were not predictive. d) The mean number of days with good weather post-fledging has decreased 1.3 ± 0.4 days per decade from 1975 to 2017. Solid lines represent trendlines, shaded areas represent 95% confidence intervals, and points represent estimates of juvenile survival (panel a-c) or annual mean days of good weather (panel d).

The weather conditions during the month after fledging also correlated with juvenile survival (weather, $F=8.76$, $p=0.006$) and there are differences in the strength of the correlation depending on whether the population was growing or declining (weather: time-period, $F=2.92$, $p=0.097$; Fig. 3.4c). When the population was growing, when there were more days with good weather post fledging, juvenile survival was higher ($\beta=0.69 \pm 0.29$, $t=2.44$, $p=0.02$). However, weather conditions post-fledging did not correlate with juvenile survival when the population was declining ($\beta=0.1 \pm 0.2$, $t=0.51$, $p=0.61$). The number of good weather days in the 28 days after the mean fledging date has decreased by 1.3 ± 0.4 days per decade since 1975 ($t=-3.37$, $p=0.002$; Fig. 3.4d).

Hurricanes in the North Atlantic basin did not correlate with juvenile survival (hurricanes, $F=1.78$, $p=0.19$). Juvenile survival was also not correlated with sugar cane and seed acreage in the United States (sugar, $F=0.14$, $p=0.71$).

Juvenile survival correlates most strongly to weather environmental variables. When we compared the top models to explain variation in juvenile survival, including the null model of time-period alone using AICcs, we found that the winter ENSO model was the best performing

model. However, neither the ENSO model nor the weather post-fledging model was substantially better fit than the null model ($\Delta AICc < 2$, Table B1).

Discussion

Tree swallows and other avian aerial insectivores are declining (Nebel *et al.* 2010; Shutler *et al.* 2012; Smith *et al.* 2015; Michel *et al.* 2016), but a lack of long-term data has made it challenging to determine why. We found that adult survival was stable overtime, in agreement with Clark *et al.* (2018). Instead, declining juvenile survival, declining fledging success, and elevated predation risk correlated with declining population size. These demographic changes are unlikely to be caused by density dependence and are more likely the cause of population declines in tree swallows. Other species have increased survival and fledging at low population densities because of decreased competition (Torok & Toth 1988; Sillett & Holmes 2005), the opposite trend shown in this population. Additionally, the dynamics of this tree swallow population are particularly sensitive to changes in overwinter survival or fledging success (Cox *et al.* in press).

Variation in fledging success, independent of nest failure due to predation, was primarily associated with weather conditions during early nestling development. With more days with “good weather” (maximum temperature $> 18.5^{\circ}\text{C}$, no rain) during the first nine days of nestling development, nestlings were more likely to survive and fledge. During these “good weather” days, insects are more active. Increased insect availability likely improves parents’ ability to feed their nestlings and reduces death by starvation. Additionally, nestlings that stay warm during development grow faster and survive better because of lower energetic costs of thermoregulation (Krijgsveld *et al.* 2003; Dawson *et al.* 2005).

Weather conditions during nestling development at this location have gotten progressively worse. There are two non-exclusive explanations for this change. First, in response to climate

change, tree swallows are nesting earlier in the season (Dunn & Winkler 1999) with the mean laying date shifting 1.29 ± 0.03 days per decade earlier at this site (Fig. B7). By breeding earlier, parents may expose their offspring to more early spring rainfalls (Parmesan *et al.* 2013). Second, because of climate change, it rains more and temperatures are more variable in the study region (Kunkel *et al.* 2013), also exposing nestlings to more days of inclement weather.

Predation was also more common when the population was declining than when it was growing. Although there are many predators, snakes, particularly grey ratsnakes (*Pantherophis spiloides*), are the most common predators at this site. Predators attacked more nests when temperatures were above 15°C. However, 81% of nests experienced fewer than two days with temperatures below 15°C so weather likely plays a relatively minor role in determining predation risk at this site. Instead, snake population dynamics may be more important. The Committee on the Status of Endangered Wildlife in Canada listed the gray ratsnake as a threatened species in 1998, putting in place protections for the species (Environment and Climate Change Canada 2017). Snake predation has increased exponentially since, suggesting that snake populations may be recovering, to the detriment of this AAI population.

Declining juvenile survival likely contributed strongly to this population's decline, but we are cautious about inferring causation. Juvenile survival correlated with both weather conditions post-fledging on the breeding ground and broad-scale climate during the overwintering period (ENSO). Only weather conditions post-fledging deteriorated over time, perhaps due to changing climate or earlier breeding (as above). However, post-fledging weather conditions only predicted juvenile survival while the population was growing. We see the same pattern in older-female survival (Fig. B3). This suggests that post-fledging conditions were an important source of mortality for juveniles and older females while the population was growing, but another

unknown factor has exerted more influence on mortality since the population began to decline. One possibility is that juveniles fledging in increasingly poor conditions require large amounts of supplemental parental feeding to survive, levels which may be unsustainable regardless of post-fledging weather conditions (Cox *et al.* in review). Although, adult overwinter survival has not declined overtime at this site, overwintering location and broadscale climate overwinter do not correlation to adult survival at other sites (Clark *et al.* 2018), suggesting that perhaps it is conditions on the breeding ground that drive changes in juvenile survival.

One limitation of our analysis is that it is unclear where this population of tree swallows overwinters. Most likely, they overwinter in the southern United States with other eastern tree swallow populations (Knight *et al.* 2018) but their specific wintering location is unknown, making it impossible to collect local environmental data overwinter. As it was, U.S. sugarcane acreage, the best available quantification for winter habitat availability, was not predictive of juvenile survival.

Trends in local box occupancy follow trends in abundance based on regional Breeding Bird Survey (BBS) data (Nebel *et al.* 2010). In 1975, when we started monitoring this population, tree swallow populations in the Northeast were increasing (Nebel *et al.* 2010), although our focal population was increasing more quickly. This discrepancy is likely due to tree swallows' preference for artificial nest boxes over natural cavities (Rendell & Robertson 1989, 1990) which caused heavy immigration into these newly established study populations from the surrounding natural populations. Juvenile survival was also increasing during this period which would have contributed to the growing population. In 1992, our focal population began to steadily decline. Based on BBS data, regional tree swallow abundance had begun declining approximately 5-10 years earlier, as had declines in AAIs more generally (Nebel *et al.* 2010). Again, timing

discrepancies are likely due to immigration from the surroundings. In recent years, box occupancy in this population has been increasing. Other nest box grids in the Northeast (e.g., Quebec) have seen similar promising trends, but only time will tell whether the AAI decline abates or continues (M. Bélisle, personal communications).

This study focused on a single population of tree swallows, but other locations may expose birds to different suites of local challenges. For instance, at this site, gray ratsnake predation has increased, likely due to increasing ratsnake populations, a factor unlikely to influence most other locations where gray ratsnakes have either always been common or are absent. Similarly, this breeding site is located within a natural landscape and therefore escapes most if not all challenges of agricultural intensification that may challenge swallows at other locations. We suggest using the network of tree swallow grids set up across North America to test whether nests at all locations have reduced fledging success and juvenile survival during inclement weather and whether weather conditions during nestling development and post-fledging have deteriorated most at locations where populations are declining.

Although local challenges may compound its effects, declining fledging success and juvenile survival likely are not specific to this tree swallow population but rather likely affect tree swallows across their breeding range, as well as most AAIs. These changes appear to be largely driven by the increasingly inclement weather on the breeding grounds, due to climate change. Because the most plausible root cause of this challenge, inclement weather's negative effects on insect abundance, is not specific to the tree swallow lifecycle, climate likely affects all AAIs. Any temporal and spatial synchrony of decline supports this conclusion (Nebel *et al.* 2010; Inger *et al.* 2015, Michel *et al.* 2016). However, within the AAIs, flycatchers show spatially variable trends in population decline while swifts, swallows, and nightjars have

declined steadily since the 1980s (Smith *et al.* 2015). Swifts, swallows, and nightjars forage almost exclusively on flying insects, caught on the wing. In contrast, flycatchers also glean insects from the ground or foliage when flying insects are absent, perhaps making them less sensitive to short-term shortages of flying insects driven by inclement weather. Regardless, flycatchers are also declining (Smith *et al.* 2015), suggesting that flycatchers have not escaped the negative effects of food shortages.

Though not without challenges, long-term monitoring projects are invaluable for documenting and understanding population declines. Without access to this continuous 43-year data set chronicling tree swallow population dynamics, we would have been unable to attribute population declines to declining fledging success and juvenile survival. We find that poor survival and fledging are likely due to increasingly variable weather conditions on the breeding grounds, a common outcome of climate change, which makes flying insects an unreliable food source for avian aerial insectivores. We may need to reckon with humanity's collective impact on the global climate to stem the decline of these birds.

abundance by creating mismatches between offspring demand and the timing of food abundance peaks, as species at differing trophic levels shift their phenology to different degrees (Walther *et al.* 2002). Such mismatches have been linked to population declines in a number of species (Post & Forchhammer 2008; Gaston *et al.* 2009; McKinnon *et al.* 2012; Visser *et al.* 2012). Further, spatial mismatches can be as important as temporal ones. As ranges shift in response to climate change and populations go locally extinct (Parmesan & Yohe 2003; Van der Putten *et al.* 2010), species at higher trophic levels may face food shortages, particularly in the case of specialists (Dunne *et al.* 2002). Although less common in the literature, local extinction of prey species has been documented to lead to their predators' extinction (Durance & Ormerod 2010).

Avian aerial insectivores, a taxonomically diverse guild of birds that feed on flying insects, may also experience food shortages due to climate change. These birds are declining worldwide, with particularly strong declines in northeastern North America (Nebel *et al.* 2010; Shutler *et al.* 2012; Hallmann *et al.* 2014; Inger *et al.* 2015; Smith *et al.* 2015; Michel *et al.* 2016). Although the causes of decline are as yet unknown, insect shortages are a commonly cited hypothesis (Winkler *et al.* 2013; English *et al.* 2017, 2018). As the climate changes, northeastern North America is experiencing increased precipitation and more variable weather, with both more warm and cold spring days (Kunkel *et al.* 2013). When local weather conditions are wetter, colder, or windier, aerial insects decrease activity (Williams 1951; Taylor 1963; Gruebler *et al.* 2007; Winkler *et al.* 2013), potentially subjecting avian aerial insectivores to short-term but drastic reductions in food availability, even though overall food abundance is unaffected. In contrast, in cases of phenological or spatial mismatch, local food abundance is reduced over a longer time span, or even permanently (in the case of local extinction of a prey population). The relative importance of short-term reductions in food availability driven by inclement weather

would be dependent on its coincidence with periods of high demand for food by dependent offspring.

When weather conditions are poor, parents may be able to compensate for low food availability by increasing their foraging effort, perhaps at the cost of self-maintenance. Although the effects of weather-related food shortages are unknown, avian parental effort has been experimentally altered through handicapping and brood size manipulation experiments. In response to these manipulations, parents of many species increase offspring provisioning rates at the expense of their own body condition (Dijkstra *et al.* 1990; Lendvai *et al.* 2017). However, other studies have found that parents do not increase effort to compensate for food shortages to the nestlings, suggesting that parents already provision at maximal levels for their local conditions (Winkler & Allen 1995; Moreno *et al.* 1999).

Alternatively, declines in the total aerial insect abundance may be causing population declines in avian aerial insectivores. Although long-term records are uncommon, those available show that insect abundance has declined worldwide (Cane & Tepedino 2001; Thomas 2005; Conrad *et al.* 2006; Shortall *et al.* 2009; Cameron *et al.* 2011; Hallmann *et al.* 2017). Widespread insect declines have been linked to agricultural intensification and our increasing reliance on pesticides and monocropping (Cane & Tepedino 2001; Rioux Paquette *et al.* 2013). Intensive agriculture has been linked to declines in farmland birds, including aerial insectivores (Donal *et al.* 2001; Jerrentrup *et al.* 2017; Stanton *et al.* 2018). If widespread insect declines caused population declines, then we would expect adults to begin breeding at lower body mass and lose more mass throughout the season and nestlings to grow more slowly. We would not expect these changes to be linked to short-term weather patterns.

