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Differential Vulnerability to Window Collision Mortality Among Migratory Songbird Species

Olivia M. Colling, *The University of Western Ontario*

Supervisor: Morbey, Yolanda E., *The University of Western Ontario*
Joint Supervisor: Guglielmo, Christopher G., *The University of Western Ontario*
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Abstract

Millions of birds die annually in North America by colliding with windows. I
investigated differential vulnerability to window collision among migratory songbird
species using long-term citizen science datasets from two bird banding stations and the
fatal light awareness program. I used negative binomial regressions to model species-
specific catch ratios, a mixed-effects negative binomial regression to model trophic
guild-specific catch ratios and mixed-effects logistic regressions to model the odds of
catching different age classes. Species-specific vulnerability varied significantly. Blue-
headed Vireos, Yellow-rumped Warblers and Ruby-crowned Kinglets were least
vulnerable, while Ovenbirds, Common Yellowthroats, Fox Sparrows and Bay-breasted
Warblers were most vulnerable. Foraging height influenced vulnerability with ground
foragers being most vulnerable. The effect of age varied across species, with only some
species showing significant effects. This study contributes to the growing foundation
that is required for future studies to investigate why these factors influence vulnerability
and how to minimize future collision mortality.

Keywords

Summary for Lay Audience

There are many songbirds in North America that migrate in the fall to wintering grounds as far south as South America. During this annual fall migration, millions of birds die by colliding with windows. For my thesis, I investigated if some species of songbirds die from window collisions during fall migration more than others. I investigated this differential vulnerability using long-term datasets from three citizen science projects. Two of the datasets were from bird banding stations that collect regional bird abundance data (Tommy Thompson Park, Toronto, ON and Long Point Bird Observatory, Long Point, ON) and one was from the fatal light awareness program that collects bird-window collision data (FLAP, Toronto, ON). I used a variety of statistical models to compare the number of birds caught, or collected, by each citizen science program. These comparisons determined if different species of songbirds collided with windows at the same rate (equal vulnerability), or if they collided at different rates (differential vulnerability). Using this method, I investigated differential vulnerability in 36 species, as well as across 3 trophic guilds and 2 age classes. I found that species varied significantly in their relative vulnerabilities, and that Blue-headed Vireos, Yellow-rumped Warblers and Ruby-crowned Kinglets were least vulnerable, while Ovenbirds, Common Yellowthroats, Fox Sparrows and Bay-breasted Warblers were most vulnerable. Additionally, I found evidence that the trophic guild an individual belong to, specifically the height at which the bird forages, influences vulnerability with ground foragers being most vulnerable. Lastly, I found that the extent that age affects vulnerability varied across species, with only some species showing significant effects. This study contributes to the growing foundation that is required for future studies to investigate why these factors (i.e. species, trophic guild and age) influence vulnerability and how we can minimize future window collision mortality.

Co-Authorship Statement

All work presented in this thesis was completed under the supervision of Dr. Yolanda E. Morbey and Dr. Christopher G. Guglielmo at the University of Western Ontario who helped develop the study objectives and methodology. Statistical analyses were developed in collaboration with Dr. Simon J. Bonner. Data collection and analysis was completed by Olivia M. Colling. This thesis has been written by Olivia M. Colling and will be published with Simon J. Bonner, Yolanda E. Morbey and Christopher G. Guglielmo.

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List of Abbreviations

AHY – After-hatch year

ALAN – Artificial light at night

API – Application programming interface

CI – Confidence interval

CMMN – Canadian Migration Monitoring Network

DI – Dispersion index

DR – Dispersion ratio

FLAP – Fatal Light Awareness Program

GLM – Generalized Linear Model

GLMM – Generalized Linear Mixed-effects Model

GPS – Global Positioning System

HY – Hatch year

LPBO – Long Point Bird Observatory

ROM – Royal Ontario Museum

TTP – Tommy Thompson Park

Introduction

1.1 Avian migration in North America

Migration is an adaptation that is driven by temporal and spatial variability of resources (Dingle & Drake 2007). Dingle and Drake (2007) describe four different, non-mutually exclusive concepts that define migration: (1) persistent, undistracted and straightened out locomotory activity, (2) relocation on a greater scale and movement of longer duration than in normal daily activities, (3) seasonal to-and-fro movement between regions that alternate between favourable and unfavourable conditions, and (4) movements resulting in redistribution within a spatially extended population (Dingle & Drake 2007). These four concepts are applicable to many species across the animal kingdom. Models for studying aspects of migration have ranged from whales to butterflies, however the models of greatest interest tend to be fish for their economic value, insects for their economic impact on agriculture, and birds for their visibility and impressive distances travelled (Dingle & Drake 2007).

Every year billions of migrating birds traverse North America, and in some cases Central and South America as well (Dokter et al. 2018). Within this group of migratory birds are species from the order Passeriformes (the passerines). Passerines are known as "perching birds", as all individuals within this order have three forward-facing toes and one backward-facing toe giving them the characteristic perching ability (Raikow 1982). Many species within this order have evolved a specialized vocal organ called the syrinx that is capable of high frequency muscle contractions which produce song (Elemans et al. 2008). The passerines that produce song via the syrinx are collectively referred to as songbirds. North American migratory songbirds generally breed in the northern regions of North America during the summer, commonly along the boreal forest, before migrating to more southern regions, or to Central or South America depending on the species, for the winter (https://birdsna.org/Species-Account/bna/species).

