Annual Survival of Winter Residents in an Urban Wetland

Kevin Perozeni

Advisor: Dr. Christopher Tonra

School of Environment and Natural Resources

College of Food, Agriculture, and Environmental Sciences, The Ohio State University

Kottman Hall, 2021 Coffee Road, Columbus, OH 43210

Abstract

Winter can have important demographic consequences for wintering resident avian species that reside in the temperate zone. Shortened days and inclement weather challenge survival, with urbanization and climate change only heightening these affects. Survival during the wintering period can even be the main limitation to a population's growth, a direct factor to population size. Thus, understanding the characteristics that determine which species may be more vulnerable to the effects of urbanization and climate change during winter is of high conservational value. To address these questions, I investigated apparent annual survival probabilities for three focal species that varied in life history characteristics within an urban wetland. Specifically, I studied one resident species (Carolina chickadee *Poecile carolinensis*), one partial migratory species (Song Sparrow *Melospiza melodia*), and one obligate migratory species (White-throated Sparrow *Zonotrichia albicollis*). I applied mark-recapture methods over a 5-year period to create capture histories and estimate apparent annual survival for both immature and adult birds. Apparent annual survival was consistent across years and ages in resident and partial migratory species, but varied by both year and age within the fully migratory birds. Additionally, White-throated and Song Sparrows averaged a higher apparent survival than the Carolina Chickadees. My results suggest that migratory species exhibit higher survival than resident birds, which may be a tradeoff with reproduction, based on known clutch sizes. I also conducted a preliminary examination of annual environmental trends with White-throated Sparrow survival. This suggested survival was lowest in harsher winters with lower average temperatures or higher amounts of snowfall. These results have potential implications for the conservation of winter residents in the temperate zone, but further work is required to establish environmental relationships.

Introduction

Human activities are leading to rapid and substantial environmental transformations (Vitousek et al. 1997). The conversion from rural to urban land continues to grow within the United States (Alig et al. 2004) with the impacts of climate change becoming increasingly impactful on ecological communities (Lemoine et al. 2007). These changes have direct impacts, with a decline of 33% of all birds in North America since 1970 (Rosenberg et al. 2019). However, not all birds respond equally to change, with responses varying based on different life history traits that tradeoff with survival (Clark & Martin 2007). For instance, understanding how different birds with varying life histories differ in their vital rates within an urban setting is important given the increases in urban landcover globally (Seto et al. 2011). Following how these birds are responding to environmental conditions within an urban landscape is critically important information to monitor and predict future biodiversity (Opdam & Wascher, 2004).

One way bird species differ significantly from each other in their life histories is through the act of migration, or the annual movement between the breeding and wintering grounds. Resident species complete all annual cycle stages (e.g. breeding, molts, overwintering) within a single geographic location, with large scale movement outside that range being limited to a few circumstances such as natal dispersal (Paradis et al., 1998). In obligate migrant species, all individuals move between breeding and wintering areas each year. Variation in migratory life history can also exist within a population of partially migratory species. In these cases a portion of a population migrates each year, while another portion of individuals remains resident. Partial migration can be a factor of physiological, morphological, or behavioral variation, but typically occurs where winter conditions are neither extremely harsh or extremely benign (Lundberg, 1988). Migratory birds experience multiple habitats at different latitudes depending on the timing within each year, with each habitat holding their own challenges. Weather can directly affect birds and their body condition during the overwintering months in avian species (Studds & Marra, 2007; Cooper et al. 2015; Krause et al. 2017). Nocturnally migrating birds can strike buildings after becoming disoriented from artificial lighting (Longcore & Rich, 2004), and breeding sites can change drastically while the birds are away.

Winter can be one of the harshest time periods on birds due to fierce competition, lack of food, and variable conditions. Winter has been shown to be the limiting factor in populations of many species of small wintering birds, with food strongly influencing winter survival (Jansson et al. 1981). Species must forage to survive, but more foraging can increase the risk of predation. Winter sharpens this trade-off, with both food availability and predation risk influencing microhabitat use by sparrows during winter (Beck & Watts, 1997). Severe weather events can also play a role in winter mortality, with population crashes noted following severe winter weather in a resident population of Song Sparrows (*Melospiza melodia*) (Rogers et al. 1991). These challenges suggest the overwintering period is the most important time to track bird survival, and how birds might respond to future changes regarding food availability and climate.

Within the overwintering period different species can also vary in other life history characteristics, such as foraging and roosting behavior. Arboreal species tend to spend their time foraging within the tree canopy. Foraging for these species can change dramatically depending on what the context is, with habitat type and inclement weather changing the height at which the species forage (Grubb, 1977; Brewer, 1963). Other species tend to forage on the lowest level of an ecosystem, the ground. Seeds, fruits, and any invertebrates along the ground or leaf litter are the main foods taken (Aldrich 1984). Typically ground foragers, such as sparrows, create loose flocks near dense underbrush or grassy areas for predator protection in the winter period and can congregate at feeding sites (Schneider 1984). In a study with uniformly and patchy distributed food, White-throated Sparrows (*Zonotrichia albicollis*) depleted sources nearest cover first before moving to more exposed areas next. This suggests a tradeoff between reducing predation risk at the expense of foraging efficiency (Schneider 1984). Also, ground foragers depend on patches of snow-free ground. Extended periods of snow cover can lead to starvation, with birds that overwinter in the northern latitudes depending on regions of snow-free patches to forage (Mehlman, 1997). After foraging during the day, most species will roost individually within natural or artificial cavities or thickets in the vegetation.

Age can also have an effect on winter survival rates in birds, with immature birds being more prone to stress or having less access to food resources from adult competition or inexperience within a wintering site (Sandercock & Jaramillo 2002). In one study, immature sparrows took greater risks during foraging and had greater rates of poor physiological condition (Piper and Wiley 1995). Studies have only been conducted on a limited number of species, but they can help draw a picture of why immature birds might be experience a lower survival rates regardless of the area they might live.