Whether short or long-term, food shortages could contribute to aerial insectivore decline by reducing nestling growth. With less food available, we would expect nestlings to grow more slowly and have higher mortality on cool, wet days. For tree swallows (*Tachycineta bicolor*), a common avian aerial insectivore, nestlings are more likely to die when the daily maximum temperature does not exceed 18.5°C, a critical threshold for flying insects (Winkler *et al.* 2013). However, the relative importance of temperature, wind speed, and precipitation to nestling growth and survival is still unknown (Winkler *et al.* 2013). In many species, poor nestling growth is linked to lower fledging success (Magrath 1991; Smith & Bruun 1998; Krebs 1999; Whittingham *et al.* 2003) and survival post-fledging (Tinbergen & Boerlijst 1990; Hochachka & Smith 1991; Naef-Daenzer *et al.* 2001; Monros *et al.* 2002; Greño *et al.* 2008; Sagar & Horning 2008), when most juvenile mortality occurs (Grüebler *et al.* 2014). Thus, food shortages have the potential to cause population declines by reducing fledging success and juvenile survival (Cox *et al.* in press).

Tree swallows are an ideal model avian aerial insectivore for studying the effects of climate change on nestling and adult body condition. They are secondary cavity nesters, naturally nesting in holes in trees formed by other species, but will preferentially nest in artificial nest boxes when available (Robertson & Rendell 1990), allowing researchers to easily monitor breeding success and track adults and nestlings throughout the breeding season. Because they are such a tractable study organism, their natural history is well documented. For instance, tree swallows are one of the few avian species where young nestlings are able to reduce their metabolism and go into torpor when cold before developing homeothermy as they mature (Dunn 1979; Marsh 1980a). Additionally, tree swallow populations show similar spatial and temporal demographic declines to other avian aerial insectivores (Nebel *et al.* 2010; Shutler *et al.* 2012;

Smith *et al.* 2015; Michel *et al.* 2016), with marked declines in northeastern North America, suggesting that the cause of these declines may be shared.

Here, we use a combination of long-term monitoring data from a box-nesting population of tree swallows (1975-2017) and short-term intensive monitoring (2017) to determine how shifting local weather conditions affect tree swallow body mass. Using the long-term record, we first determined whether nestling body mass had declined, indicating reduced growth rates and poor parental provisioning. We also assessed whether adults lost more body mass during the breeding season than previously, indicating that parents increased foraging effort to provision offspring and/or that food availability had declined to the point where adults were unable to forage enough to meet their personal needs. We assessed the relative effects of temperature, wind, and rain on nestling growth and parental effort during the 2017 breeding season and assessed whether weather parameters that predicted nestling growth or parental effort had changed across time. Overall, we find evidence that increasingly rainy weather conditions are decreasing nestling growth.

Methods

Long-term monitoring field methods

We monitored a box-nesting population of tree swallows at the Queen's University Biological Station in southeastern Ontario, Canada (44.521°N, 76.385°W) regularly during the annual breeding season (May to July) from 1975-2017. Nest boxes in this population are arranged in grids to mimic the natural distribution of cavities (Robertson & Rendell 1990). From 1983-2017, we captured adults during breeding. Adults were sexed based on the presence of a brood patch (female) or cloacal protuberance (male). In most years, we also measured adult body mass (Pesola spring scale, $\pm 0.25\text{g}$) and wing chord (wing rule, $\pm 1\text{mm}$). From 1977-2017,

nestlings were ringed at 10-16 days old, at which time their body mass and wing chord were also measured. Across the dataset used in this study, we measured 1,437 females, 585 males, and 10,232 nestlings.

Field methods monitoring nestling development in 2017

We expected that slowed nestling growth and changing patterns of adult body mass evident in the long-term data might be explained by changing local weather patterns. To elucidate associations between nestling growth and daily weather conditions, we closely tracked the growth of 445 nestlings from 91 nests from April 25 to July 25, 2017, for a total of 1,723 measurements. We measured nestling body mass every other day from two to twelve days old (i.e., at day 2, 4, 6, 8, 10, and 12). We did not measure nestlings on days when it was raining so heavily that we were unable to keep them dry, resulting in some gaps in the measurement records. At twelve days old, we fitted nestlings with a numbered aluminum Canadian Wildlife Service ring.

We caught adults between day 10 and 12 of incubation using a combination of mist netting (males and females) and hand trapping techniques (females). At this time, we fitted each adult with a passive integrated transponder (PIT) tag embedded in a leg band. On day ten of nestling development, we used radio-frequency identification (RFID) at the entrance to the nest box to determine parental provisioning rates using the set up developed in (Lendvai *et al.* 2015). Provisioning rates (i.e., numbers of visits by the parent to the nest box) accurately reflect the amount of food nestlings receive because tree swallows bring similar amounts of insects each trip (McCarty 2002). We were unable to deploy RFID readers on rainy days. We were able to measure provisioning rates for 55 females and 17 males, including 15 nests where both parents were measured.

Statistical Analyses

All analyses were conducted in R version 3.4.3 (2017-11-30) (R Core Team 2016). Assumptions of normality were verified via histograms, quartile-quartile plots, and the Shapiro-Wilks tests. The fit of the global model was verified by plotting residuals against all predictors and response variables, verifying for homoskedasticity and the absence of trends, indicating a well-fitting model. We retained all significant variables (as calculated using the *lmerTest* package for models with random effects (Kuznetsova *et al.* 2017)). We retained random effects when the variance explained was greater than the standard deviation. We assessed the need for first, second, and third order polynomials by comparing AICc scores.

We compiled wind speed data from weather stations at the Queen's University Biological Station and all other weather data from Environment Canada's Hartington Court weather station (~30km from the site) (Environment Canada 2018). Variables included maximum daily temperature, daily rainfall, and mean wind speed during hours of active foraging (5:30am-8pm), from which we extracted weather conditions on specific days and over three day windows for key dates.

To determine whether nestling body mass declined over the long-term record, we used linear mixed models (LMMs). We tested whether body mass varied with the fixed effects of nestling age, year, and their interaction. Nestling growth rates may have declined over time if food availability became limited. We included a random intercept for nest ID to account for similar growth trajectories of nestmates. To determine if nestling body size had changed, we repeated this analysis using nestling wing chord as the response variable.

Adult body mass might also be affected if food abundance during the breeding season had declined. We expected adult body mass to decline as offspring developed because both

parents expend energy to care for their offspring. Therefore, we determined if adult body mass had changed from 1983 to 2017 using LMMs with body mass as the response variable and number of days since the first egg was laid, year, and their interaction as fixed effects. Because males and females have different roles (females incubate the eggs and provision nestlings; males only provision nestlings and do so to a lesser degree than females (Whittingham *et al.* 2003)) and because males were typically caught only after nestlings hatched compared to females which were also caught during incubation, we conducted separate analyses for the two sexes. Body mass might not be lost linearly during breeding, so we tested for first through third order polynomial relationships between adult mass and days since the first egg was laid. Some birds were measured more than once, either within a year or in multiple years, so we included a random intercept for bird ID. To determine if overall body size had changed through time, we conducted similar LMM with wing chord as the response variable and year as the predictor, conducting separate LMMs for each sex. As moulting occurs prior to the breeding season, we did not include days since the onset of egg laying in these models.

To determine nestling growth trajectories in 2017, we conducted a linear model with nestling body mass as the response variable and age as the predictor. As growth rate is often not linear, we assessed the fit of first through third order polynomials and logistic regression, settling on a third order polynomial as the best fit based on AIC_c score. Younger nestlings had less variation in mass than older nestlings, so we used the “varFixed” function in the *nlme* package to allow variation in mass to increase with age (Pinheiro *et al.* 2017). Residual body mass from this model reflects whether individual nestlings were heavy or light for their age.

To assess relations between weather, nestlings’ ability to go into torpor, and nestling growth in 2017, we conducted an LMM from the *lme4* package (Bates *et al.* 2015) with residual

mass as the response variable and thermoregulatory strategy, weather conditions, and the interaction as predictor variables. We included thermoregulatory strategy because poikilothermic nestlings (0-6 days old) might be less affected by inclement weather than nestlings just developing temperature regulation (7-8 days old) or fully homeothermic nestlings (9+ days old) because they are able to go into torpor in cold conditions (Dunn 1975; Marsh 1980a). For our weather variables, we considered total rainfall, mean windspeed, and mean maximum daily temperature during the three days prior to measurement because tree swallow nestling development suffers most when inclement weather lasts for three or more days (McCarty & Winkler 1999b). All three weather variables and their interaction with thermoregulatory strategy were included in one LMM. We also included nested random intercepts for nestling ID within nest ID to account for the fact that a poor-quality nestling might always be lighter than average, or that parental quality could influence the entire brood's growth.

We calculated hourly provisioning rates for PIT-tagged males and females in 2017 based on two hours of RFID readings at the nest following Lendvai *et al.* 2015. Then we conducted two linear regressions to assess the effects of local weather conditions with provisioning rate as the response variable and weather conditions and brood size as additive predictor variables. We expected parents to provision less often when they had fewer offspring demanding food. For weather variables, we considered maximum temperature and mean windspeed on the day of provisioning measurements, and, for the females, whether or not it had rained in the preceding three days (as it never rained during our recordings and only 3 males had experienced no rain). We conducted separate linear regressions to test for associations between local weather and provisioning rate for each sex because males and females typically provision at different rates (Leonard & Horn 1996; Whittingham *et al.* 2003) and our unequal sample sizes prevented us

from modeling both sexes together. Finally, for the 15 nests where both male and female provisioning rates were available, we regressed male provisioning rate against female provisioning rate to assess the degree to which parents matched or compensated for their partner.

Because we found that rainfall and maximum temperature were predictive of nestling body mass in 2017, we calculated the total rainfall and average maximum temperature experienced from hatching to fledging for each nest across the long-term dataset. Then, we calculated annual mean rainfall and maximum temperature experienced by developing nestlings from 1975 to 2017. We used linear regression to assess whether rainfall or temperature had changed over time. Long-term wind speeds are unavailable for the area.

Results

Long-term trends in body size

Nestling growth patterns have changed over the long-term study period (Fig. 4.1). Nestlings are not gaining body mass as much as they used to (age * year, $F_{1,3466.2}=26.56$, $p<0.001$, $N=10,232$). In 1977, when we first began measuring nestlings, 10-day-old to 16-day-old nestlings were growing at a rate of 0.77 ± 0.08 g per day (~3.5% of adult body mass). In contrast, by 2017, nestlings were not growing at all during this period (-0.05 ± 0.09 g per day). The effect of nest ID explained a substantial portion of the variation ($\sigma=6.80$, $SD=2.61$). The decline in body mass is not simply due to nestlings being generally smaller; nestling wing chord has grown at the same rate from 1988 to 2017 (2.5 ± 0.2 mm per day; age, $F_{1,1460.6}=164.1$, $p<0.001$).

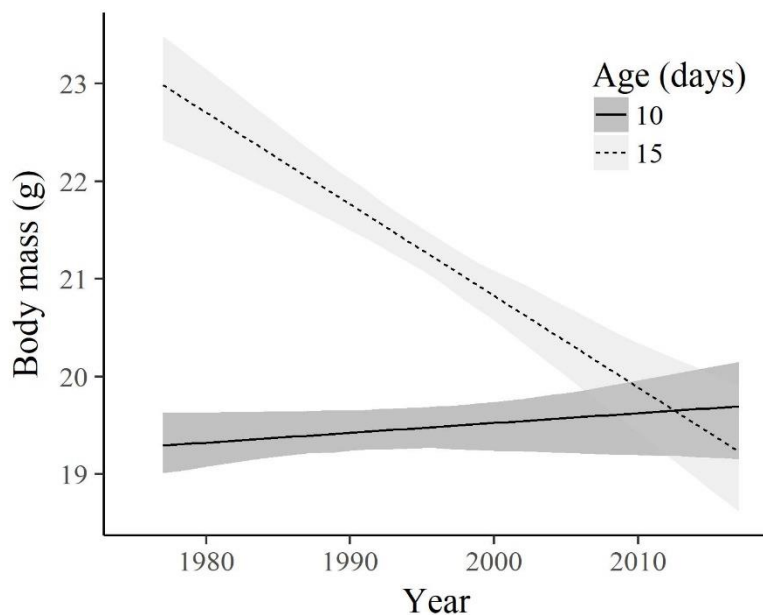


Figure 4.1: Nestling tree swallows have not gained as much body mass in recent years as they did in the past (age * year, $F=26.56$, $p<0.001$), illustrated here with data from 10- and 15-day-old nestlings. In 1977, 15-day-old nestlings were considerably heavier than 10-day-old nestlings ($23.0\pm 0.3\text{g}$ and $19.3\pm 0.2\text{g}$ respectively). In contrast, by 2017, model predictions show 10 and 15-day-old nestlings both weighing similar amounts (19.7 ± 0.3 and $19.2\pm 0.4\text{g}$ respectively). The solid line represents model-projected body mass of a 10-day-old nestling from 1975 to 2017. The dashed line represents projected body mass of a 15-day-old nestling from 1975 to 2017. Shaded areas represent 95% confidence intervals on the projections (dark grey for 10-day-old, light grey for 15-day-old). For plots of raw data, see Fig. C1.