Thus, within the annual cycle of migratory songbirds there are two migration events: (1) the spring migration where birds migrate from their respective wintering grounds to their

respective breeding grounds and (2) the fall migration where they migrate back to their respective wintering grounds. During these migrations, individuals need to stop and refuel along the way, a phenomenon known as stopover. Individuals make multiple stopovers throughout their migration spending more time on the ground refueling than in migratory flight. Hedenström and Alerstam (1997) estimated that the ratio of time spent in migratory flight to the time spent refueling during stopover is approximately 1:7 during migration (~87.5% of migration time is spent on the ground refueling). The duration of each stopover can vary from hours to days (Moore 2018). The frequency of stopovers and the route travelled also vary among individuals, species and years (Stanley et al. 2012). For example, studies have found that in some species younger birds stopover longer than adult birds, possibly due to inexperience and low social status resulting in lower rate of refueling (Yong et al. 1998, Rguibi-Idrissi et al. 2003, Mackenzie 2010, Dossman et al. 2016, Morbey et al. 2018).

1.2   The dangers of migration

Individuals are exposed to multiple dangers during migration. Some of these dangers are naturally occurring such as predation, disease, exhaustion and weather (Newton 2007, Sillett & Holmes 2002), while others are anthropogenic dangers that coincide with urbanization. Anthropogenic threats are largely an issue when birds are stopping over in urban centers, however they can also affect individuals stopping over in less developed suburban and rural areas (Klem 2008, Machtans et al. 2013, Hager et al. 2017). The most significant anthropogenic threats to migrating songbirds in North America include: predation by cats, window collisions, power line collisions, vehicle collisions and wind turbine collisions (Calvert et al. 2013). The annual mortality for each of these sources in Canada was summarized by Calvert et al. (2013). They reported that the estimated number of birds killed annually by both domestic and feral cats ranged between 76 million to 418 million. The number killed annually from collisions with windows ranged between 16.1 million and 42 million. Power line collisions were estimated to be responsible for 10.1 million to 41.2 million deaths annually, while annual death tolls from vehicle collisions and wind turbine collisions were estimated to range between 8.9

million and 18.7 million, and 13 thousand and 22 thousand, respectively (Calvert et al. 2013).

1.3   Bird-window collisions

In Canada, Machtans et al. (2013) estimated that approximately 17.7 million birds die annually from window collisions. Window collisions can occur year-round at any time of day. During the night, it is suspected that artificial light at night (ALAN) attracts and disorients nocturnal migrants bringing them into the vicinity of buildings, where their probability of collision is increased (Van Doren et al. 2017, Machtans et al. 2013). ALAN is suggested to have a beacon effect that traps birds in the apparent safety of the light, which can lead to exhaustion, collision and increased stopover duration (Van Doren et al. 2017, Machtans et al. 2013, Drewitt & Langston 2008, Avery et al. 1976). However, it is becoming more evident that most window collisions occur during the day (Gelb & Delacretaz 2009, Aymí et al. 2017, Hager & Craig 2014, Klem 1989). In the daylight, birds behave as if they cannot perceive windows suggesting that, to birds, windows are invisible barriers that reflect surrounding trees and sky (Klem 1990, Gelb & Delacretaz 2009, Klem et al. 2004). Some studies have found that the rate of window collisions peaks in the hours after dawn when nocturnal migrants are descending to rest (Borden et al. 2010, Aymí et al. 2017), while others have found that peak collisions occur in daylight when birds are foraging (Gelb & Delacretaz 2009, Hager & Craig 2014). Window collisions increase when birds are more abundant overall, such as during spring and fall migration, and occur more frequently in the fall than in the spring (Klem 1989, Borden et al. 2010, Bracey et al. 2016, Loss et al. 2014, Hager et al. 2008, Ocampo-Peñuela et al. 2016).

1.4   Differential vulnerability to window collisions

Differential vulnerability of birds to window collisions has been suggested among feeding guilds, with birds that forage for insects in the canopy having a higher risk than birds that forage for insects and/or seeds closer to or on the ground (Wittig et al. 2017, Cusa et al. 2015). This is thought to be due to behavioural differences in foraging

techniques between canopy foraging insectivores who dart quickly through small openings between branches and ground foragers who hop along the ground (Wittig et al. 2017, Aymí et al. 2017). There is also evidence for differential vulnerability between migrant and resident species, with migrants having a higher risk of death by collision than residents (Hager & Craig 2014, Wittig et al. 2017, Borden et al. 2010, Sabo et al. 2016). This difference has been attributed to the degree of familiarity to the area, as migrants travel through many unfamiliar areas while residents generally stay within familiar territory (Hager & Craig 2014, Wittig et al. 2017, Borden et al. 2010, Sabo et al. 2016). Furthermore, within migrant species there are findings that support that nocturnal migrants are more vulnerable to window collisions than diurnal migrants based on observed proportions of species known to be nocturnal migrants and species known to be diurnal migrants in carcass surveys (Nichols et al. 2018, Aymí et al. 2017). Nichols et al. (2018) propose multiple reasons why nocturnal migrants could be at higher risk including sleep deprivation, physical and mental exhaustion, low light levels during descent and attraction to the artificial light of urban centers drawing individuals into high risk areas.

Nocturnal flight calling in migratory species as a way of collectively navigating has also been found to influence window collision vulnerability, with migratory species that flight call in the night being at higher risk than migratory species that do not use nocturnal flight calls (Winger et al. 2019). It is proposed that when birds that use flight calls during migration are attracted to the artificial light produced by buildings at night and become disoriented, they produce flight calls as an attempt to receive assistance in navigation from nearby conspecifics (Winger et al. 2019). These flight calls attract more individuals to the building's vicinity resulting in higher mortality (Winger et al. 2019).