I examined apparent annual survivorship of three focal species at a wintering site in an urban wetland of Columbus, Ohio. The three species range from resident, partial migrant, to a obligate migrant that travels out of the state to breed. My objectives were to determine apparent annual survival probability for juvenile and adult birds for our site, compare apparent survival probability between three bird species with differing migration strategies, and evaluate potential trends for estimating apparent survival from populations of wintering birds with compiled environmental data. I predicted that immature birds would have a lower survival than the adults in the population. I also predicted that migratory species would have a higher survival estimate than the residents. Additionally, I predicted that inclement weather such as higher snowfall or colder temperatures will coincide with lower apparent survival.

Methods

Study Area

The Tonra Lab of Avian Ecology studies wintering songbird species at The Wilma H. Schiermeier Olentangy River Wetland Research Park of the Ohio State University, Columbus, OH (40.019854, -83.018239) over a 5-year period from October 2015 to March 2020. The area is approximately 52 acres. Habitats include riparian forest vegetation with two large freshwater emergent wetlands, one freshwater pond, and restored prairie. Eastern cottonwood (*Populus deltoides*), white ash (*Fraxinus americana*), and American sycamore (*Platanus occidentalis*) dominate the canopy while box elder (*Acer negundo*) and black willow (Salix nigra) populate the understory. Amur honeysuckle (*Lonicera maackii*) densely crowds parts of the understory, but some areas were cleared by restoration work during 2019. The two wetlands have water pumped in, while the pond floods seasonally with the river. The Olentangy River flows adjacent to the eastern side of the site with a walking path connecting suburban/urban development (Figure 1). Meanwhile, a cemetery borders the western side of the study area.

Study Species

Three focal bird species were examined in this study. The species vary in their migratory strategies, but are all common wintering birds within central Ohio. Each bird species could be readily identified to species and age by features of plumage, bill color, eye color, and wing length (Pyle 1997). Carolina Chickadees (*Poecile carolinensis*) are nonmigratory residents of the central and southern portions of Ohio with no hybridization occurring with Black-capped

Chickadee (*Poecile atricapillus*) noted within or surrounding the area. They are the smallest species studied with an average tarsus of 15.8 mm and a mass of around 11 grams (Mostrom et al. 2020). Males average slightly larger (Pyle 1997). Chickadees form flocks in the winter made up of both sexes. Song Sparrows are partial migrants across the site with an unknown proportion of the wintering population leaving for the breeding season. Males tend to be larger with a range of 21.25-27.49 mm tarsus as compared to the average female range of 20.92-27.03 mm (Arcese et al. 2020). The tarsus lengths are positively correlated between sexes. However, the range of mean tarsus lengths overlaps extensively and can be slightly different depending on the subspecies (Arcese et al. 2020). White-throated Sparrows are an obligate migrant. They form flocks with other sparrow species and are resident at the Wetlands and surrounding area throughout the winter. Similar to other sparrows they are a primarily ground foraging species. No major body size differences should be found, with males measuring an average tarsus length of 23.6 mm and females at 23.1 mm (Falls & Kopachena, 2020).

Capture, banding, aging, and resighting of birds

The Lab captured all three species using two methods. Up to 10, 6 or 12-meter mist nets were set in fixed locations utilized throughout the study, with the number run depending on weather, available technicians, and flooding. Generally the

Figure 1. Mist net and Potter Trap locations across the Wilma H. Schiermeier River Wetlands Research area

Lab maintained nets beginning at sunrise until midday, however adverse weather, such as high winds, created conditions where some nets locations were not feasible to keep open, due to risk of damage to the net or injury to the birds. On occasion, additional "supplementary" nets were operated in different orientations or slightly different locations to increase re-capture rates. In addition to mist nets, walk-in Potter ground traps, baited with commercial bird seed, were set in up to 6 locations and operated in addition to or instead of mist nets. This method was useful during windier days and allowed for capturing of birds even when mist nets could not be run, as well as offered a second method of capture for "trap-shy" birds.

Once captured, we carefully extracted birds and brought them back to the central banding station to be processed. One uniquely numbered metal leg band and 2-3 colored bands to create a color combination for visual identification in the field was placed on each of the study birds. Although different species could have the same color combination, no two birds of the same species overlapped. We weighed and classified the birds as young/immature (Fall HY = Hatch Year, Spring SY = Second Year) or adult (Fall SY = Second Year, Spring ASY = After Second Year). On January 1st, every bird moves up in age class (i.e. HY to SY or AHY to ASY). Since annual survival between winters was studied, birds could be an immature SY in the spring, or an adult SY in the following fall. AHY birds caught in the fall had to be adults as well, because all fall immature birds would be considered HY at that point. The species studied were all monochromatic, and there was substantial overlap in size between the sexes so sex was not included as a parameter. The lab took body size by measuring wing chord, tail length, and tarsus length. Tarsus became the primary indicator of body size because it does not change over time, although there can be a slight observational bias. After birds had been fully processed, we released them back into the wetlands from the central banding location. In the case of recaptures, band number was written down and measurements were taken as normal unless the bird had been caught within the same day, in which case it was released.

In addition to recapture in traps, we worked to resight any birds while nets were up during banding sessions. Lab members and the ENR5364.02 Avian Wildlife Biology and Management class taught in the spring also worked weekly to resight birds in the wetlands. Every student within the class was required to resight birds around the wetlands for a minimum of 2 hours, 2 separate times across the year, as well as during class on 6 occasions. Times had to be reserved to maintain a constant resighting effort each year. This resighting data was a significant part of the study, because it could be used to track birds from year to year even if an individual was never caught again. To help check if enough effort was being put into the banding and resighting, effort hours were tracked (Table 1). I calculated the net hours by adding up the total amount of hours a net had been up. For example, if 6 nets were run for 5 hours, 30 net hours would be written down for that day. I calculated trap hours a similar way, with each set of potter traps adding one hour for every hour they were open and active (Table 1). Finally, I calculated resighting effort by adding one hour every time someone spent an hour actively resighting birds in the wetland site (Table 1). If 2 people worked together for 2 hours, 4 resighting effort hours would be calculated. These effort hours were tracked against recapture rate over time to find whether the amount of effort hours directly impacted the encounter rate of bird species in our study.