It is not just nestlings that are losing body condition. Adult females have always lost body mass throughout the breeding season as they incubate and provision their nestlings. However, in recent years adult females began breeding at lower body mass and spent more time during incubation recouping body mass before losing body mass again during nestling provisioning, as compared to females earlier in the long-term study (Fig. 4.2a; $(\# \text{ days since first egg})^2 * \text{ year}$, $F_{2,2885.2}=30.96$, $p<0.001$, $N=3,176$). Males were typically not caught prior to incubation so we focused on changes in body mass after hatching, while males were provisioning. Males lose more body mass during nestling provisioning than in the past (Fig. 4.2b; $\# \text{ days since first egg} * \text{ year}$, $F_{1,1141.0}=5.78$, $p=0.016$, $N=1,148$). As with nestlings, changing body mass cannot be

explained by changes in body size in males or females; wing chord has not declined through time (females, year, $F_{1,1529.1}=0.004$, $p=0.95$; males, 0.3 ± 0.01 mm/decade, year, $F_{1,760.04}=6.93$, $p=0.009$, $N_{\text{females}}=3,170$, $N_{\text{males}}=1,477$).

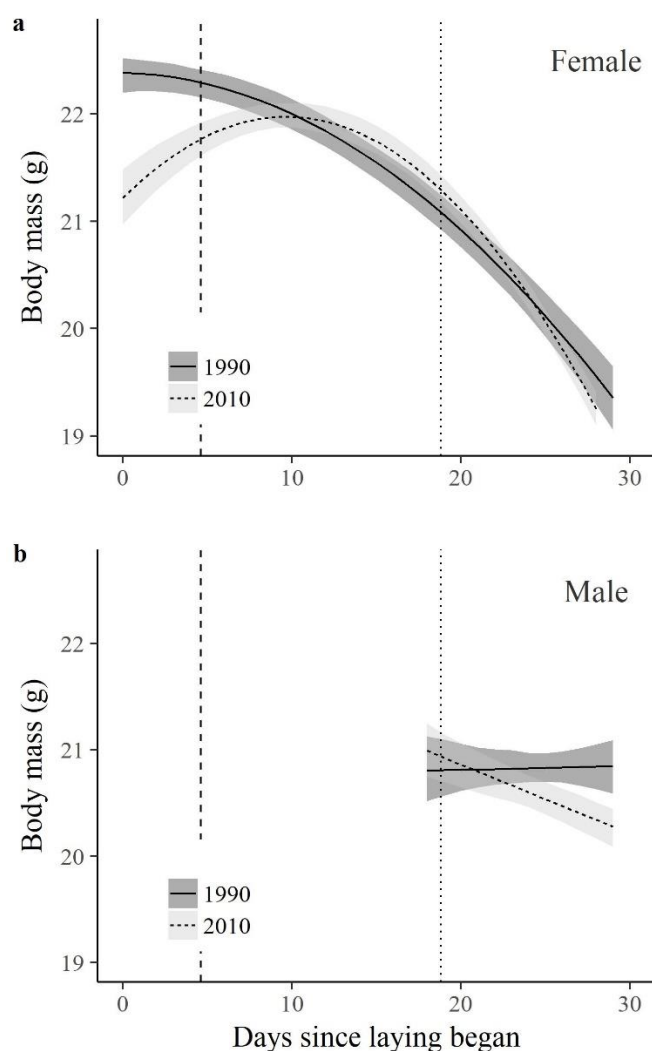


Figure 4.2: Adult tree swallow body mass fluctuates throughout the breeding season, but these fluctuations have changed from 1983 to 2017, illustrated here with data from 1990 and 2010. a) For females, body mass has always declined throughout the breeding season. However, in recent years (e.g., 2010), females have started breeding with lower body mass and spending egg laying and the beginning of incubation gaining mass. b) In the past (e.g., 1990), male body mass did not change over the breeding period, but in recent years males lose body mass during nestling provisioning (e.g., 2017). The solid lines represent model projected adult mass throughout the breeding season in 1990 and the dashed lines represent adult mass during 2010. Shaded areas represent 95% confidence intervals (dark grey for 1990, light gray for 2010). The vertical dashed

line represents the mean start of incubation (4.6 days after the first egg was laid) and the vertical dotted line represents the mean day of hatching (18.8 days after the first egg was laid). For plots of raw data, see Fig. C2.

Effects of local weather conditions in 2017

As expected, nestling body mass increased as nestlings got older (age³, $F_{3,1719}=4205.7$, $p<0.001$, $N=1,723$). Nestling residual body mass was associated with total rainfall, mean windspeed, and mean maximum daily temperature in the three days preceding measurement but the strength of the association depended on the thermoregulatory strategy employed by the nestling (rain*thermoreg., $F_{2,1379.9}=5.13$, $p=0.006$; wind*thermoreg., $F_{2,1372.7}=5.60$, $p=0.004$; temp.*thermoreg., $F_{2,1374.2}=6.01$, $p=0.003$). As in the long-term dataset, there was a strong nest effect, with some nests and nestlings more likely to be light for their age than others (random intercept for nest ID, $\sigma=2.66$, $SD=1.56$; random intercept for nestling ID, $\sigma=0.63$, $SD=0.79$). Older nestlings who had developed homeothermy were generally more sensitive to weather conditions than poikilothermic or intermediate nestlings (Fig. 4.3). Nestlings were more likely to be light for their age (i.e., low residual body mass) if it had been cold or rainy previously. High windspeeds were associated with decreased residual body mass of homeothermic nestlings and increased residual body mass of intermediate and poikilothermic nestlings.

Female provisioning rates were predicted by whether it had rained in the preceding three days or not (Fig. 4.4b; $F_{1,50}=5.91$, $p=0.019$). If it had rained, female provisioning rate increased by an average of 4 ± 2 visits per hour. Female provisioning rate also increased as the number of nestlings in the nest increased (Fig. 4.4a; 2.0 ± 0.7 visits/hr per nestling, $F_{1,50}=7.69$, $p=0.008$). Male provisioning rates were not associated with local weather conditions or brood size but did

increase with increasing female provisioning rates (Fig. 4.4c; 0.5 ± 0.2 male visits/female visit, $F_{1,13}=5.47$, $p=0.036$).

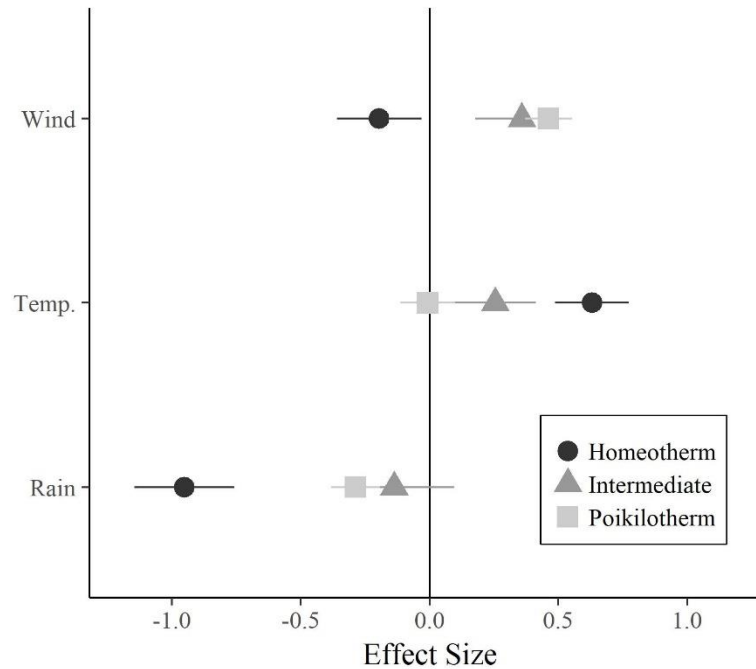


Figure 4.3: In 2017, nestling tree swallows were lighter (residual body mass, controlling for a relationship with age) when there was more rainfall or colder weather during the three days before measurement, particularly in the case of older, homeothermic nestlings. Note that the largest effect sizes and lowest residual body mass were seen in homeothermic nestlings during rainy weather. Points represent mean effect sizes of mean windspeed, mean daily maximum temperature, and total rainfall in the preceding three days on nestling residual body mass with error bars representing standard error. Positive effect sizes mean that nestlings were heavier for their age when this weather parameter was higher; negative effect sizes mean that nestlings were lighter for their age when this weather parameter was higher. To facilitate comparison, all effect sizes have been calculated with rescaled weather parameters (mean=0, SD=1). For plots of raw data, see Fig. C3.

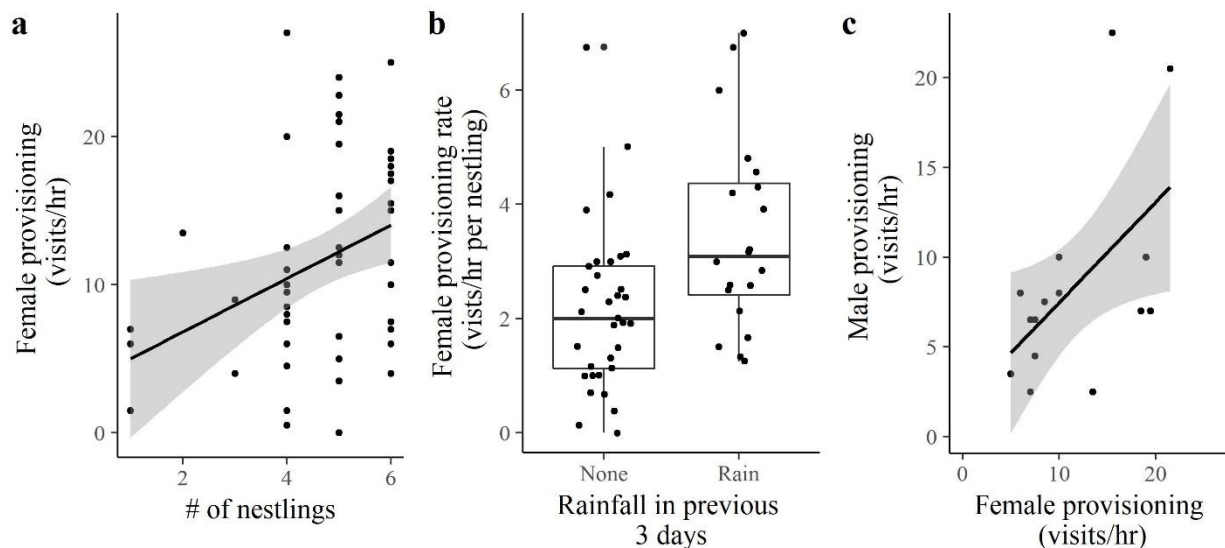


Figure 4.4: Offspring provisioning rates in male and female tree swallows were best predicted by different variables. Female provisioning rate was greater when a) there were more nestlings in the nest (2.0 ± 0.7 visits per hr/nestling, $F=7.75$, $p=0.008$) and b) there had been rain in the preceding three days (rain, $F=6.58$, $p=0.013$). c) Male provisioning rate was unrelated to brood size or weather but tended to increase with increasing female provisioning ($\beta=0.5 \pm 0.2$, $F=5.47$, $p=0.036$). All lines represent trendlines with shadings to show the 95% confidence intervals. Boxplot hinges show first and third quartiles, with whiskers extending to the farthest point within 1.5 times the distance of interquartile range, and points spread across the x-axis for readability only. All points represent unique males and females. Note that in panel a only, plotted female provisioning rates are controlled for the number of nestlings in the nest.

Long-term changes in weather patterns

Since 1975, the mean rainfall during nestling development, which was associated both with nestling growth and female provisioning, has increased by 9.3 ± 0.3 mm per decade (Fig. 4.5; $F_{1,39}=9.17$, $p=0.004$). The mean of maximum daily temperature during nestling development, which was associated with nestling growth, has not changed over the course of the study period ($F_{1,39}=1.26$, $p=0.27$).