Certain species have also been consistent colliders across studies. For example, Ovenbirds (Nichols et al. 2018, Winger et al. 2019, Wittig et al. 2017), Common Yellowthroats (Nichols et al. 2018, Winger et al. 2019), Swamp Sparrows (Winger et al. 2019, Arnold & Zink 2011), Dark-eyed Juncos (Nichols et al. 2018, Winger et al. 2019), Fox Sparrows (Winger et al. 2019, Arnold & Zink 2011), Hermit Thrushes (Winger et al. 2019, Kahle et al. 2016), Lincoln's Sparrows (Winger et al. 2019, Kahle et al. 2016), Swainson's Thrushes (Winger et al. 2019, Kahle et al. 2016) and Brown Creepers

(Winger et al. 2019, Arnold & Zink 2011) were all reported as overrepresented, suggesting higher vulnerability to dying from window collisions, in carcass surveys in multiple studies. Red-eyed Vireo (Wittig et al. 2017), Yellow-rumped Warbler (Sabo et al. 2016) and Black-throated Blue Warbler (Arnold & Zink 2011) were also overrepresented in some studies, however other studies reported that these three species were under- or proportionally represented in surveys (Nichols et al. 2018, Winger et al. 2019). Thus, there is not enough evidence to classify these three species as consistent colliders.

Despite these findings, differential vulnerability among species has yet to be properly measured or understood. This is likely due to early studies only using carcass surveys to estimate vulnerabilities without accounting for local abundance (Borden et al. 2010, O'Connell 2001, Klem 1989, Klem 1990). It is important to consider local abundance when investigating differential vulnerability via carcass surveys because without having a baseline proportion of a species to compare the carcass survey results to, it is impossible to know how many individuals one should expect to find and whether the observed amount is greater or less than expected.

Recent studies of bird-window collisions account for local abundance by conducting either point count surveys (counting birds from a specific location over a specified time), or mist net surveys (passive capture of flying birds) to estimate differential vulnerability (Kahle et al. 2016, Sabo et al. 2016, Wittig et al. 2017, Aymí et al. 2017, Nichols et al. 2018, Winger et al. 2019). These studies generally consider local abundance estimates based on one or two years of observations, with the exceptions of Aymí et al.'s (2017) four-year study and Winger et al.'s (2019) study that used 40 years of window collision data at one site and one year of window collision data at another site. Longer studies are ideal for determining the vulnerability of a species as there are significant year to year variations in migratory populations that cannot be accurately represented in a single year of observations, thus using long-term datasets allows a more accurate representation of the various populations of migratory species.

In addition to differences among species, there are also differences among individuals within species that have the potential to influence window collision vulnerability. Whether differential vulnerability to window collision mortality within species is a general phenomenon is unknown. Some findings support differential vulnerability based on age (Kahle et al. 2016, Hager & Craig 2013, Hager & Craig 2014), however others do not (Klem 1989, Sabo et al. 2016). Many have proposed that window collision mortality is higher in the fall than the spring due to the addition of hatch year birds (or juveniles) to the population (Borden et al. 2010, O'Connell 2001, Hager et al. 2008, Loss et al. 2014). The inexperience of the hatch year birds has been suggested to play a role in this increased mortality (Kahle et al. 2016), however it has also been proposed that it is simply the increase in population size that accounts for this higher fall mortality (Hager et al. 2008, Hager et al. 2014). Another difference between hatch year and after-hatch year (or adult) birds that could contribute to differential vulnerability, and to my knowledge has yet to be investigated, is the degree of cranial pneumatization for each age class. Generally, hatch year skulls are not fully pneumatized in the fall (Pyle 1997). This weaker braincase could increase the probability of death given a collision, since a common cause of death after a collision is internal brain injuries (Veltri & Klem 2005).

1.5   Using citizen science datasets

The use of citizen science datasets in scientific studies is becoming more common (e.g., Arnold & Zink 2011, Nichols et al. 2018, Winger et al. 2019, Hassall et al. 2019, Forrest et al. 2019). A citizen scientist is a volunteer who assists in data collection and/or processing (Silvertown 2009). One of the earliest citizen science projects is the Christmas Bird Count which originated in 1900 and consists of volunteer birders completing a census of birds over the winter holiday season (Silvertown 2009). Nowadays, there is a multitude of citizen science projects that monitor bird populations around the globe at various scales, such as eBird (global; https://ebird.org), Breeding Bird Survey (continental; https://www.pwrc.usgs.gov/bbs/) and the Fatal Light Awareness Program (local; https://www.flap.org/). These projects monitor many aspects of avian ecology including, but not limited to, migration timing, population trends, species range and distribution, and sources of mortality (e.g., bird-window collisions).

These types of monitoring projects have provided invaluable evidence for scientific research (see Dickinson et al. 2010). For example, citizen science breeding bird atlases in Europe provided significant evidence supporting poleward shifts in species ranges as a response to climate change (Thomas & Lennon 1999, Brommer 2004, Brommer 2008). While birds are a popular topic for citizen science projects, there is a wide range of ecological topics that citizen scientists can contribute to, from invasive species, to ecological restoration, to water quality monitoring (Silvertown 2009). Using amateur volunteers in the field of ecology has significantly increased and Silvertown (2009) attributes this great expansion to three factors: (1) accessibility and user-friendly software (i.e., internet and mobile applications), (2) cost-effectiveness (i.e., free labour at a large geographic scale), and (3) government research funds that are conditional on project-related public outreach (e.g., National Science Foundation in the USA).

There are advantages and disadvantages to using citizen science datasets in scientific research. The main advantage of citizen scientist participation in scientific research projects is that the scale of the project can be increased to a size that would be impossible without the efforts of the many volunteers (Loss et al. 2015, Silvertown 2009, Tulloch et al. 2013). The main disadvantages of citizen science are inconsistent effort across space and time, and diminished data quality. The inconsistent survey effort is a result of variable availability, interest and convenience for volunteers throughout the year (Tulloch et al. 2013). The lowered quality of data stems from inconsistencies and errors in surveys and records as a result of varying degrees of structure and direction in projects, as well as volunteer background knowledge and skill (Tulloch et al. 2013). Biases that also affect data quality are observer biases related to identification and detection skill levels, and species preferences (i.e., only looking for and/or recording favourite, rare or interesting species), and location biases such as preferences for nearby, accessible locations or known high density and diverse areas (Johnston et al. 2019).