Table 1. Net, trap, and resighting effort hours over the 5-year study period at the Wilma H. Schiermeier Olentangy River Wetlands

Year	Net hours	Trap Hours	Resighting Effort
2015/2016	210.5	0	0
2016/2017	289.2	0	353.7333333
2017/2018	384.09	0	387.1166667

2018/2019	348.5	225.55	316.5
2019/2020	234	280.25	166.2666667

Encounter histories

All species were present at the wetlands by mid-October when the banding and resighting season started. Banding effort was limited during early fall and early spring to restrict the amount of non-wintering birds being color banded. In order to conduct apparent annual survival analysis, I recorded each bird banded during the study as present or absent each year, based on the three possible modes of detection (mistnet, trap, resight). A bird got a 1 if it was caught for the first time during the winter it was banded. The bird got a single mark of 1 to note its presence even if it was seen multiple times during that particular winter. Another 1 would be marked if that bird was seen or captured in the nets again for any of the following winters. If the bird was not resighted or seen, the space was filled in with a 0. This was done for every individual bird, resulting in a variety of encounter histories such as 10000, 10110, or 01100. In the second example, the bird was caught in the first winter and encountered in the third and fourth year. With the third example, the bird was first caught in the second winter, and then encountered in the third winter as well.

Survival analyses

I compiled encounter histories for Carolina Chickadee, White-throated Sparrow, and Song Sparrow in separate text documents compatible for mark-recapture analyses with the Program MARK. I used Program MARK to run Cormack-Jolly-Seber (CJS) survival models comparing different combinations of the parameters age, time, and body size (tarsus). These models estimate two parameters: apparent survival probability (ϕ) and recapture/resighting probability (p) based on the encounter histories. To determine which models best fit the data, I ranked models by Akaike's Information Criterion (AICc) and compared with model weights (w_i) and deviations in AIC from the top model (ΔAICc). The AICc value increases as more parameters are brought into the model, and decreases based on how much variability it explains within the dataset. Recapture/resighting probability allow for comparisons of apparent survival from year to year, even if there were lower detection rates in a particular year. Survival probability is an estimate of the probability of an individual bird surviving from one year to the next.

Prior to running final CJS models for my objectives, I first modeled apparent survival as a function of age to see if age was a strong predictor of survival. This excluded any birds with an unknown/imprecise age. I modeled age within MARK assuming any effect of age only spanned the first year of life, with the young individuals then being switched to an adult survival parameter with all following years. This led to only two categories, immature and adult birds, in the models. I modeled all apparent survival and recapture probabilities with and without time dependence (t) in the survival and recapture rates, as well as with and without age dependence (t/t).

I considered any models with ΔAICc>4 unlikely to be unsupportive of my dataset relative to the other models. Thus, in this first pass of the analysis, if all age models were uninformative, I chose to eliminate them from the final analysis and include individuals with unknown ages in the dataset to increase the sample size. If age was removed, only four models were run with the new datasets, constant ϕ and p, both time dependent, or each combination of one time dependent and one constant. In the event of multiple models being within 4 AICc, models were averaged. This took into account each model's weight, with the more likely models having more weight in the final apparent survival and recapture estimates. I averaged the estimates and standard error across the results of all the models run using the program MARK model-averaging function, and output into a final model averaged result.

Finally, I added body size after age had or had not been ruled out of the dataset. I measured body size by the individual covariate of tarsus length, because the length of a bird's tarsus does not change over its lifespan. Other body size covariates, such as wing or tail length, could have changed each year and resulted in inaccurate data. Every model was run with the additional covariate, to see if body size had an effect on apparent survival within a species, or even within a given year of the study. If all models including this covariate were >4 ΔAICc, I excluded them from the final model set.

Weather variables

To examine possible correlations between time dependent apparent survival and weather, I obtained data for each year of the study from the John Glenn Columbus International Airport weather station accessed through Weather Underground. I did not run any in-depth statistical tests due to the small sample size of years, but descriptive results were still drawn based on apparent relationships for exploratory purposes. I obtained average temperatures obtained for every month between October-March, along with the average high and average low. I also quantified temperatures by counting up the number of days with a high temperature below 32°F or 20°F, and with a low temperature below 20°F or 10°F. I added snowfall for the entire winter, along with total rainfall and precipitation. To help quantify extreme cold events, temperatures with lows below 10 degrees for at least 3 consecutive days were also added and marked under a prolonged cold category.

Results

Carolina Chickadee

Across the 5-year study, the lab marked total of 50 Carolina Chickadees from the winters of 2015/2016 to 2019/2020 with 41 of those chickadees having a known age. My modeled results indicated that apparent annual survival of Carolina Chickadee was not influenced by age, with age-incorporated models running above a ΔAICc of 10. Thus, individuals omitted from models due to unknown starting age were added back into the sample with the most likely model finding no variation by time with recapture or apparent survival (Table 2). Apparent annual survival probability was estimated at 46% with a recapture probability of 61% (Table 5). The mean tarsus length was 15.5 mm, with a Beta estimate of -0.256 and a CI between -0.878 and 0.365. A likelihood ratio test found the P-value = 0.40, suggesting both models fit the data equally well (P>0.05). However, body size was not found to be a significant parameter in determining chickadee apparent survival because of both negative and positive values within the CI, but was noted to have a slight negative correlation with survival as body size increased.

Table 2. Most likely models of apparent annual survival ranked with respective AICc values for Carolina Chickadee within the Wilma H. Schiermeier Olentangy River Wetlands over the 5-year study.

Carolina Chickadee – Without Age AIC Table

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.
Phi(.)p(.)	93.5154	0.0000	0.8493	1.0000	2
Phi(.)p(t)	98.3850	4.8696	0.0744	0.0876	5
Phi(t)p(.)	98.5517	5.0363	0.0685	0.0806	5
Phi(t)p(t)	102.8940	9.3786	0.0078	0.0092	7

Song Sparrow

From 2015-2020 we marked 134 Song Sparrows across the 5-year study period, and 115 of those sparrows had a known age. Age was not found to be a significant influence on apparent annual survival across the sparrows. Models also revealed that time had an unlikely influence on apparent survival, with time incorporated models falling outside of ΔAICc values of 4 (Table 3). Thus, individuals omitted from models due to unknown starting age were added back into the sample with the most likely model finding no variation by time with recapture or apparent survival (Table 3). Apparent annual survival probability was estimated at 65% with a recapture probability of 46% (Table 5). The mean tarsus length was 21.2 mm, with a Beta estimate of 0.125 and a CI between -0.195 and 0.447. A likelihood ratio test found the P = 0.44, suggesting both models fit the data equally well (P>0.05). Body size was not found to be a significant parameter determining Song Sparrow apparent survival because of both negative and positive values within the CI, but was noted to have a slight positive correlation with apparent survival as body size increased.