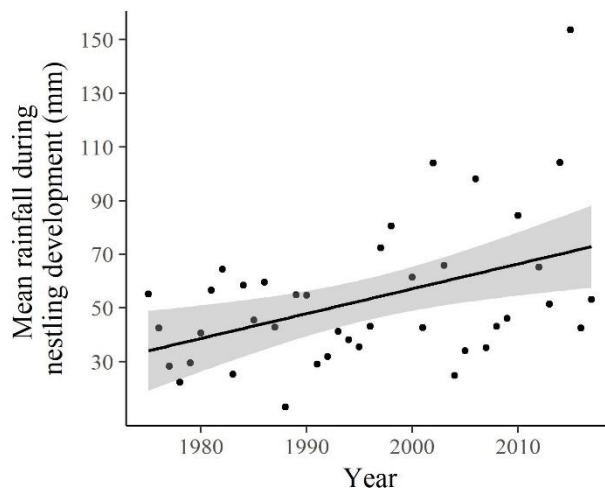


Figure 4.5: Since 1975, mean rainfall during nestling development has increased by 9.3 ± 0.3 mm per decade ($F=9.17$, $p=0.004$). For each nest, we calculated the total rainfall between hatching and fledging. From there we calculated the mean annual rainfall during nestling development for each year between 1975 and 2017. The black line represents the trendline and the shaded area represents the 95% confidence interval.

Discussion

Avian aerial insectivore population sizes have declined dramatically across the globe (Nebel *et al.* 2010; Inger *et al.* 2015; Smith *et al.* 2015; Michel *et al.* 2016) but the underlying causes remain unclear. It is often suggested that declines are due to widespread declining insect abundance caused by agricultural intensification (Cane & Tepedino 2001; Gruebler *et al.* 2007; Shortall *et al.* 2009; Cameron *et al.* 2011; Hallmann *et al.* 2014, 2017). Here we show that an alternative mechanism, short-term food shortages due to effects of climate change on local weather patterns, may also drive population declines. After periods of rainy, cold weather when insects are less active (Williams 1951; Taylor 1963; Gruebler *et al.* 2007), tree swallow nestlings are more likely to be light for their age, indicating constrained growth during food shortages (Fig. 4.3). We found that rainfall during nestling development has increased at this study site over the past four decades, following climate change projections for the area (Kunkel *et al.* 2013). Correspondingly, tree swallow nestlings have become lighter. Therefore, we suggest that

nestlings may be experiencing a lack of food, not necessarily because of low insect abundance, but rather because increasingly rainy weather causes short-term insect shortages.

Like previous studies, we saw that cold weather reduced nestling growth (McCarty & Winkler 1999b; Nooker *et al.* 2005; Jenni-Eiermann *et al.* 2008; Winkler *et al.* 2013). However, we found that rainfall was a more important predictor. Previous work did not test for effects of rainfall or wind which we found to be correlated with temperature, so it is possible that some of the negative temperature effects described in these previous studies were driven by rain instead. Tree swallows are advancing their phenology in response to changing precipitation and wind conditions, rather than changing temperatures (Irons *et al.* 2017), supporting the conclusion that precipitation may matter more than temperature for this species.

Declining nestling mass likely has negative consequences at the population level. Larger nestlings are more likely to survive to fledging in tree swallows (Whittingham *et al.* 2003) and other bird species (Magrath 1991; Smith & Bruun 1998; Krebs 1999). In great and coal tits, most juvenile mortality occurs shortly post-fledging, while juveniles are learning to fly and forage for themselves and are particularly susceptible to predation and starvation (Naef-Daenzer *et al.* 2001). Across several species, nestlings that fledge with greater body mass survive this post-fledging period better, probably by relying on their larger energy reserves to help them survive periods of low foraging success (Tinbergen & Boerlijst 1990; Hochachka & Smith 1991; Naef-Daenzer *et al.* 2001; Monros *et al.* 2002; Greño *et al.* 2008; Sagar & Horning 2008). For this population, during cold snaps and heavy, sustained rainfall, nestling mortality regardless of body mass is high but heavier nestlings are slightly more likely to survive, suggesting a frailty effect (Ouyang *et al.* 2015). Such a selection for heavier nestlings during cold, rainy weather may cause us to underestimate the strength of the effect of poor weather conditions on nestling growth and

subsequent consequences for fledging success and juvenile survival. Fledging success and juvenile survival strongly influence population dynamics in this population (Cox *et al.* in press), so declining nestling body mass is likely contributing to overall declines in this tree swallow population.

We found that young nestlings' body mass (0-8 days old, here classified as having poikilothermic or intermediate thermoregulatory strategies) was less affected by weather than older nestlings. There are two possible explanations. First, young tree swallow nestlings have a natural defense against inclement weather conditions: torpor. Nestlings in some insectivorous species are known to go into torpor, reducing basal metabolic rate in response to starvation and cold temperatures (Dunn 1975; Prinzinger & Siedle 1988) which may allow young nestlings to maintain body condition during short-term insect shortages. Alternatively, younger, smaller nestlings require less food to maintain body condition, perhaps so much less that their parents are able to supply sufficient food, even during poor weather. However, if this were the case, one would expect nestling age to be more predictive than thermoregulatory strategy (based on age classes) which was not the case (data not shown).

Females increased provisioning rates when the previous days were wet and rainy (Fig 4.5). While we were unable to assess provisioning rate during rain events, nestlings were lighter following rain events suggesting that rain reduced provisioning. We hypothesize that following rain events, females respond to increased nestling demand for food and attempt to compensate for earlier food shortages through increased effort as has been shown in barn swallows (Schifferli *et al.* 2014). These efforts do not seem to fully compensate for rainy weather as nestlings were still light for their age following rain events. Because of increased rainfall during nestling development, females are likely working harder to provision their nestlings.

In contrast, male provisioning rates did not directly respond to weather conditions in the preceding three days. Because we saw no response to previous weather conditions in males and our analyses and previous work (Lendvai *et al.* 2017) shows tree swallow males match their provisioning rate to their partners, we suggest that males rely on females' assessment of the broods' need to determine provisioning effort. By responding to females' increased effort, males may be increasing provisioning following rain events as well, but we did not have the data to assess such an effect.

Although adult provisioning effort was only moderately responsive to weather conditions, from 1983 to 2017 parental self-maintenance suffered (Fig. 4.2). Females are beginning incubation with progressively lower body mass and spending the incubation period foraging to improve their body condition. This is consistent with other tree swallow populations which have found that females have lost mass over a relatively short time-period across different breeding habitats (Rioux Paquette *et al.* 2014). Returning to the breeding ground with low body mass suggests that foraging conditions on the overwintering grounds may have deteriorated. By the time the brood hatches, females have regained body condition to pre-decline levels and lose mass throughout nestling development similarly across the study period. In contrast, males have lost an increasing amount of body mass while provisioning nestlings. Male provisioning was not linked to local weather conditions suggesting that increased provisioning effort during rainier springs does not explain faster body mass declines. Instead, males may be finding it difficult to feed themselves adequately during wet weather or feeling the effects of widespread insect declines (Cane & Tepedino 2001; Gruebler *et al.* 2007; Shortall *et al.* 2009; Cameron *et al.* 2011; Hallmann *et al.* 2017).

We present evidence that climate change may be affecting tree swallow food availability through short-term insect shortages, but overall declining insect abundance may also be a factor (Thomas 2005; Conrad *et al.* 2006; Shortall *et al.* 2009; Cameron *et al.* 2011; Hallmann *et al.* 2017). However, we suspect that weather-induced food shortages may be more important. Tree swallows and other avian aerial insectivores show the most notable declines in northeastern North America, where climate change is causing increasingly rainy spring weather (Kunkel *et al.* 2013). In contrast, the most intensive agriculture in North America occurs in the Midwest, a region where most aerial insectivores are not declining (Nebel *et al.* 2010; Shutler *et al.* 2012; Smith *et al.* 2015; Michel *et al.* 2016). If agriculture was responsible for the decline, one might expect the fastest aerial insectivores declines to occur in regions with the most intensive agriculture. In contrast, climate change is causing increasingly rainy weather in the Northeast (Kunkel *et al.* 2013), a pattern consistent with climate-driven declines in aerial insectivores.

In conclusion, the effects of short-term, weather-driven food shortages, outside of overall food abundance, appear strong enough to reduce body condition and offspring development. For tree swallows, a declining avian aerial insectivore, reduced nestling growth may be caused by increasingly rainy weather that prevents adequate provisioning by the parents. Climate change likely affects other aerial insectivores similarly, as they all rely on the same flying insects. Therefore, we suggest that consideration of food availability, as distinct from food abundance, may be important for predicting long-term impacts of climate change.

Chapter 5: General discussion

Avian aerial insectivore declines are widespread (Nebel *et al.* 2010; Inger *et al.* 2015; Smith *et al.* 2015; Michel *et al.* 2016), but it has been difficult to determine their cause. Because the main commonality among these taxonomically-diverse birds is that they forage on flying insects, their rapid decline may be linked to their shared diet (Nebel *et al.* 2010). However, there are numerous mechanistic hypotheses to explain this decline, ranging from increasing pesticide use to decreasing open habitat for foraging to climate change's impact on insect availability.

I turned to a population of tree swallows, a model avian aerial insectivore, to investigate demographic and environmental causes of population decline in aerial insectivores. In chapter 2, I conducted a life-stage simulation analysis to determine which demographic transitions (egg to nestling to juvenile to one-year-old to older bird) had the largest impact on population growth rates. Fledging success and overwinter survival of juveniles, one-year-olds, and older birds all had the potential to substantially influence population growth of tree swallows. To determine which of these potentially important transitions were changing and driving population decline, in chapter 3, I analysed long-term nest and banding records. Adult survival had not changed over time so was not likely to be responsible for population decline; however, declining fledging success and juvenile survival coincides with population declines. Poor fledging success was linked to increasingly poor weather conditions during nestling development and increased predation. Both fledging success and survival overwinter are heavily influenced by body mass in many species including tree swallows (Tinbergen & Boerlijst 1990; Hochachka & Smith 1991; Magrath 1991; Smith & Bruun 1998; Krebs 1999; Naef-Daenzer *et al.* 2001; Monros *et al.* 2002; Greño *et al.* 2008), so in chapter 4 I analysed the effects of local weather on body mass. In 2017, nestlings were lighter when it had rained in the preceding three days and rainfall during nestling

development in the area has increased by 9.3 ± 0.3 mm/decade (Chapter 4). Increasing rainfall may explain the fact that nestlings are fledging in poorer condition than they had in the past.

Our results show that demographically, poor juvenile survival and fledging success are likely responsible for the decline, a finding generally consistent with other populations. Adult survival has remained relatively stable over time in this population and others (Weegman *et al.* 2017; Clark *et al.* in press), as expected given that both declining and stable populations share a migratory corridor and overwintering grounds (Knight *et al.* in press). Fledging success has also declined in multiple bank and barn swallow populations (Imlay *et al.* 2018), although Weegman *et al.* (2017) found that juvenile tree swallow survival had not declined since 1991. However, the declines we saw in juvenile survival after 1991 were subtle, and differences were most notable when compared to juvenile survival before the population began to decline, years not available in studies of other populations.

My results suggest that declining fledging success and juvenile survival are due, at least in part, to poor food availability on the breeding ground brought on by climate change. In the northeast where the most marked avian aerial insectivore declines occur, climate change has led to wetter springs (Kunkel *et al.* 2013) with more rain during nestling development (chapters 3 and 4). During cold, rainy weather flying insects are inactive, effectively reducing food availability for tree swallow nestlings (Williams 1951; Taylor 1963; Gruebler *et al.* 2007; Winkler *et al.* 2013). Although I do not have detailed growth curves for nestlings from 1975-2016, in 2017 I collected data to estimate growth curves and found that nestlings were more likely to be light for their age if the preceding days were rainier (chapter 4). As expected if the increasingly rainy weather prevents parents from adequately feeding their offspring, older nestlings now have lower body mass than they did at the start of the long-term study. If there is a

frailty effect, whereby nestlings in poor body condition have higher mortality, these effects of rainy weather on nestling growth are likely underestimates. Poor nestling growth is associated with decreased fledging success and juvenile recruitment, two important vital rates in many species (e.g., Maness and Anderson 2013, Tinbergen and Boerlijst 1990, Michaud and Leonard 2000) and may help explain trends in declining fledging success and juvenile survival in this population.