Research on how to develop successful citizen science projects and how to best use the resulting data have greatly increased the effectiveness of such datasets. Some solutions are as simple as having a regional program coordinator communicating with volunteers and validating the collected data (Tulloch et al. 2013). Other techniques involve

professional scientists assisting program coordinators on data collection design, using a stratified sampling design, accounting for variation during modelling via covariates, and excluding data from less reliable volunteers, such as first-time volunteers, volunteers with erratic submissions and volunteers with erroneous submissions (Loss et al. 2015, Dickinson et al. 2010, Johnston et al. 2019). In the scientific field, solutions to these challenges exist in thorough sampling protocols, however the implementation of these rigorous protocols in citizen science programs presents a new challenge of keeping volunteers interested and capable of participating (Dickinson et al. 2010).

1.6   Study objectives and overview

My thesis had two objectives: (1) to determine if there is differential vulnerability to dying from window collisions among migratory songbird species using long-term bird monitoring data to estimate local abundance, and (2) to determine if there is differential vulnerability to dying from window collisions within migratory songbird species, specifically looking at the effect of age in the fall.

For objective (1), I hypothesized that there is differential vulnerability among migratory songbird species and that trophic guild contributes to window collision mortality vulnerability because some guilds are more active fliers than others (Wittig et al. 2017, Hager & Craig 2014, Sabo et al. 2016, Aymí et al. 2017). I tested differential vulnerability among species using three temporally-overlapping datasets (one bird-window collision monitoring dataset and two bird population monitoring datasets) to estimate and compare window and mist net catch ratios for each species using species-specific negative binomial regressions. To test the effect of trophic guild, I grouped the species by trophic guild and estimated and compared window and mist net catch ratios for each guild using a mixed-effects negative binomial regression. I predicted that if trophic guild contributes to window collision mortality vulnerability, then insectivorous migrants would be more vulnerable than granivorous migrants, as they are the more active feeding guild (Wittig et al. 2017, Hager & Craig 2014). For objective (2), I hypothesized that age contributes to window collision mortality vulnerability because hatch years are inexperienced and generally, have less pneumatized skulls (Kahle et al.

2016, Pyle 1997). To test this, I collected age data from the carcasses that were collected for the window collision dataset in two years. Then, using this age data along with the age data from the two population monitoring datasets, I estimated the odds of catching a hatch year bird at each site using species-specific mixed-effects logistic regressions. I predicted that if age contributes to window collision mortality vulnerability, then hatch years would be more vulnerable than after-hatch years.

Methods

2.1 Datasets

2.1.1 Window collision data

I used a window collision monitoring dataset spanning the years 2000-2018 from the Fatal Light Awareness Program (FLAP; www.flap.org) a citizen science program in Toronto, Ontario (43°39'11.6"N 79°22'59.5"W). FLAP volunteers collect and record window collision data by completing daily surveys. FLAP volunteers survey year-round (permitted volunteers are available), however peak window collisions occur during spring migration (April-June) and fall migration (August-November). The peak during fall migration is larger than the spring migration peak, with the majority of the fall activity occurring in September and October. Thus, I set the temporal extent of my study as 1 September to 31 October for each year to overlap with the period of greatest abundance of data. FLAP began surveying downtown Toronto in 1993 for birds that collided with windows and coverage has expanded to include the Greater Toronto Area (Figure 1). Despite starting data collection in 1993, data is only available from 2000 to present due to a technical issue with the computer that was storing the 1993-1999 data. Volunteers record where a bird was found, the day and time it was found, the species (if able), the bird's status (e.g., dead, alive, sent to rehabilitation center) and any notes of interest. FLAP has developed an online mapping program that enables people to report window collisions globally (Global Bird Collision Mapper; https://birdmapper.org/app/), which has greatly expanded the surveys beyond the Greater Toronto Area. Carcasses are brought to FLAP headquarters or the Royal Ontario Museum (ROM) for storage at -20°C and confirmation of species identification. FLAP retains carcasses for one year, at the end of which they display the collection at an annual layout to raise public awareness, and then FLAP donates the carcasses to various interested parties, including, but not limited to, the ROM, universities, and environmental consulting firms. Data is recorded throughout the year by FLAP volunteers in an online program designed specifically for FLAP. When the birds are delivered to FLAP headquarters the species identification for each individual is verified.

Figure 1. Comparison of the Fatal Light Awareness Program's (FLAP) survey areas in 2000, 2003, 2006, 2009, 2012 and 2017. Shown in red are the locations that birds were collected by FLAP in the fall of each year. The transparency of the dots reflects the number of carcasses found at that location, with darker red signifying higher numbers. Outlined in black is the area that my study focuses on as it is consistently surveyed over the years. Map sourced from Google Maps using the ***ggmap*** package in R (Kahle & Wickham 2013).

2.1.2 Mist net data

I used two different regional mist net datasets to account for local abundance of each bird species. The first mist net dataset came from the Long Point Bird Observatory (LPBO) banding program, Long Point, Ontario (42°34'58.5"N 80°23'54.5"W; Long Point Bird Observatory 2008). LPBO is the oldest banding station in Bird Studies Canada's Canadian Migration Monitoring Network (CMMN). The CMMN is a network of independent bird banding stations that was formed in 1998 to improve migration monitoring in Canada and to increase the information used to monitor population trends of Neotropical migrant birds that have largely inaccessible breeding and wintering habitats (https://www.birdscanada.org/volunteer/cmmn/). At LPBO mist net surveys are performed daily (unless rain or wind prevent surveying) during spring and fall migration at three field sites: Old Cut, Breakwater and The Tip. In my study, I used the mist net dataset from the Old Cut field site because it is the most reliably surveyed and has the most constant survey effort.