Table 3. Most likely models of apparent annual survival ranked with respective AICc values for Song Sparrow within the Wilma H. Schiermeier Olentangy River Wetlands over the 5-year study.

Song Sparrow – Without Age AIC Table

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.
Phi(.)p(.)	255.2131	0.0000	0.7801	1.0000	2
Phi(t)p(.)	259.2971	4.0840	0.1012	0.1298	5
Phi(t)p(t)	260.2344	5.0302	0.0631	0.0809	7
Phi(.)p(t)	260.4934	5.2803	0.0557	0.0714	5

White-throated Sparrow

From 2016-2020 we followed 179 White-throated Sparrows, but we only analyzed 149 over the study period because of unknown age. Age was found to be a likely parameter that influenced sparrow apparent annual survival, with two age models within 4 ΔAICc of the top model. Similarly, apparent survival was also influenced by time, with different apparent survival estimates across the years for young and adult birds (Table 4). Estimates were averaged on account of the likelihood of multiple models, ending with both adult and young apparent survival and recapture returns. Young birds had apparent survival probabilities of 65%, 55% and 57% between the winters of 2016 – 2020 (Table 5). The adult White-throated Sparrows averaged higher with apparent survival probabilities of 77%, 68%, and 64% (Table 4). Recapture rates were almost identical between the two groups, with each estimate being within 1-2% of each other (Table 5). The mean tarsus length was 23.3 mm, with all models incorporating tarsus as a covariate outside of ΔAICc values of 4. Thus, body size was not found to be a significant parameter to predict sparrow apparent survival, and had no correlation across the range of tarsus values.

Table 4. Most likely models of apparent annual survival ranked with respective AICc values for White-throated Sparrow within the Wilma H. Schiermeier Olentangy River Wetlands over the 5-year study.

White-throated Sparrow – With Age, Without First Year AIC Table

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.
Phi(.)p(t)	219.0835	0.0000	0.3740	1.0000	4
Phi(t/t)p(t)	220.4872	1.4037	0.1854	0.4957	8
Phi(t)p(t)	221.2305	2.1470	0.1278	0.3418	5
Phi(t/t)p(.)	221.5562	2.4727	0.1086	0.2904	7
Phi(.)p(.)	222.1793	3.0958	0.0796	0.2127	2

Phi(t)p(.)	222.6283	3.5448	0.0636	0.1699	4
Phi(t/t)p(t/t)	224.2757	5.1922	0.0279	0.0746	10
Phi(.)p(t/t)	224.6056	5.5221	0.0237	0.0632	7
Phi(t)p(t/t)	226.4283	7.3448	0.0095	0.0254	8

Given the small sample size of years, I only visual examined apparent survival probabilities in relation to weather data. White-throated Sparrow apparent survival probability was lower in years with more snowfall amounts in adults and young (Figure 2). Similarly, apparent survival probability was estimated lower in both age classes in years with lower January temperatures (Figure 3).

Table 5. Apparent annual survival probabilities for three focal species at the Wilma H. Schiermeier Olentangy River Wetlands from 2015-2019.

Age/Year	Species Survival and Recapture Estimates						
	Species	Phi	SE	CI	p	SE	CI
	CACH	0.4616	0.0903	0.2960, 0.6361	0.6112	0.1568	0.3013, 0.8514
	SOSP	0.6479	0.0730	0.4958, 0.7750	0.4619	0.0815	0.3110, 0.6202
Young, 16/17	WTSP	0.6485	0.1379	0.2867, 0.8944	0.5878	0.1342	0.2781, 0.8408
Young, 17/18	WTSP	0.5501	0.1471	0.1527, 0.8928	0.3215	0.1049	0.1213, 0.6191
Young, 18/19	WTSP	0.5723	---	---	0.4370	---	---
Adult 16/17	WTSP	0.7782	0.1279	0.3082, 0.9651	0.5946	0.2879	0.2879, 0.8418
Adult 17/18	WTSP	0.6842	0.1597	0.2528, 0.9328	0.3190	0.1019	0.1223, 0.6114
Adult 18/19	WTSP	0.6446	---	---	0.4363	---	---

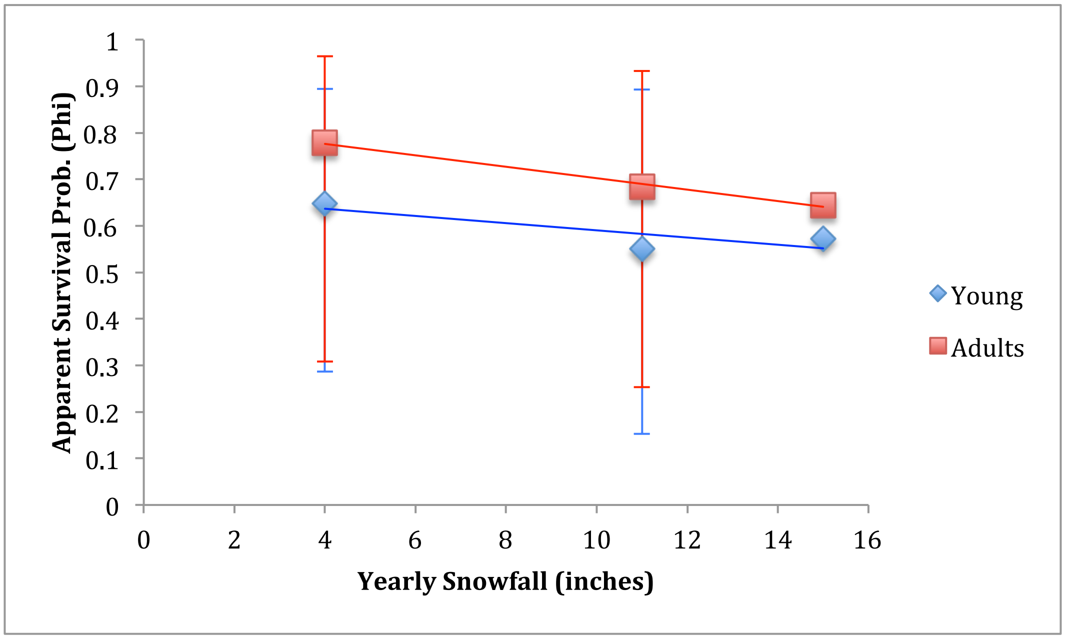

Figure 2. Apparent annual winter snowfall predicting annual variation in apparent survival of immature and adult White-throated Sparrows at the Wilma H. Schiermeier Olentangy River Wetlands. Error bars were calculated from confidence intervals estimated by Program MARK.