Poor fledging success was linked to both deteriorating weather conditions during breeding and increased predation. I found that nests were less likely to fledge offspring when there were more rainy, cold days during early nestling development, indicating that temporary, weather-driven food shortages might be causing nestling mortality by starvation and hypothermia (chapter 3). Additionally, predation rates have increased substantially over time, further challenging tree swallow nestlings. This increase in predation may be driven by grey ratsnakes (*Pantherophis spiloides*), the dominant nest predator in this system, which were listed by COSEWIC as a threatened species in 1998 and are now protected in Canada (Environment and Climate Change Canada 2017).

Before the population began declining, juvenile survival was linked to weather conditions in the first month post-fledging but this association broke down when the population started to decline (chapter 3). In many species, most juvenile mortality occurs during the post-fledging period (Grüebler *et al.* 2014; Klaassen *et al.* 2014) and food shortages during rainy weather likely increase mortality. One possible explanation for the breakdown of this association as the population began to decline is that fledging at low body weight reduces survival post-fledging as juveniles learn to fly and forage (Tinbergen & Boerlijst 1990; Michaud & Leonard 2000; Maness & Anderson 2013). Perhaps parents were no longer able to supplement juveniles'

(in increasingly poor body condition) food intake during this post-fledging period, regardless of weather conditions.

As I conducted this analysis using data from a single population, there may be different challenges facing tree swallows at other locations. The nest-box grids are located at an expansive biological station surrounded mainly by natural habitat. In contrast, other regions are facing agricultural intensification, which can decrease insect abundance (Evans *et al.* 2007; Gruebler *et al.* 2007; Rioux Paquette *et al.* 2013; Stanton *et al.* 2016). Challenges from agricultural intensification potentially compound the effects of climate change that we see in this population. Similarly, local pollution of PCBs and methyl mercury may reduce nestling growth and subsequent fledging success and recruitment at some sites (Maul *et al.* 2006, Brasso and Cristol 2008, but see Bonier 2016). At this site, we see increasing predation by gray ratsnakes (*Pantherophis spiloides*), likely due to successful efforts to protect this threatened species. Increasing predation is likely to be anomalous to my site, as similar predator population dynamics do not play out in other locations (i.e., gray ratsnakes and other nest predators having either always been common, or were never present). I do not wish to minimize the effects these environmental challenges may have on local tree swallow population dynamics. These local effects may well drive year to year differences in population dynamics, perhaps even explain the recent post-decline period at this location. However, I suggest that these challenges are unlikely to be the predominant driver of population decline across tree swallow populations in the region, as declines are widespread and occur in areas not facing these challenges. In contrast to small-scale local challenges, due to climate change, weather conditions are deteriorating in Northeastern North America (Kunkel *et al.* 2013), the region experiencing the most marked tree

swallow and avian aerial insectivore declines (Nebel *et al.* 2010; Shutler *et al.* 2012; Smith *et al.* 2015; Michel *et al.* 2016).

Much as weather conditions likely affect all populations of tree swallows in similar ways, most avian aerial insectivores are also likely to be affected. Because all aerial insectivores forage on flying insects to feed their nestlings, reduced insect availability is detrimental to all. A notable exception is those aerial insectivores, like the flycatchers, that will glean insects off the ground or foliage when there are few flying insects. Flycatchers began declining later than other aerial insectivores (Smith *et al.* 2015), so perhaps the ability to glean has somewhat protected them from short-term, weather-induced declines in aerial insects. However, ultimately, regardless of feeding flexibility, avian aerial insectivores have declined, suggesting that climate change is affecting this diverse array of species (Nebel *et al.* 2010; Smith *et al.* 2015; Michel *et al.* 2016).

Unfortunately, if climate change is the primary driver of avian aerial insectivore population declines, there is little that we can do to prevent decline, or at least little we should not already be doing. Without wrestling with our greenhouse gas emissions and climate change, avian aerial insectivores will remain subject to the increasingly variable weather conditions that make flying insects an unreliable food source for nestlings. In the meantime, we can and should be focusing on providing high-quality foraging habitat, free from aquatic pollutants and agricultural intensification on the breeding, migratory, and overwintering grounds. However, the outlook may be bleak for avian aerial insectivores unless we can curb climate change.

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Appendix A: Supplemental material for chapter 2

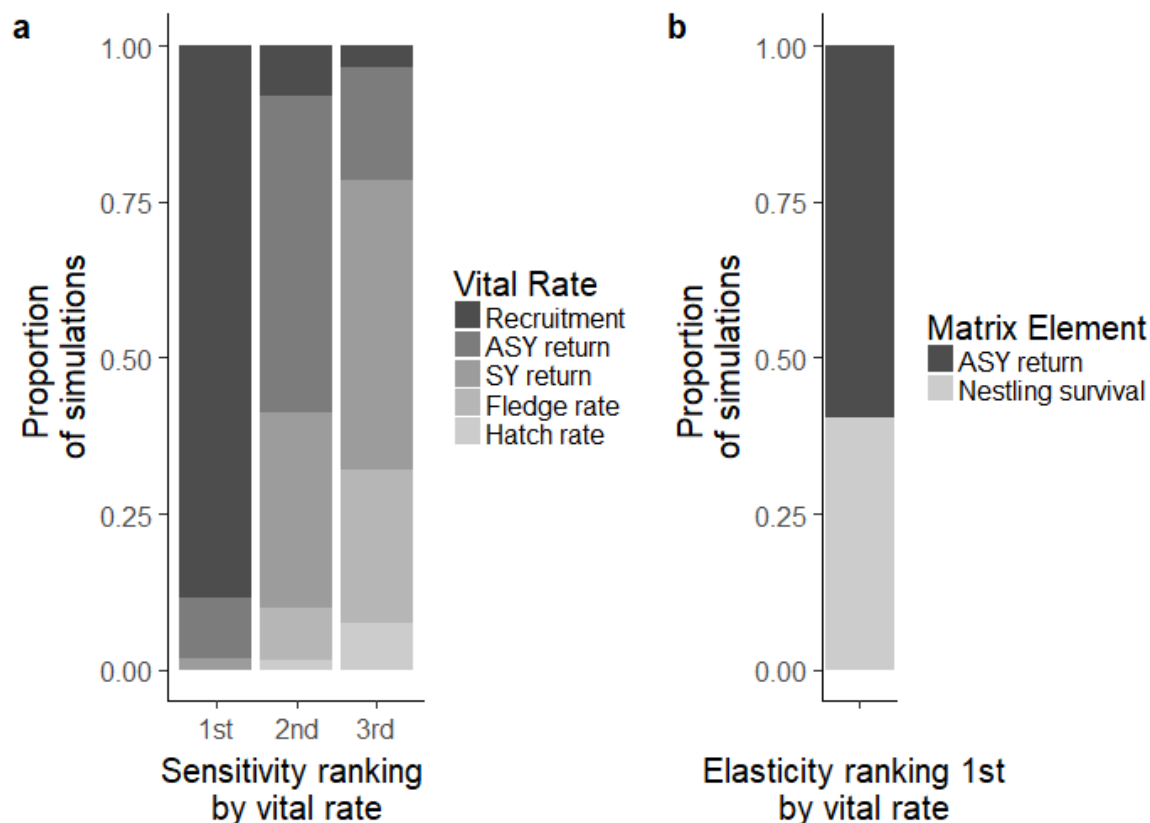


Figure A1: Proportion of analysis iterations a) where each vital rate ranked 1st through 3rd most sensitive (i.e., greatest influence of a small change in the vital rate on population growth) and b) where matrix elements ranked most elastic when correlations between vital rates were not included in the analysis. a) In 88.3% of the simulations, juvenile recruitment had the highest sensitivity ranking (2.22 ± 1.19). ASY female return (51.1%, 0.53 ± 0.25) most commonly ranked second in sensitivity, but SY female return (30.6%, 0.43 ± 0.34), fledging (8.7%, 0.23 ± 0.13), recruitment (8.2%) and hatch rates (1.4%, 0.18 ± 0.10) all ranked second in some iterations. Usually, SY female return (47.4%) ranked third in sensitivity but fledging (23.9%), ASY female return (18.7%), and other vital rates (10.0%) were other candidates. b) Of five matrix elements (SY female fertility, ASY female fertility, SY female return, ASY female return, and nestling

survival), ASY return (0.42 ± 0.28) had the highest elasticity in 60.6% of the iterations, and nestling survival (0.23 ± 0.12) had the highest elasticity in 39.4% of iterations.

Table A1: Overall means and standard deviation of the annual means for nine vital rates estimated for the Tree Swallow population.

<i>Vital Rate</i>	<i>Mean</i>	<i>SD across years</i>	<i>Years sampled (N)</i>
<i>Nests per SY female</i>	1.05	0.16	42
<i>SY clutch size</i>	5.05	0.57	42
<i>Nests per ASY female</i>	1.08	0.15	43
<i>ASY clutch size</i>	5.46	0.31	43
<i>Hatch rate</i>	0.77	0.08	43
<i>Fledge rate</i>	0.60	0.16	43
<i>Recruitment</i>	0.07	0.04	42
<i>SY female return</i>	0.23	0.17	37
<i>ASY female return</i>	0.41	0.16	37

Table A2: Mark-recapture analysis shows that female Tree Swallow survival varies based with female age and year, based on model comparison with AICc. Survival rate (ϕ) could vary by age (categorical variable with age set to 1-year old or older), year (categorical), the combination (with or without interacting), or remain constant (depicted as 1). Capture probability (P) could vary between years (categorical) or remain constant. The global model was (ϕ : year * age)(P: year). We present here all models with $\Delta AICc < 5$ and the null model for comparison.

<i>Model</i>	<i>Parameters</i>	<i>AICc</i>	<i>$\Delta AICc$</i>	<i>Deviance</i>
ϕ : year * age P: year	114	6128	0	774.5
ϕ : year + age P: year	80	6129	1.33	846.7
ϕ : 1 P: 1	2	6448	320.1	1324.2

Table A3: Mark-recapture analysis shows that survival for all Tree Swallows fledged in this population varies with age and year, based on model comparison with AICc. Survival rate (ϕ)

could vary by age (categorical variable with age set to fledgling, one-year-old or older), year (categorical), the combination (with or without interacting), or remain constant (depicted as 1). Capture probability (P) could vary between years (categorical) and/or ages (categorical) or remain constant. The global model was (ϕ : year * age)(P: year + age). We present here all models with $\Delta AICc < 5$ and the null model for comparison.

<i>Model</i>	<i>Parameters</i>	<i>AICc</i>	$\Delta AICc$	<i>Deviance</i>
ϕ : year * age P: year + age	162	13427	0	1632.4
ϕ : 1 P: 1	2	16517	3090.2	5045.3

Table A4: Sensitivity, elasticity, and coefficients of determination for each vital rate as determined from a correlated life-stage simulation analysis. SY refers to vital rates of one-year-old females and ASY refers to those of older females.

<i>Matrix Element</i>	<i>Vital Rate</i>	<i>Sensitivity</i> ¹	<i>Elasticity</i> ¹	<i>Coefficient of determination (R²)</i>
<i>SY fertility</i>	Nests per SY female	0.07±0.06	0.13±0.12	0.017
	SY clutch size	0.02±0.02		0.011
<i>ASY fertility</i>	Nests per ASY female	0.06±0.03	0.11±0.04	0.00086
	ASY clutch size	0.014±0.008		0.017
<i>Nestling survival</i>	Hatch rate	0.19±0.11	0.25±0.12	0.015
	Fledge rate	0.24±0.12		0.31
	Recruitment	2.25±0.88		0.24
<i>SY female return</i>	SY female return	0.44±0.31	0.11±0.04	0.37
<i>ASY female return</i>	ASY female return	0.50±0.24	0.39±0.25	0.50

¹Mean and SD reported

Table A5: Sensitivity, elasticity, and coefficients of determination reported by vital rate for the uncorrelated life-stage simulation analysis. SY refers to vital rates of one-year-old females and ASY refers to those of older females.