Long Point, Ontario is approximately 145 km southwest of Toronto, Ontario. Thus, I also used a second mist net dataset from Tommy Thompson Park (TTP), which is located in Toronto, Ontario (43°37'37.4"N 79°19'50.7"W; Tommy Thompson Park Bird Research Station 2008; Figure 2). TTP is a newer banding station in CMMN that started operating in 2003. Since TTP began operation later than FLAP and LPBO, I excluded data prior to 2003 from these two sites in order to achieve consistent timeframes across sites. Thus, in my catch analysis I used the fall data collected at each site from 2003 to 2017. TTP has one field site with 20 mist nets (30 mm mesh size) where staff survey birds daily (weather permitting) during spring and fall migration for six hours starting 30 minutes before sunrise. This banding station is operated by volunteers who are trained on-site to capture and band birds, and record measurements. Standard bird banding measurements are taken for each individual, including variables such as species, date, time captured, age and mass. The fall of 2008 was excluded from my TTP analyses as no banding data was recorded that season since the program did not have a master bander at the time. Using both the LPBO and TTP mist net datasets allowed me to compare the two banding stations to determine if collision vulnerability results differed depending on
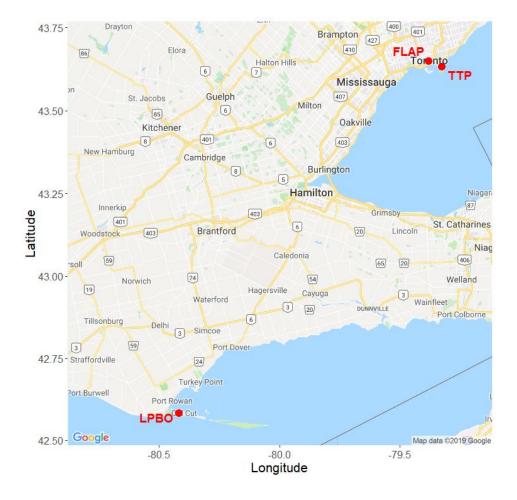
Figure 2. Map showing the three sites of data collection used in the study. The mist net banding data came from the Long Point Bird Observatory (LPBO) and Tommy Thompson Park (TTP), and the window collision data came from the Fatal Light Awareness Program (FLAP). Map sourced from Google Maps using the ***ggmap*** package in R (Kahle & Wickham 2013).

banding station. When there were differences in results between LPBO and TTP, I favoured TTP due to its proximity to downtown Toronto, even though the LPBO dataset was more complete.

Mist net survey effort is recorded in mist net hours (the number of hours a net is open in a day) for all nets. At Old Cut, there are 14 mist nets (30 mm mesh size) that are opened daily for six hours starting 30 minutes before sunrise. This banding station is also operated by volunteers who are trained to capture and band birds, and record measurements. The same measurements are taken for each captured individual as at TTP. The hardcopies of all banding records are proofread and, if necessary, corrected by a qualified bander (generally, the master bander) before they are scanned and digitized using a customized windows-based program. The digital versions of the records are also proofread to ensure that any misinterpretations of the program are corrected. Copies of these verified datasets are backed-up and kept on site. The data are also sent to the Canadian Wildlife Service banding office. I obtained these banding records and the effort dataset, however incomplete entries and a lack of data verification post-digitization (all records are originally hand-written) made total net hours an unreliable measure of effort. Instead, I controlled for effort using total net days (number of days the nets were open) for each species' fall catch season (the period in the fall when the species is present), assuming that each day the nets were open at least one bird was caught and processed. This measure of effort also worked for the FLAP survey effort, since FLAP does not record effort. For FLAP, I considered the total net days as the total number of survey days for each species' fall catch season, assuming that each day the volunteers surveyed at least one bird was recovered (see Appendix 1 for the annual total net days at each site from 1 September to 31 October). I defined the catch season for each species and each year as the earliest capture of the species by FLAP, TTP or LPBO to the latest capture by FLAP, TTP or LPBO. Each species requires a unique catch season because the timing of migration varies among species; some species are only present in early September, while others are only present in late October. My definition of catch season includes all recorded captures at each program and uses the same timeframe across the three programs for each species without overestimating effort by using the whole season for each species.

2.2 Data preparation

2.2.1 Filtering & geocoding data

The FLAP data was recorded by various citizen scientists with varying degrees of quality within and among years. As such, there were issues with missing data and inconsistencies in how variables were recorded within the dataset that had to be resolved before I could use the dataset in my analysis. Entries with missing data for address/location and/or date that a carcass was found were excluded. Entries that were located outside of Toronto, Ontario (e.g. Mississauga, Ontario) were also excluded. The address/location variable required significant quality checking to ensure that each location had one address associated with it. To standardize the addresses I fixed spelling errors, removed any additional notes/descriptions following addresses, removed any irregular spacings, changed building names to their respective addresses, formatted intersection records consistently and changed the various formats of the same address to a single, consistent address.