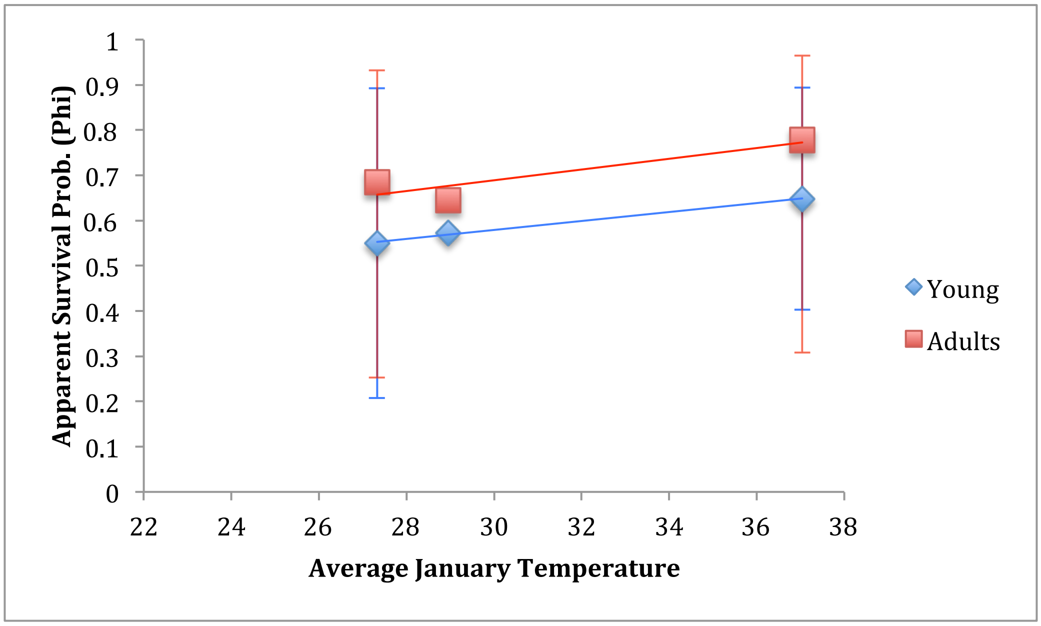

Figure 3. Average January temperature predicting annual variation in apparent survival of immature and adult White-throated Sparrows at the Wilma H. Schiermeier Olentangy River Wetlands. Error bars were calculated from confidence intervals estimated by program MARK.

Effort Hours

Net hours (time spent banding) and resighting hours were compared against White-throated Sparrow recapture estimates across the three years. The amount of time resighting did not appear to vary with resighting/recapture probability (Figure 4). Resighting/recapture probability was lower in years with more capture effort (Figure 5).

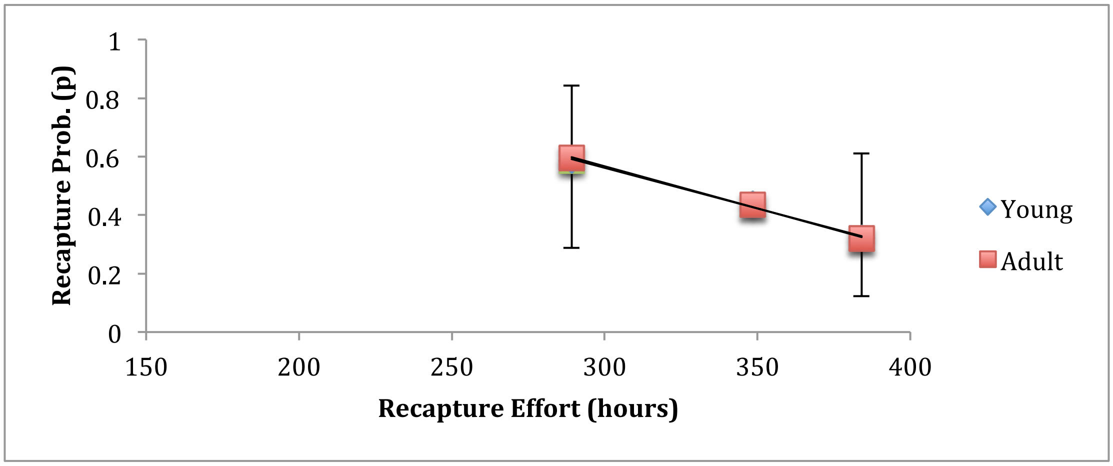

Figure 4. Annual recapture effort hours (Net Hours + Trap Hours) compared to annual recapture rates of immature and adult White-throated Sparrows across the study period within Wilma H. Schiermeier Olentangy River Wetlands, 2015-2019.

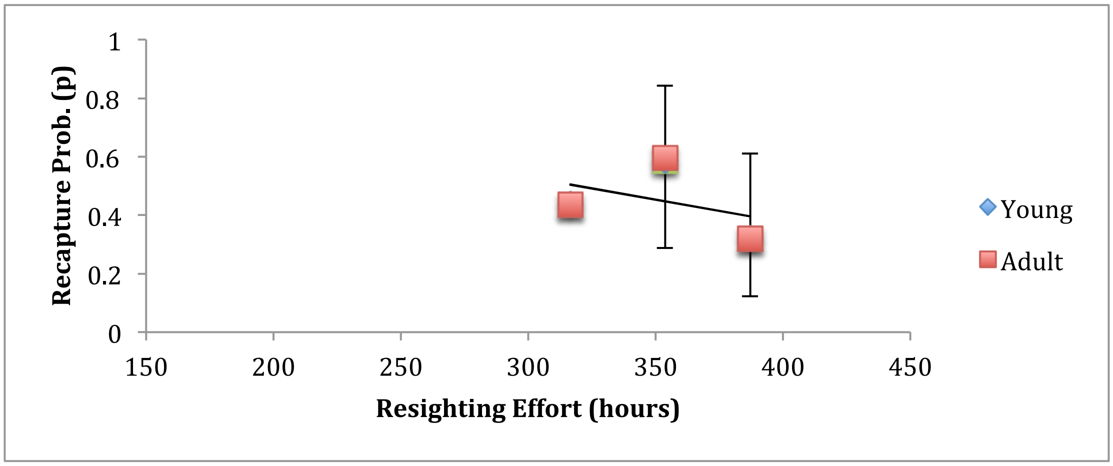

Figure 5. Annual resighting hours influence on annual recapture rates of immature and adult White-throated Sparrow across the study period within Wilma H. Schiermeier Olentangy River Wetlands, 2015-2019.