<i>Matrix Element</i>	<i>Vital Rate</i>	<i>Sensitivity¹</i>	<i>Elasticity¹</i>	<i>Coefficient of determination (R²)</i>
<i>SY fertility</i>	Nests per SY female	0.07±0.06	0.12±0.10	0.007
	SY clutch size	0.02±0.01		0.0015
<i>ASY fertility</i>	Nests per ASY female	0.06±0.03	0.11±0.05	0.002
	ASY clutch size	0.014±0.07		0.0003
<i>Nestling survival</i>	Hatch rate	0.18±0.10	0.24±0.12	0.010
	Fledge rate	0.24±0.14		0.078
	Recruitment	2.2±1.2		0.29
<i>SY female return</i>	SY female return	0.4±0.3	0.11±0.05	0.13
<i>ASY female return</i>	ASY female return	0.5±0.2	0.4±0.3	0.38

¹Mean and SD reported

Appendix B: Supplemental material for Chapter 3

Appendix B1: Supplemental population size analysis

Methods

We conducted an additional analysis to evaluate the robustness of our analysis determining breakpoints in population trends. To do this, we ran piecewise regressions with box occupancy (our estimate of population size) as the response variable and year as the fixed effect. We compared piecewise regressions that split the years into two time periods at every year from 1975 to 2017. We selected the best breakpoint year as the one that minimized residual standard error across the regressions. Because we suspected that there might also be a second breakpoint in more recent years, after the period of steep decline in the population, we conducted an additional analysis, restricted to the years 2001-2017, and again selected the breakpoint that minimized residual standard error.

Results

The first analysis identified 1991 as a breakpoint in trends in population size over time, and the second analysis (restricted to 2001-2017) identified 2013 as a breakpoint. These are the same years that were identified as breakpoints in our main analysis (Figure 1, main text), and delineate an initial period of population growth (1975-1991), a period of steep decline (1992-2013), and a recent period of four years of growth (2014-2017).

Appendix B2 Supporting Information 2: Supplemental fledging success and predation analyses

Methods

In addition to our binary analysis of fledging success, we conducted a Cox-proportional hazards analysis to analyze age-dependent nest failure through nestling development using the

‘survival’ package (Therneau 2015). As in our binary analysis, we excluded nests that failed due to predation. First, we analysed the daily risk of nest failure (0=alive, 1=dead in nest) based on the fixed effects of year, age, time-period (growing, declining, post-decline), and all possible interactions. As tree swallow nestlings age, they transition from being poikilothermic (able to go into torpor to survive cold weather), to homeothermic, where they require constant energy input to maintain their body temperature (Dunn 1979; Marsh 1980b). Nestlings employing these different thermoregulatory strategies are likely to be affected by weather differently, so we treated age as a categorical variable based on thermoregulatory strategy: poikilothermic (0-6 days old), intermediate (7-8 days old), and homeothermic (9+ days old) (Dunn 1979; Marsh 1980b).

We were also interested in how weather conditions the previous day affected age-dependent nest failure. We modelled the daily risk of nest failure based on weather conditions the previous day, age, time period, and all interactions. We tested for effects of three weather parameters: minimum temperature, maximum temperature, mean temperature, and whether or not it had rained using data from a weather station located ~30km from the study site (Environment Canada 2018). Because weather variables were highly correlated, we used principal components to assess whether the combination of weather variables predicted nest failure better than any single weather variable (Table B2). Together PC1 and PC2 account for 92% of the variation in weather (66.5 % and 25.8% respectively).

We also conducted a Cox-proportional hazards analysis to analyze age-dependent predation, excluding nests that failed due to causes other than predation. First, we analysed the risk of predation (0=alive, 1=predation event) based on the fixed effects of year, age (poikilothermic, intermediate, homeothermic), time period (growing, declining, post-decline),

and all two-way interactions. Second, we modelled whether a nest had been depredated with the fixed effects of the weather conditions during the previous day, age, time period and all interactions using the same weather parameters as for nest failure.

Results

The age-dependent risk of nest failure changed across years in different ways during the three time periods (year*age*time-period, $\chi^2=20.95$, $p<0.001$) (Fig B1). While the population was growing, nest failure risk was increasing for poikilothermic nestlings (OR=4.1±1.1 per decade, $z=5.31$, $p<0.001$), and higher but steady for older nestlings. When the population started to decline, risk of nest failure steadily increased for all age classes (poikilotherms, OR=2.6±0.7 per decade, $z=3.37$, $p<0.001$; intermediates, OR=7±3, $z=4.67$, $p<0.001$; homeotherms, OR=2.8±0.5, $z=5.66$, $p<0.001$). In recent years, nest failure risk has been lower again. Although the binary analysis did not differentiate between ages, increasing nest failure risk during the decline parallels the trend of decreasing binary fledging success during the decline.

As in the binary analysis, nest failure was more likely with more inclement local weather. Of all the weather parameters, maximum temperature during the previous day was most predictive of nest failure risk (Table B3). Nest failure risk was highest when maximum daily temperature was low for all nestling ages (OR= 0.87±0.01 per °C, $z=-13.58$, $p<0.001$). Homeothermic nestlings had lower failure risk than intermediate nestlings (OR=0.81±0.11, $z=-1.48$, $p=0.14$) and poikilothermic nestlings (OR=0.51±0.07, $z=-5.21$, $p<0.001$) experiencing the same temperatures.

Predation risk also changed across years in different ways during the three time-periods (year: time-period, $\chi^2= 18.2$, $p<0.001$) (Fig. B2a). Predation risk was consistently low while the population was growing (OR=0.7±0.2 per decade, $z=-1.24$, $p=0.21$). However, when the

population began to decline, predation risk increased two-fold per decade (OR= 2.0 \pm 0.3, $z=3.95$, $p<0.001$). Predation risk did not differ between age classes of nestlings (age, $\chi^2=3.40$, $p=0.18$). Whether analysed using a Cox proportional hazard or binary GLM method, depredation increased during the decline.

Maximum daily temperature was also predictive of predation risk (Table B4; Fig. B2b) but its effect varied between nestling ages (age*max temp, $\chi^2=5.88$, $p=0.053$). Predation risk for homeothermic nestlings increased when the weather the previous day was warmer (OR=1.09 \pm 0.03, $z=3.36$, $p<0.001$) and to a lesser degree for nestlings with an intermediate thermoregulatory strategy (OR= 1.08 \pm 0.05, $z=1.56$, $p=0.12$). However, predation risk for poikilothermic nestlings was not related to maximum temperature (OR=0.99 \pm 0.03, $z=-0.36$, $p=0.72$). Across age classes, independent of temperature, predation risk was lower while the population was growing than during the decline or post-decline.

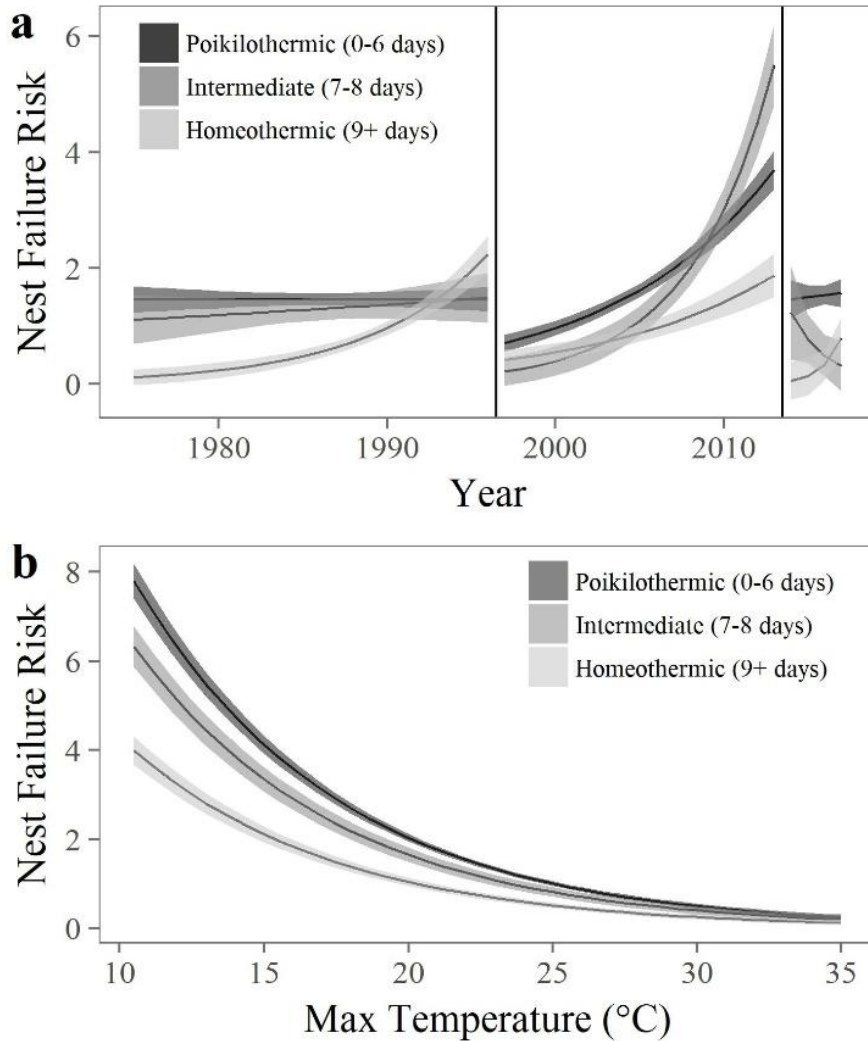


Figure B1: a) Nest failure risk, excluding predated nests, increased substantially for all nestling ages while the population was declining (poikilotherms, $OR=2.6\pm0.7$ per decade, $z=3.37$, $p<0.001$; intermediates, $OR=7\pm3$, $z=4.67$, $p<0.001$; homeotherms, $OR=2.8\pm0.5$, $z=5.66$, $p<0.001$). However, in recent years, risk of nest failure has been lower again. b) Nest failure for all ages, excluding predation, was lower when the previous day was warmer ($OR=0.87\pm0.01$ per °C, $z=-13.58$, $p<0.001$). Predicted risk (black lines) is plotted with standard error (gray shaded area).

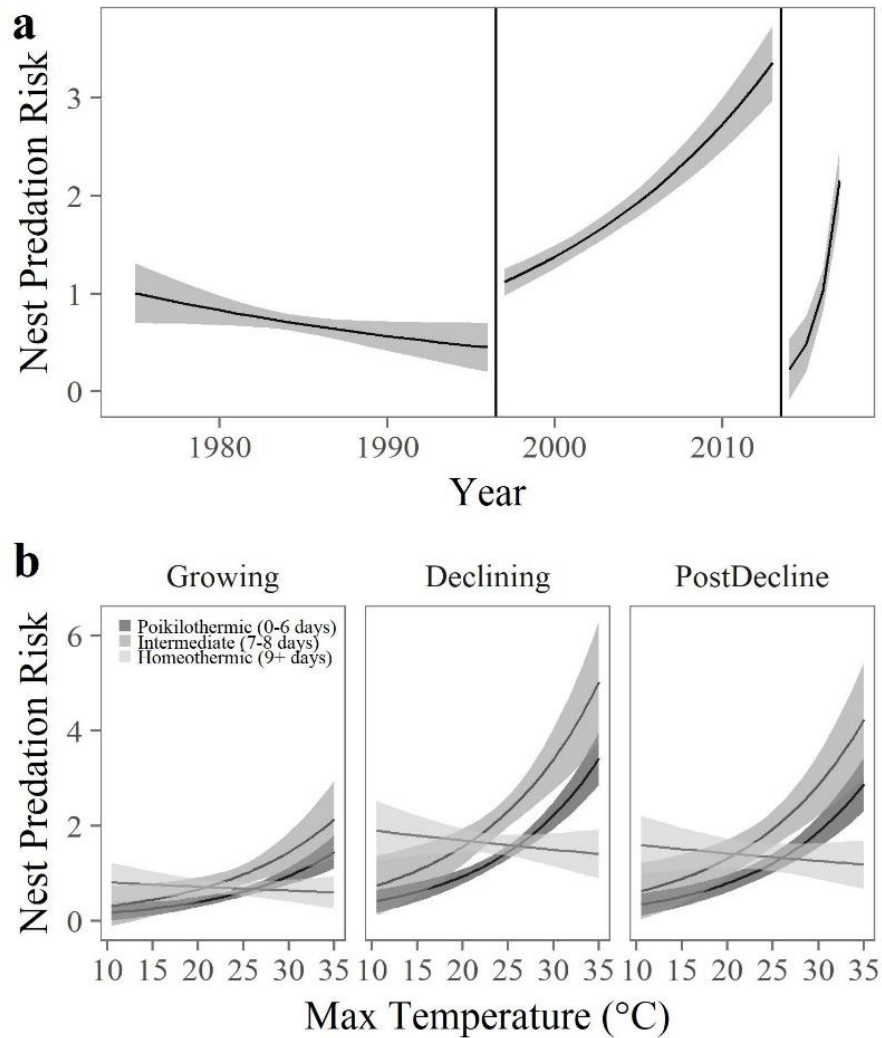


Figure B2: a) Nest predation increased substantially while the population was declining. b) Warmer maximum temperatures the previous day increased predation rates for homeothermic nestlings (OR=1.09±0.03, z=3.36, p<0.001) and intermediate nestlings to a lesser extent (OR=1.08±0.05, z=1.56, p=0.12). Independent of age class and temperature, predation risk was lower while the population was growing than during the decline or post-decline. Predicted risk (black lines) is plotted with standard error (shaded areas).