All data cleaning and filtering steps were completed using R version 3.4.1 in order to maintain a record of changes (R Core Team 2017). I then made a master list of all the unique addresses and geocoded these locations using a batch geocoding function developed by Shane Lynn using the ***ggmap*** package in R and Google's geocoding API (https://www.shanelynn.ie/massive-geocoding-with-r-and-google-maps/). Once I had the longitude and latitude of each address, I added these variables to the cleaned dataset. This dataset was filtered to only include entries where the bird's status was "Dead" since my study was focused on window collision mortality. The data was then further filtered for entries within the spatial and temporal extents of my study. Since the FLAP survey area is so far-reaching and variable from year-to-year, I narrowed down the spatial extent to an area in Toronto where surveying was consistent from 2000-2017 (Figure 1). To decide where this area would be, I plotted the FLAP data on a map using the ***ggmap*** package in R (Kahle & Wickham 2013) to evaluate the survey area. After comparing survey areas over the years, I chose to use the core downtown Toronto area as the spatial extent of the analysis, since it was consistently surveyed from 2000-2017 (Figure 3). I filtered the data for individuals found between the latitudes 43.644 and 43.652 and the
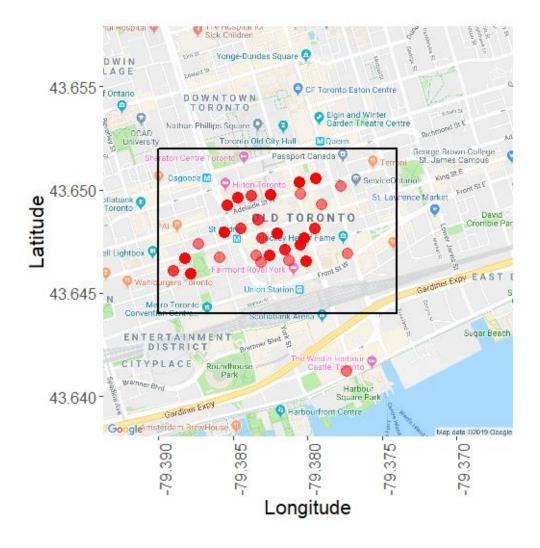
Figure 3. Map of downtown Toronto displaying the spatial extent (black outline) and locations of birds (red dots) collected in the fall of 2017. The transparency of the dots reflects the number of carcasses found at that location, with darker red signifying higher numbers. Map sourced from Google Maps using the ***ggmap*** package in R (Kahle & Wickham 2013).

longitudes -79.39 and -79.374, which are the boundaries of downtown Toronto, Ontario, and then I filtered for entries between 1 September and 31 October.

I filtered both the LPBO and TTP banding datasets for mist net records between 1 September and 31 October, and then selected data for the years 2003-2017. In addition to filtering for temporal extent, I also only included the first capture of individuals that were caught multiple times. This was intended to standardize the trapping results between mist nets and windows, since the birds that are recovered in FLAP's carcass surveys can only collide with windows once. Net days were calculated for each species each year within this temporal extent to estimate effort. Differences in the number of nets between sites was not accounted for in net days since it is unknown how many nets were open on a given day. The number of nets opened can vary day-to-day depending on the direction of strong winds (nets face different directions thus some can be affected while others are not) and the catch volume (if the catch is overwhelming the available volunteers some nets will be closed).

2.2.2   Species selection & classification

To determine which species to use in the catch analysis, I calculated the total count per fall season for each species at LPBO using the LPBO fall mist net data. I then selected species with counts greater than or equal to 20 individuals to prevent uncommon captures from skewing the data. I filtered the remaining species to only include those from the Order Passeriformes. The remaining songbird species were checked against the FLAP and TTP data, as well as eBird data (https://ebird.org) to ensure their presence in Toronto, Ontario in the fall. eBird is a citizen science project where volunteer observers report bird observations online. I examined the fall 2017 eBird data for Toronto to confirm that each of the remaining songbird species found at LPBO were also seen in Toronto during fall migration. All 37 remaining songbird species occurred in both areas in the fall.

I classified 37 species by Family and trophic guild (i.e. diet and foraging height). Family classifications were obtained from Birds of North America (birdsna.org/Species-Account/bna/species). The trophic guild diet and foraging height information was

obtained from Gonzalez-Salazar et al. (2014). If the species was not included in their table, then the information was obtained from Birds of North America (birdsna.org/Species-Account/bna/species). One species (Black-capped Chickadee) was excluded as it is a resident species, and therefore not a migratory songbird. The remaining 36 species were used in the catch analysis (Table 1).

2.3 Catch analysis

2.3.1 Conceptual model

To compare species-specific catch ratios among sites (FLAP, TTP and LPBO), I made several assumptions about the migration process (Figure 4). In this conceptual model, I assumed that the birds present at each site are all part of a metapopulation (N) that breeds in Northern Ontario and divides into four subpopulations; birds that fly towards LPBO, birds that fly towards downtown Toronto, Ontario (FLAP), birds that fly towards TTP and birds that fly elsewhere. Each subpopulation represents a different migratory route and stopover site, each with its own probability that an individual follows it (P_1). Once the birds stop at a site they are vulnerable to being captured, and the probability of capture depends on the capture efficiency of the program's trap (mist net or window; P_t). These two probabilities determine how many birds are caught at each site:

Metapopulation (N_{iy}) x Stopover (P_{1ijy}) x Capture Efficiency (P_{tijy}) = Catch (C_{ijy})

where N_{iy} is the population size of species i in year y, P_{1ijy} is the probability of species i stopping over at site j in year y, P_{tijy} is the probability of species i being trapped at site j in year y and C_{ijy} is the catch of species i at site j in year y. For FLAP, the capture efficiency is further broken down into two components:

$$P_{tiFy} = \phi_{iy} + \rho_{iy} \qquad \qquad (1)$$

where P_{tiFy} is the probability that species i is found by FLAP in year y, ϕ_{iy} is the probability of species i being killed by a window in year y (window kill rate) and ρ_{iy} is the probability of species i being detected by a volunteer in the carcass survey in year y (detection rate).

Table 1. Classifications of 36 songbird species used in the catch analysis. Guild refers to the diet of the species and foraging height refers to the canopy height at which the species generally forages. The average count (± standard deviation) of carcasses collected by the Fatal Light Awareness Program from 2003 to 2017 is included for each species.