Discussion

Summary

In this study, apparent annual survival probabilities were estimated for three focal species that differed in migratory behavior and foraging strategies. Apparent survival rates of the resident Carolina Chickadees were the lowest compared to both migratory species. The obligate migrant, White-throated Sparrow had apparent annual survival rates dependent on age and variable with time. Preliminary examination of environmental factors suggests possible trends with mortality related to harsher winters. Collectively, my results suggest full and partial migratory sparrows have higher apparent annual survival than the resident species, and that snowfall and temperature may impact annual survival in an urban wetland.

Carolina Chickadee

Carolina Chickadees had an apparent annual survival estimate lower than both the Song Sparrows and both age classes of White-throated Sparrows. Lower apparent survival may have been due to differences in body size. Long hours of cold winter nights can lead to high energy expenditure, with previous studies suggesting that larger species and their higher metabolic rates could be better suited for colder temperatures (Root 1988; Brown et al. 2004). Smaller birds tend to have larger surface to volume ratios, which leads to more energy being needed to upkeep body heat. Studies of the closely related Black-capped Chickadee have shown chickadees that are too slow to adjust their metabolic performance to winter temperatures having little chance of survival (Petit et al. 2017). The larger Song and White-throated Sparrow can tolerate much lower temperatures and have similar metabolic rates, so differences in survival could be due to temperature regulation (Williams 1985; Dolby et al. 2004). Time did not come out as a factor in the Carolina Chickadee models, so the chickadees could simply have a lower tolerance to average winter conditions. Indeed, my models suggested a marginal negative trend in apparent survival with body size. However, this could be a result of sexual dimorphism, with males being larger than female birds (Pyle 1997), thus future studies should include sex as a possible predictor. Foraging strategies could also have an impact on variation among species. However, feeders surrounding the site likely created a supplemental food source for many bird species within the wetlands.

As a resident species, lack of migration has been found to lower survival rate. Several studies have also noted resident species having lower survival, possibly because of higher energy expenditure into fecundity during the longer but less abundant breeding season (Sandercock & Jaramillo 2002). This life history tradeoff results in residents expending more energy into reproduction, but at the cost of lower survival. On the other hand, migrants tend to have higher annual survival than residents, but are shown to have a lower average of number of broods and number of offspring per brood (Nicols 1996). Resident northerly populations of certain species have also been noted to have low overwinter survival (Ketterson & Nolan 1982) as compared to overwinter survival of migratory passerines (Marra, Sherry, Holmes 1989). This aligns with our results with Carolina Chickadee having the lowest survival but having the highest average clutch size of 6 eggs, while White-throated and Song Sparrow averaged 4 eggs (Mostrom et al. 2020; Arcese et al. 2020; Falls et al. 2020).

Song Sparrow

Apparent annual survival estimates for partial migrant Song Sparrows were intermediate relative to the other species. Since the Song Sparrows were partial migrants, there could have been differences between the migrant and resident populations. In fact, mark-recapture models in a study of partial migrant American Dippers (*Cinclus mexicanus*) suggested that the migratory individuals have somewhat higher survival than the residents but a lower reproductive output (Gillis et al. 2008). Since there was no way to split the data between the two groups, this converging of both migratory and resident individuals could have led to an "averaging" of the survival estimate in this study. Studies on species such as the American Dipper reaffirm life history tradeoffs, and we would predict survival to be higher in the migratory Song Sparrows than the resident ones. Foraging and life history characteristics overlapped substantially with the White-throated Sparrow as well, helping explain the overlap of survival estimates between the sparrows while having estimates higher than the Carolina Chickadee (Falls et al. 2020).

White-throated Sparrow

The apparent annual survival of White-throated Sparrow varied in time and with age class. Immature birds had lower apparent annual survival than the adults. This could have been due to inexperience, with immature birds needing to acquire behaviors such as predator avoidance, foraging, and social interaction (Wunderle, 1991). However, migratory species of birds have to deal with a long flight in unfamiliar terrain as well. A study looking at migratory kites found that over 60% of the juvenile birds died during their first year due to movement, adverse conditions, and unpredictability (Sergio et. al. 2019). Another paper on Wood Thrush found that there are lower survival rates during the migration period for young birds than adults (Rushing et al. 2017). This could explain why an age effect was only found in the fully migratory species, rather than the other two partial or fully resident birds. However, migratory sparrows also tend to have larger natal dispersal distances, and have been known to switch their overwintering site after their first year (Barrentine & McClure 1993). This could also help explain why survival was lower between the age classes for the sparrows. Finally, immature and adult survival could be influenced by social interaction of the White-throated Sparrow flocks that feed within the wetlands. White-crowned Sparrow (*Zonotrichia leucophrys*) studies found that on average, adults foraged closer to cover than immature birds (Slotow & Paxinos 1997). If immature sparrows are being pushed to forage in areas with higher predation, it could lead to a lower survival within the wetland population.

Apparent survival estimates for both immature and adult White-throated Sparrows dropped during the same years, indicating the drivers of poor survival years were consistent across age classes. One environmental factor that could negatively impact survival is snowfall, especially for a ground foraging species. Since White-throated Sparrows almost exclusively feed on the ground on their wintering grounds, snow can prevent feeding for prolong periods if it covers the ground (Rogers 1987). When compared to the total snowfall for the year within the wetlands, the years of higher snowfall coincided with lower apparent survival. Lower average January temperatures also coincided with lower apparent survival. Savannah Sparrows (*Passerculus sandwichensis*) can experience strong positive effects on survival with above-average temperatures (Woodworth et al. 2017). If White-throated Sparrows in our study area exhibit the same pattern, it could help explain why apparent survival was highest during the first year of study (2016/2017) with a warm average January temperature, but declined in the following years with two colder averages.