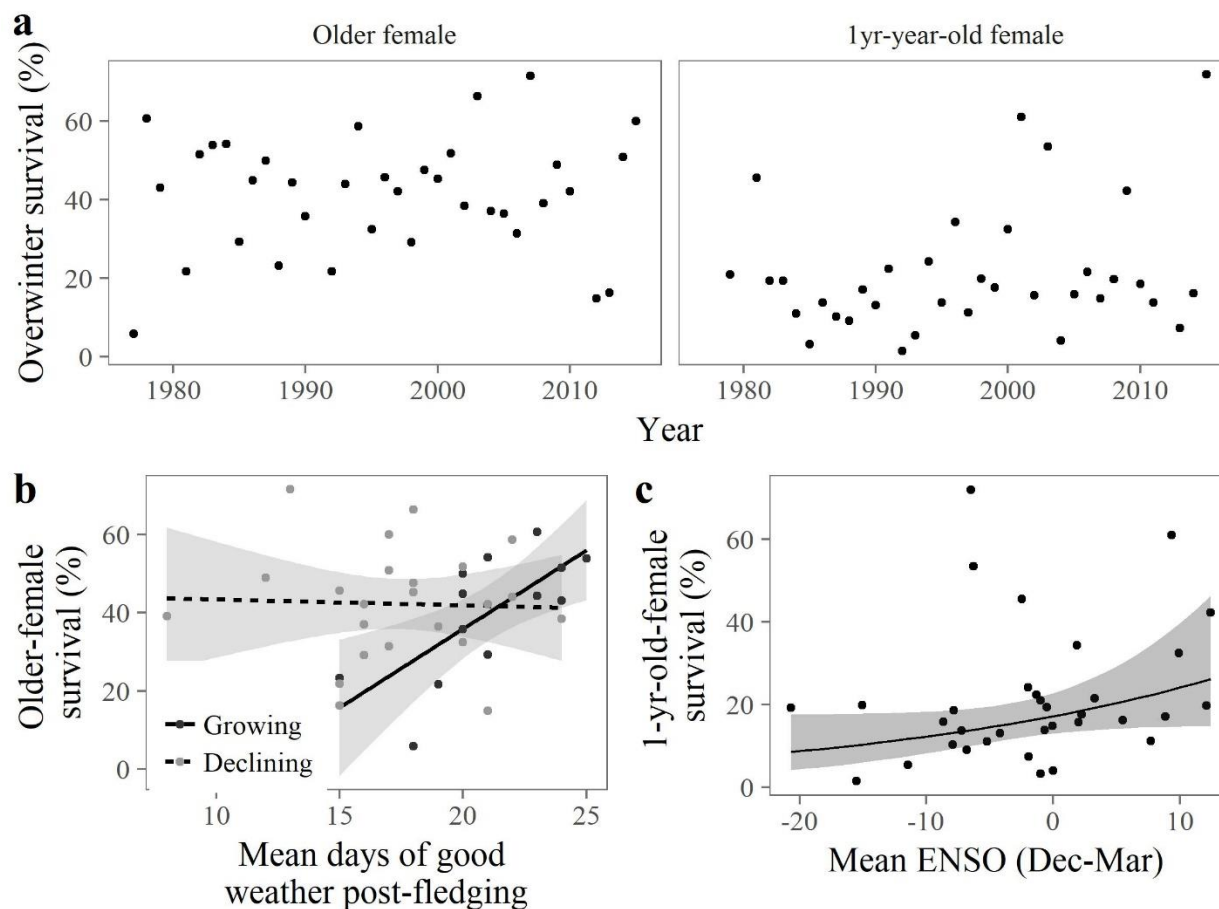


Figure B3: a) One-year-old survival overwinter has not changed over time ($21 \pm 16\%$). Older female survival also has not changed overtime but is slightly higher than one-year-old female survival ($41 \pm 15\%$). Points represent survival estimates b) When the population was growing (solid line), older female survival was higher when weather conditions post-fledging were better but post-fledging conditions were not predictive when the population was declining (dashed) (Post-fledging weather * Time period, $F= 6.50$, $p=0.016$). Trends while the population was growing (solid line) and declining (dashed line) are plotted with 95% confidence intervals (shaded areas) and points representing survival estimates. c) Mean ENSO during the winter months was weakly predictive of one-year-old female survival (ENSO, $F=3.81$, $p=0.060$).

Predicted survival (black lines) is plotted with 95% confidence limits (shaded areas). Points represent annual survival estimates.

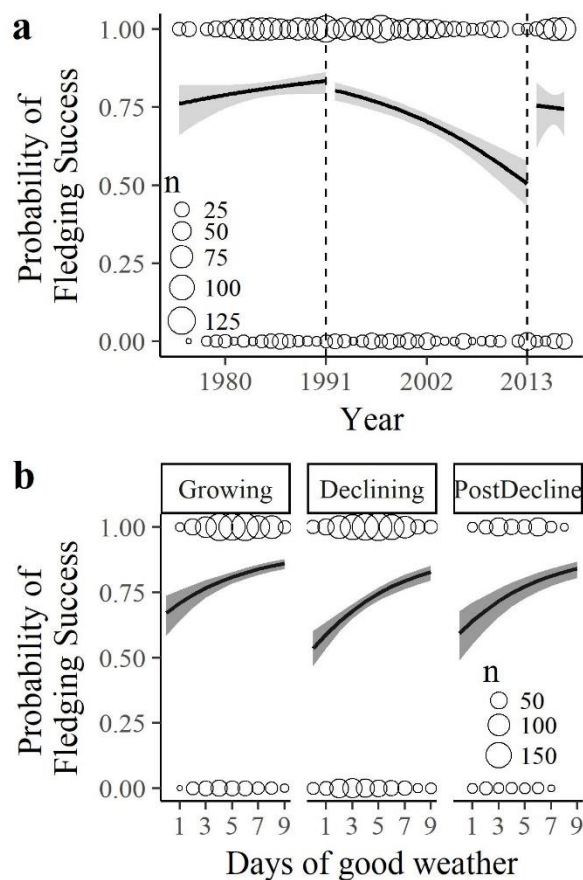


Figure B4: Environmental correlates of fledging success in a box-nesting population of tree swallows. a) Fledging success (excluding failures of nests due to predation) was high and stable while the population was growing and declined by half each decade during population decline ($OR=0.51\pm 0.05$ per decade, $z=-6.37$, $p<0.001$). Post-decline, fledging success has been higher, comparable to fledging success before the decline. b) Fledging success increased when there were more days with temperatures above $18.5^{\circ}C$ and no rain (“good weather” days) during the first eight days of nestling development ($OR=1.19\pm 0.03$ per day, $z=6.23$, $p<0.001$). Solid lines

represent trendlines and shaded areas represent 95% confidence intervals. Circles represent the number of nests that fledged (1) or failed (0).

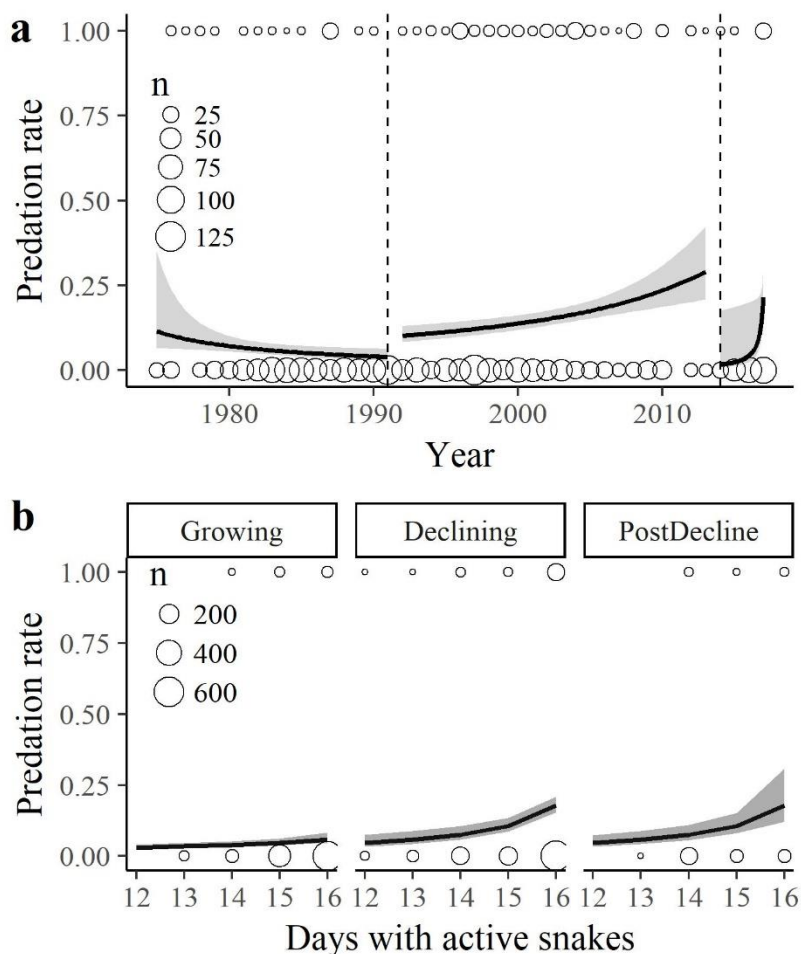


Figure B5: Environmental correlates of predation rate in a box-nesting population of tree swallows. Predation rate refers to the likelihood that a nest would be depredated before fledging if nestlings were not found dead in the nest from other causes. a) Until 1991, while the population was growing, predation rate was stable. From 1992 to 2013 predation increased three-fold every decade (OR=2.9 ±0.8 per decade, z=4.05, p<0.001). When the population was growing (2014 on) predation rate has been lower but increasing. b) Predation increased when there were more days with maximum temperatures above 15°C (“days with active snakes”; OR=3.7±1.2, $\chi^2=25.09$, p<0.001). However, even when accounting for weather conditions, predation

rates have been elevated since 1991 when the population began to decline. Solid lines represent trendlines and shaded areas represent 95% confidence intervals. Circles represent the number of nests that were depredated (1) or fledged (0).

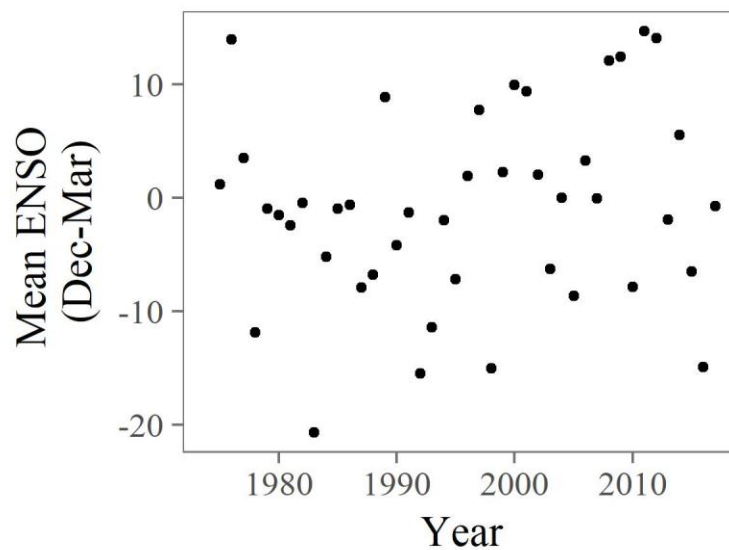


Figure B6: While tree swallows are on the over-wintering ground, mean ENSO has been stable from 1975 to 2017 (means calculated from December to March monthly values). Points represent annual winter ENSO indices.