Common Name	Family	Species	Guild: foraging height	Average Count ± SD
Brown Creeper	Certhiidae	*Certhia americana*	Insectivore: bark	11.4 ± 3.96
Gray Catbird	Mimidae	*Dumetella carolinensis*	Insectivore: ground	1.80 ± 1.78
Wilson's Warbler	Parulidae	*Cardellina pusilla*	Insectivore: lower	1.93 ± 2.22
Common Yellowthroat		*Geothlypis trichas*	Insectivore: lower	15.7 ± 9.95
Orange-crowned Warbler		*Oreothlypis celata*	Insectivore: lower	0.40 ± 0.51
Tennessee Warbler		*Oreothlypis peregrina*	Insectivore: lower	2.40 ± 1.80
Nashville Warbler		*Oreothlypis ruficapilla*	Insectivore: lower	5.53 ± 3.91
Ovenbird		*Seiurus aurocapilla*	Insectivore: ground	26.3 ± 18.1
Northern Parula		*Setophaga americana*	Insectivore: lower	0.53 ± 0.92
Black-throated Blue Warbler		*Setophaga caerulescens*	Insectivore: lower	10.8 ± 11.3
Bay-breasted Warbler		*Setophaga castanea*	Insectivore: lower	2.67 ± 2.13
Yellow-rumped Warbler		*Setophaga coronata*	Insectivore: lower	1.67 ± 1.91
Magnolia Warbler		*Setophaga magnolia*	Insectivore: lower	12.8 ± 9.24
American Redstart		*Setophaga ruticilla*	Insectivore: aerial hawker	3.47 ± 1.96
Blackpoll Warbler		*Setophaga striata*	Insectivore: lower	1.20 ± 1.15
Cape May Warbler		*Setophaga tigrina*	Insectivore: upper	0.27 ± 0.46
Black-throated Green Warbler		*Setophaga virens*	Insectivore: lower	2.87 ± 2.90
Dark-eyed Junco	Passerellidae	*Junco hyemalis*	Granivore: ground	13.1 ± 9.02
Swamp Sparrow		*Melospiza georgiana*	Insectivore: ground	2.00 ± 1.36
Song Sparrow		*Melospiza melodia*	Granivore: ground	3.53 ± 2.88
Fox Sparrow		*Passerella iliaca*	Granivore: ground	4.60 ± 5.59
American Tree Sparrow		*Spizelloides arborea*	Granivore: ground	0.40 ± 0.74

Common Name	Family	Species	Guild: foraging height	Average Count ± SD
White-throated Sparrow		*Zonotrichia albicollis*	Granivore: ground	45.1 ± 24.7
White-crowned Sparrow		*Zonotrichia leucophrys*	Granivore: ground	2.07 ± 2.15
Ruby-crowned Kinglet	Regulidae	*Regulus calendula*	Insectivore: lower	3.67 ± 2.79
Golden-crowned Kinglet		*Regulus satrapa*	Insectivore: lower	11.0 ± 8.49
Red-breasted Nuthatch	Sittidae	*Sitta canadensis*	Insectivore: bark	2.13 ± 2.13
Winter Wren	Troglodytidae	*Troglodytes hiemalis*	Insectivore: lower	2.60 ± 1.84
Veery	Turdidae	*Catharus fuscescens*	Insectivore: ground	0.20 ± 0.41
Hermit Thrush		*Catharus guttatus*	Insectivore: ground	14.5 ± 8.25
Gray-cheeked Thrush		*Catharus minimus*	Insectivore: ground	1.27 ± 1.44
Swainson's Thrush		*Catharus ustulatus*	Insectivore: lower	3.67 ± 1.84
Eastern Phoebe	Tyrannidae	*Sayornis phoebe*	Insectivore: aerial hawker	0.27 ± 0.59
Red-eyed Vireo	Vireonidae	*Vireo olivaceus*	Insectivore: lower	1.47 ± 0.99
Philadelphia Vireo		*Vireo philadelphicus*	Insectivore: lower	0.33 ± 1.05
Blue-headed Vireo		*Vireo solitarius*	Insectivore: lower	0.07 ± 0.26

Metapopulation (N_{iy})

P_{1L} P_{1F} P_{1T}

LPBO (N_{iLy})   FLAP (N_{iFy})   TTP (N_{iTy})

Capture Efficiency

Kill Rate ϕ_i

Detection ρ

Capture Efficiency

Capture Efficiency

P_{tL} P_{tiF} P_{tT}

LPBO Catch (C_{iLy})   FLAP Catch (C_{iFy})   TTP Catch (C_{iTy})
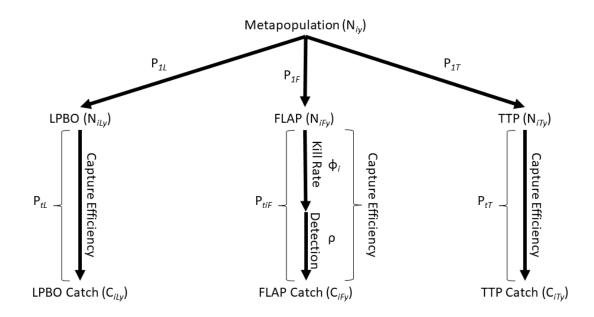
Figure 4. Schematic of the catch model used to develop the statistical models used in the catch analyses. This model assumes that the species (or trophic guild) is one metapopulation (N_{iy}) that divides into three distinct subpopulations (N_{iLy}, N_{iFy} and N_{iTy}) during fall migration. It is further assumed that each subpopulation migrates through its respective site. (*i*: species/trophic guild *i*, *y*: year *y*, P_1: probability of stopping over at specific site, P_t: probability of being trapped at specific site, ϕ: window kill rate, ρ: detection rate, C: total catch, *L*: Long Point Bird Observatory (LPBO) site, *F*: Fatal Light Awareness Program (FLAP) site, *T*: Tommy Thompson Park (TTP) site).