Finally, recapture and resighting effort across the study related to a decreasing trend for the recapture estimates of the White-throated Sparrows (Figure 4; Figure 5). It is unlikely that increasing the effort decreased the recapture probability, but too much banding effort could potentially result in birds becoming more “trap-shy” or avoiding net areas. However, this suggested trend was more likely due to a minimal sample size, and future recapture estimates need to be analyzed to see if this conflicting result continues.

Conclusions

My results suggest that apparent annual survival differs between the species with three different life histories overwintering at a common site in an urban wetland. They are consistent with life history tradeoffs with Carolina Chickadee, a resident species, having lower apparent survival than the partial and full migratory species. Further, White-throated Sparrows exhibited results in agreement with other studies of higher immature mortality, presumably from the challenges of migration. Future research, such as tagging the Song Sparrows to confirm which are migratory and which are resident, could help explain and draw more in-depth comparisons between the two sparrows studied. It would likely be fruitful to continue examining White-throated Sparrow survival in relation to weather, to conduct a more robust analysis. Working to track resident, partial, and full migratory species needs to continue as urbanization grows and the climate changes. Long-term studies on overlapping species with variable life histories will help draw conclusions about potential variation in responses to anthropogenic change.

Acknowledgements

This paper would not have been possible without the tireless effort of Dr. Christopher Tonra and the Tonra Lab of Avian Ecology. I thank their effort and commitment for research and avian conservation, and for teaching me important topics surrounding the methods and conclusions. I also want to thank all of the students in the ENR5364.02 Avian Wildlife Biology and Management course over the years of this study, who resighted birds weekly through most of the wintering period. Finally, I thank Ohio State University, specifically the School of Environment and Natural Resources, who set up timelines and helped answer any questions that were asked throughout the research study.

Literature Cited

Aldrich, J. W. (1984). Ecogeographical Variation in Size and Proportions of Song Sparrows (Melospiza melodia). *Ornithological Monographs*, *35*, iii–134. https://doi.org/10.2307/40166779

Alig, R. J., Kline, J. D., & Lichtenstein, M. (2004). Urbanization on the US landscape: Looking ahead in the 21st century. *Landscape and Urban Planning*, *69*(2), 219–234. https://doi.org/10.1016/j.landurbplan.2003.07.004

Arcese, P., M. K. Sogge, A. B. Marr, and M. A. Patten (2020). Song Sparrow (Melospiza melodia), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.sonspa.01

Barrentine, C. D. (1993). Is Site Fidelity to a Winter Area Reversible for Some Adult White-Crowned Sparrows? *North American Bird Bander*, *18*(1 (January-March)), 15–17.

Beck, C. W., & Watts, B. D. (2011). The effect of cover and food on space use by wintering Song Sparrows and Field Sparrows. *Canadian Journal of Zoology*. https://doi.org/10.1139/z97-790

Brewer, R. (1963). Ecological and Reproductive Relationships of Black-Capped and Carolina Chickadees. *The Auk*, *80*(1), 9–47. https://doi.org/10.2307/4082581

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a Metabolic Theory of Ecology. *Ecology*, *85*(7), 1771–1789. https://doi.org/10.1890/03-9000

Clark, M. E., & Martin, T. E. (2007). Modeling tradeoffs in avian life history traits and consequences for population growth. *Ecological Modelling*, *209*(2), 110–120. https://doi.org/10.1016/j.ecolmodel.2007.06.008

Cooper, N.W., Sherry, T.W. and Marra, P.P. (2015), Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. Ecology, 96: 1933-1942. https://doi.org/10.1890/14-1365.1

Dolby, A. S., Temple, J. G., Williams, L. E., Dilger, E. K., Stechler, K. M., & Davis, V. S. (2004). Facultative Rest-Phase Hypothermia in Free-Ranging White-Throated Sparrows. *The Condor*, *106*(2), 386–390. https://doi.org/10.1093/condor/106.2.386

Falls, J. B. and J. G. Kopachena (2020). White-throated Sparrow (Zonotrichia albicollis), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.whtspa.01

Gillis, E. A., Green, D. J., Middleton, H. A., & Morrissey, C. A. (2008). Life History Correlates of Alternative Migratory Strategies in American Dippers. *Ecology*, *89*(6), 1687–1695. https://doi.org/10.1890/07-1122.1

Grubb, T. C., Jr. (1977). Weather-Dependent Foraging Behavior of Some Birds Wintering in a Deciduous Woodland Horizontal Adjustments. *Condor*, *79*(2 (March-April)), 271–274. https://doi.org/10.2307/1367175

Jansson, C., Ekman, J., & Brömssen, A. von. (1981). Winter Mortality and Food Supply in Tits Parus spp. *Oikos, 37(3),* 313-322. https://doi.org/10.2307/3544122

Jesse S. Krause, Jonathan H. Pérez, Simone L. Meddle, John C. Wingfield. Effects of short term fasting on stress physiology, body condition, and locomotor activity in wintering male white-crowned sparrows, Physiology & *Behavior*, Volume 177, 2017, Pages 282-290, https://doi.org/10.1016/j.physbeh.2017.04.026

Ketterson, E. D., & Val Nolan, Jr. (1982). Role of Migration and Winter Mortality in the Life History of a Temperate-Zone Migrant, the Dark-Eyed Junco, as Determined from Demographic Analyses of Winter Populations*. The Auk, 99(2),* 243-259. https://doi.org/10.1093/auk/99.2.243

Lemoine, N., Bauer, H.-G., Peintinger, M., & Böhning-Gaese, K. (2007). Effects of climate and land-use change on species abundance in a Central European bird community. *Conservation Biology: The Journal of the Society for Conservation Biology*, *21*(2), 495–503. https://doi.org/10.1111/j.1523-1739.2006.00633.x