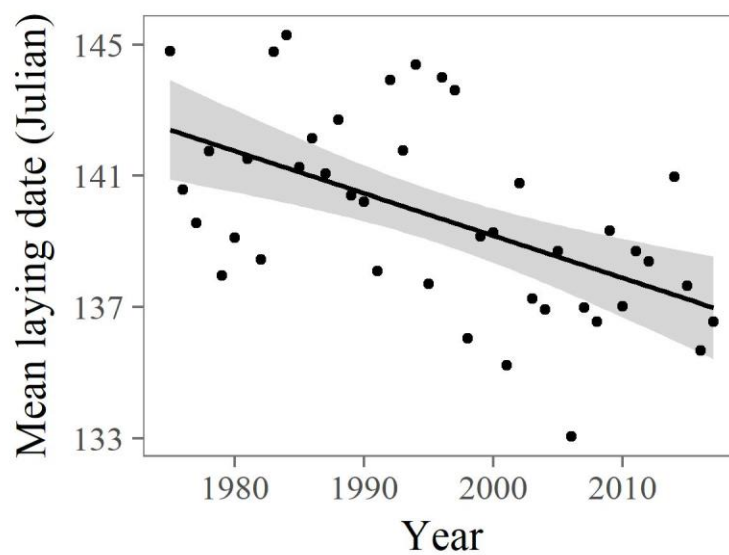


Figure B7: The mean laying date has advanced by 1.29 ± 0.03 days per decade (year, $F=8.92$, $p=0.005$). The solid line represents the trendline with shaded 95% confidence intervals. Points represent annual mean laying dates.

Table B1: Winter ENSO and post-fledging weather predict juvenile survival slightly better than time period alone

<i>Model</i>	<i>Degrees of Freedom</i>	<i>AICc</i>	$\Delta AICc$
<i>ENSO + Time-period</i>	4	207.51	0
<i>Weather post-fledging * Time period</i>	5	208.14	0.62
<i>Time period</i>	3	209.35	1.84

Table B2: Weather principal components

<i>Weather Variable</i>	<i>Correlation with PC1</i>	<i>Correlation with PC2</i>
<i>Max. temp.</i>	-0.56	0.13
<i>Min. temp.</i>	-0.55	-0.19
<i>Mean temp.</i>	-0.61	-0.03
<i>Rainfall</i>	0.05	-0.97

Table B3: Maximum daily temperature best predicted daily nest failure risk

<i>Model</i>	<i>Degrees of Freedom</i>	<i>AICc</i>	$\Delta AICc$
<i>Max. temp + Age</i>	3	7117.8	0
<i>PC1 + PC2 + Age</i>	4	7161.5	43.7
<i>Mean temp. * Age</i>	5	7162.7	44.9
<i>Min. temp * Age</i>	5	7267.9	150.1
<i>Rain + Age</i>	4	7161.53	157.6

Table B4: Maximum daily temperature best predicted daily depredation risk

<i>Model</i>	<i>Degrees of Freedom</i>	<i>AICc</i>	$\Delta AICc$
<i>Max. temp. * Age + Time Period</i>	7	2512.3	0
<i>PC1 + PC2 + Time Period</i>	4	2514.5	2.2
<i>Rain * Age * Time Period</i>	17	2514.8	2.5
<i>Mean temp. + Time Period</i>	3	2515.6	3.3
<i>Time Period</i>	2	2520.5	8.2

Appendix C: Supplemental material for chapter 4

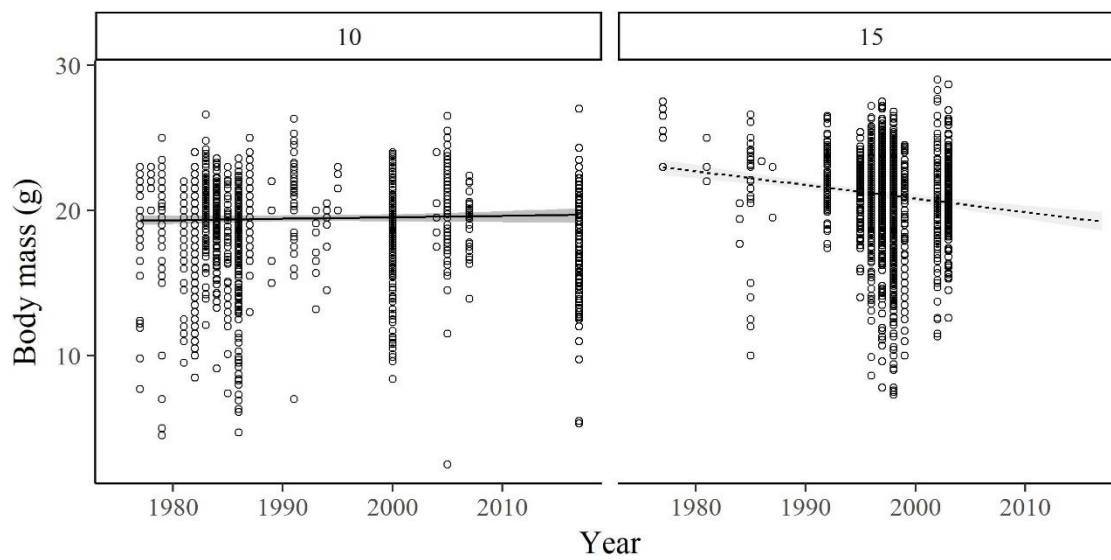


Figure C1: Nestling tree swallows have not gained as much body mass in recent years as they did in the past (age * year, $F=26.56$, $p<0.001$), illustrated here with data from 10- and 15-day-old nestlings. In 1977, 15-day-old nestlings were considerably heavier than 10-day-old nestlings ($23.0\pm 0.3\text{g}$ and $19.3\pm 0.2\text{g}$ respectively). In contrast, by 2017, model predictions show 10 and 15-day-old nestlings both weighing similar amounts (19.7 ± 0.3 and $19.2\pm 0.4\text{g}$ respectively). Model projections are based on data from 10-16 day old nestlings. Solid lines represent trendlines and shaded areas represent 95% confidence intervals. Circles represent the residual body mass for individual nestlings.

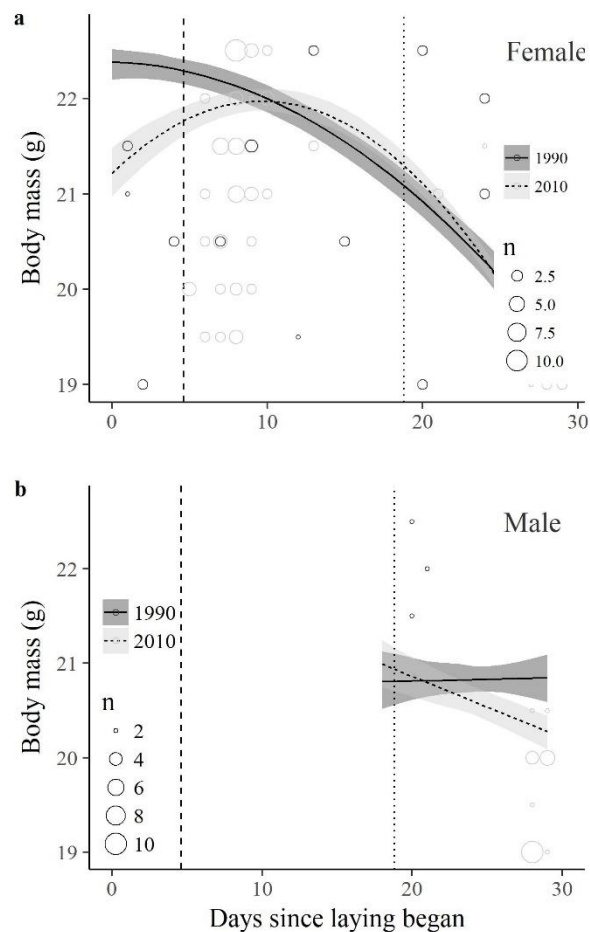


Figure C2: Adult tree swallow body mass fluctuates throughout the breeding season, but these fluctuations have changed from 1983 to 2017, illustrated here with data from 1990 and 2010. a) For females, body mass has always declined throughout the breeding season. However, in recent years (e.g., 2010), females have started breeding with lower body mass and spending egg laying and the beginning of incubation gaining mass. b) In the past (e.g., 1990), male body mass did not change over the breeding period, but in recent years males lose body mass during nestling provisioning (e.g., 2017). The solid lines represent model projected adult mass throughout the breeding season in 1990 and the dashed lines represent adult mass during 2010. Shaded areas represent 95% confidence intervals (dark grey for 1990, light gray for 2010). Circles represent overlapping points reflecting individual body mass measurements, with circle size representing the number of birds. (dark grey for 1990, light gray for 2010) The vertical dashed line represents

the mean start of incubation (4.6 days after the first egg was laid) and the vertical dotted line represents the mean day of hatching (18.8 days after the first egg was laid). Model projections are based on data from 1983 to 2017.

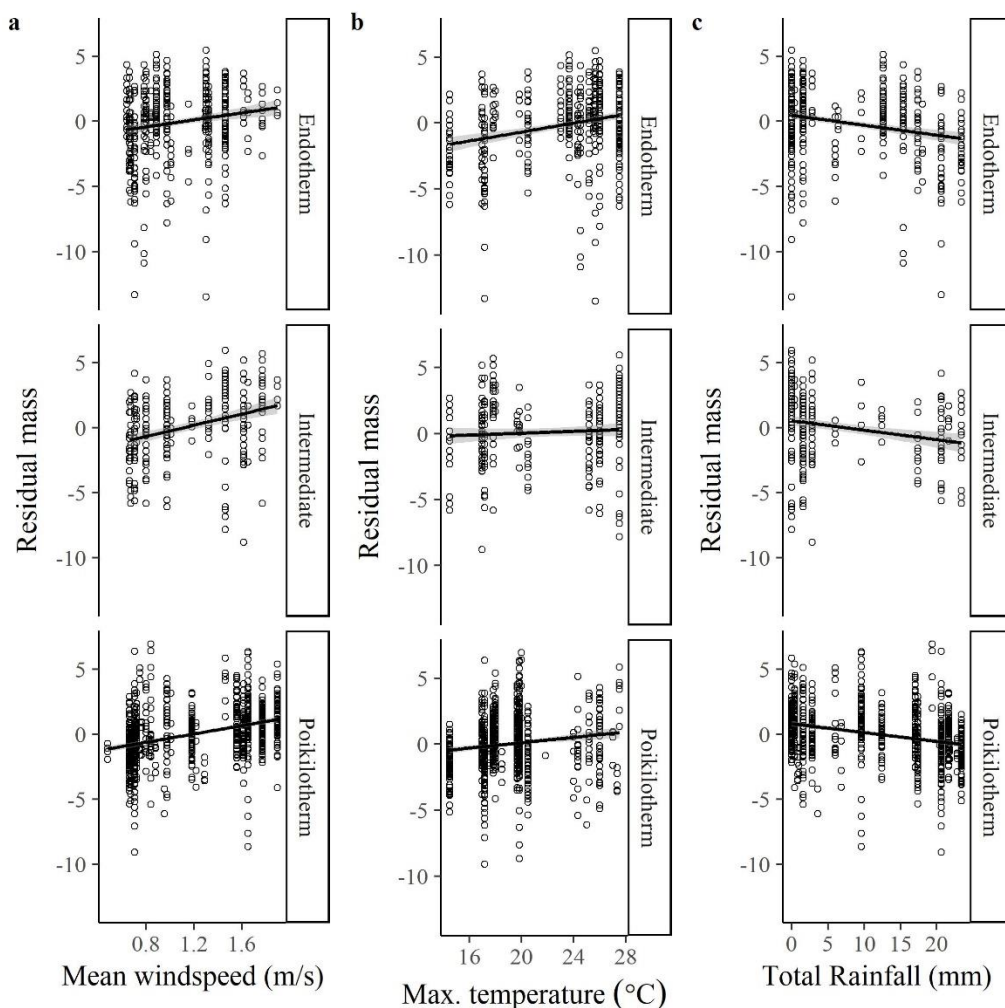


Figure C3: In 2017, nestling tree swallows were lighter (residual body mass, controlling for a relationship with age) when there was more rainfall or colder weather during the three days before measurement, particularly in the case of older, homeothermic nestlings. Pairwise correlations between residual mass and mean windspeed, average maximum temperature, and total rainfall in the preceding three days. Note that neither random effects nor collinearity are accounted for in this figure. For effect sizes, see Fig. 4.3. Solid lines represent trendlines and

shaded areas represent 95% confidence intervals. Circles represent residual body mass of individual nestlings.