Longcore, T., & Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and the Environment*, *2*(4), 191–198. https://doi.org/10.1890/1540-9295(2004)002[0191:ELP]2.0.CO;2

Lundberg, P. (1988). The evolution of partial migration in Birds. *Trends in Ecology & Evolution*, *3*(7), 172–175. https://doi.org/10.1016/0169-5347(88)90035-3

Marra, null, Hobson, null, & Holmes, null. (1998). Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science (New York, N.Y.)*, *282*(5395), 1884–1886. https://doi.org/10.1126/science.282.5395.1884

Marra, P. P., Sherry, T. W., & Holmes, R. T. (1993). Territorial Exclusion by a Long-Distance Migrant Warbler in Jamaica: A Removal Experiment with American Redstarts (Setophaga Ruticilla). *The Auk*, *110*(3), 565–572. https://doi.org/10.2307/4088420

Mehlman, D. W. (1997). Change in Avian Abundance Across the Geographic Range in Response to Environmental Change. *Ecological Applications*, *7*(2), 614–624. https://doi.org/10.1890/1051-0761(1997)007[0614:CIAAAT]2.0.CO;2

Mostrom, A. M., R. L. Curry, and B. Lohr (2020). Carolina Chickadee (*Poecile carolinensis*), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.carchi.01

Nichols, J. D. (1996). Sources of variation in migratory movements of animal populations: Statistical inference and a selective review of empirical results for birds. In Olin E. Rhodes Jr., Ronald K. Chesser, & Michael H. Smith (Eds.), *Population Dynamics in Ecological Space and Time* (pp. 147–197). University of Chicago Press; USGS Publications Warehouse.

Opdam, P., & Wascher, D. (2004). Climate change meets habitat fragmentation: Linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, *117*(3), 285–297. https://doi.org/10.1016/j.biocon.2003.12.008

Paradis, E., Baillie, S. R., Sutherland, W. J., & Gregory, R. D. (1998). Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, *67*(4), 518–536. https://doi.org/10.1046/j.1365-2656.1998.00215.x

Petit, M., Clavijo-Baquet, S., & Vézina, F. (2016). Increasing Winter Maximal Metabolic Rate Improves Intrawinter Survival in Small Birds. *Physiological and Biochemical Zoology*, *90*(2), 166–177. https://doi.org/10.1086/689274

Piper, W. H. (1995). Social Dominance in Young White-Throated Sparrows: Effects of Early Social Experience and the Unstable Period. *The Auk*, *112*(4), 878–889. https://doi.org/10.2307/4089020

Pyle, P. (1997). Identification guide to North American birds : a compendium of information on identifying, ageing, and sexing "near-passerines" and passerines in the hand. Bolinas, Calif. :Slate Creek Press.

Rogers, C. M. (1987). Predation Risk and Fasting Capacity: Do Wintering Birds Maintain Optimal Body Mass? *Ecology*, *68*(4), 1051–1061. https://doi.org/10.2307/1938377

Rogers, C. M., Smith, J. N. M., Hochachka, W. M., Cassidy, A. L. E. V., Taitt, M. J., Arcese, P., & Schluter, D. (1991). Spatial Variation in Winter Survival of Song Sparrows Melospiza melodia. *Ornis Scandinavica (Scandinavian Journal of Ornithology)*, *22*(4), 387–395. https://doi.org/10.2307/3676513

Root, T. (1988). Environmental Factors Associated with Avian Distributional Boundaries. *Journal of Biogeography*, *15*(3), 489–505. https://doi.org/10.2307/2845278

Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., Stanton, J. C., Panjabi, A., Helft, L., Parr, M., & Marra, P. P. (2019). Decline of the North American avifauna. *Science*, *366*(6461), 120–124. https://doi.org/10.1126/science.aaw1313

Rushing, C. S., Hostetler, J. A., Sillett, S. T., Marra, P. P., Rotenberg, J. A., & Ryder, T. B. (2017). Spatial and temporal drivers of avian population dynamics across the annual cycle. *Ecology, 98(11),* 2837-2850. https://doi.org/10.1002/ecy.1967

Sandercock, B. K & Jaramillo A. (2002). Annual Survival Rates of Wintering Sparrows: Assessing Demographic Consequences of Migration. *The Auk, 119(1),* 149-165. https://doi.org/10.1093/auk/119.1.149

Sæther, B.-E., Ringsby, T. H., & Røskaft, E. (1996). Life History Variation, Population Processes and Priorities in Species Conservation: Towards a Reunion of Research Paradigms. *Oikos*, *77*(2), 217–226. https://doi.org/10.2307/3546060

Schneider, K. J. (1984). Dominance, Predation, and Optimal Foraging in White-Throated Sparrow Flocks. *Ecology, 65(6),* 1820-1827. https://doi.org/10.2307/1937778

Sergio, F., Tavecchia, G., Tanferna, A., Blas, J., Blanco, G., & Hiraldo, F. (2019). When and where mortality occurs throughout the annual cycle changes with age in a migratory bird: Individual vs population implications. *Scientific Reports*, *9*(1), 17352. https://doi.org/10.1038/s41598-019-54026-z

Slotow, R., & Paxinos, E. (1997). Intraspecific Competition Influences Food Return-Predation Risk Trade-Off by White-Crowned Sparrows. *The Condor*, *99*. https://doi.org/10.2307/1370476

Studds, C., & Marra, P. (2007). Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, Setophaga ruticilla. *Climate Research*, *35*, 115–122. https://doi.org/10.3354/cr00718

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human Domination of Earth's Ecosystems. *Science*, *277*(5325), 494–499. https://doi.org/10.1126/science.277.5325.494

Williams, J. B., & Nagy, K. A. (1984). Validation of the Doubly Labeled Water Technique for Measuring Energy Metabolism in Savannah Sparrows. *Physiological Zoology*, *57*(3), 325–328. https://doi.org/10.1086/physzool.57.3.30163721

Woodworth, B. K., Wheelwright, N. T., Newman, A. E., Schaub, M., & Norris, D. R. (2017). Winter temperatures limit population growth rate of a migratory songbird. *Nature Communications*, *8*(1), 14812. https://doi.org/10.1038/ncomms14812

Wunderle, J., Joseph. (1991). Age-specific foraging proficiency in birds. *Current Ornithology*, *8*, 273–324.