I simplified the conceptual model through the following assumptions: (1) the probability of stopping over at one of the programs (P_1) is constant over years and species, (2) the capture efficiencies for LPBO and TTP (P_t) are constant over years and species, (3) the window kill rate for FLAP (ϕ) is constant over years, (4) the detection rate for FLAP (ρ) is constant over years and species and (5) all probabilities in this model conform to binomial distributions. After simplifying the model with these assumptions, the resulting chain of probabilities becomes:

Metapopulation (N_{iy}) x Stopover (P_{1j}) x Capture Efficiency (P_{tj}) = Catch (C_{ijy})

Metapopulation (N_{iy}) x Stopover (P_{1F}) x Capture Efficiency (ϕ_i x ρ) = Catch (C_{iFy})

where j is the banding program (LPBO or TTP) and F is the FLAP program.

2.3.2   Conceptual model interpretation

To determine if there are differences in the species-specific vulnerabilities to window collisions, I used the above model to estimate catch ratios between the banding programs and FLAP. This was done by first approximating the distribution of each catch (C_{ijy}) by negative binomial distributions:

$$C_{iFy} \sim \text{NBinom}(\mu_{iFy} + (\mu_{iFy})^2/k)$$

$$C_{iTy} \sim \text{NBinom}(\mu_{iTy} + (\mu_{iTy})^2/k)$$

$$C_{iLy} \sim \text{NBinom}(\mu_{iLy} + (\mu_{iLy})^2/k)$$

where μ is the mean of the distribution and k is the dispersion parameter. Then, using the previously defined chain of probabilities and the approximated distribution, the estimated catch ($E(C_{ijy})$) is:

$$E(C_{iFy}) = \mu_{iFy} + (\mu_{iFy})^2/k = N_{iy}\ P_{1F}\ \phi_i\ \rho \qquad (2)$$

$$E(C_{iTy}) = \mu_{iTy} + (\mu_{iTy})^2/k = N_{iy}\ P_{1T}\ P_{tT} \qquad (3)$$

$$E(C_{iLy}) = \mu_{iLy} + (\mu_{iLy})^2/k = N_{iy}\ P_{1L}\ P_{tL} \qquad (4)$$

Using these equations, two catch ratios can be calculated (TTP:FLAP and LPBO:FLAP) for each species:

$$\frac{E(C_{iTy})}{E(C_{iFy})} = \frac{P_{1T}\, P_{tT}}{P_{1F}\, \phi_i\, \rho} \tag{5}$$

$$\frac{E(C_{iLy})}{E(C_{iFy})} = \frac{P_{1L}\, P_{tL}}{P_{1F}\, \phi_i\, \rho} \tag{6}$$

As window kill rate (ϕ_i) is the only variable that is species-specific (or trophic guild-specific), any differences in catch ratios among species (or trophic guilds) is a result of differences in window kill rate (ϕ_i). Thus, the null hypothesis where there is no differential vulnerability among species (or trophic guilds) is: $\phi_i = \phi_m$ for any pair of species (or trophic guilds) where m represents a species different from species i. Alternatively, if there is differential vulnerability, then $\phi_i \neq \phi_m$ for at least one pair of species (or trophic guilds).

These differences can be inferred by comparing the site effects estimated by a species-specific (or trophic guild) model, since:

$$E(\mathbf{C}_{iFy}) = \log(\mu_{iFy} + {(\mu_{iFy})}^2/k) = \beta_{i0} \tag{7}$$

$$E(\mathbf{C}_{iTy}) = \log(\mu_{iTy} + {(\mu_{iTy})}^2/k) = \beta_{i0} + \beta_{i1} \tag{8}$$

$$E(\mathbf{C}_{iLy}) = \log(\mu_{iLy} + {(\mu_{iLy})}^2/k) = \beta_{i0} + \beta_{i2} \tag{9}$$

And therefore:

$$\frac{E(C_{iTy})}{E(C_{iFy})} = \log(\mu_{iTy} + {(\mu_{iTy})}^2/k) - \log(\mu_{iFy} + {(\mu_{iFy})}^2/k) = \beta_{i0} + \beta_{i1} - \beta_{i0} \tag{10}$$

$$\frac{E(C_{iLy})}{E(C_{iFy})} = \log(\mu_{iLy} + {(\mu_{iLy})}^2/k) - \log(\mu_{iFy} + {(\mu_{iFy})}^2/k) = \beta_{i0} + \beta_{i2} - \beta_{i0} \tag{11}$$

where β_0 represents the site effect of FLAP (reference level), β_1 represents the site effect of TTP and β_2 represents the site effect of LPBO. In summary:

$$\frac{E(C_{iTy})}{E(C_{iFy})} = \frac{P_{1T}\,P_{tT}}{P_{1F}\,\phi_i\,\rho} = \beta_{i1} \tag{12}$$

$$\frac{E(C_{iLy})}{E(C_{iFy})} = \frac{P_{1L}\,P_{tL}}{P_{1F}\,\phi_i\,\rho} = \beta_{i2} \tag{13}$$

Therefore, if $\phi_i = \phi_m$, then $\beta_{i1} = \beta_{m1}$ and $\beta_{i2} = \beta_{m2}$, and the null hypothesis is supported. Alternatively, if $\beta_{i1} < \beta_{m1}$, then the mist net catch of species i is more similar to, or less than, its respective window catch than the mist net catch of species m is to its respective window catch. This would suggest that species i has a higher window kill rate than species m.

2.3.3   Statistical analysis of catch

I used species-specific generalized linear models (GLM) to estimate the effect of site (i.e. trap type) on catch. The data are count data, therefore I considered Poisson regression, zero-inflated Poisson regression and negative binomial regression for modelling species-specific catch. I calculated the dispersion indices (DI) for each of these regressions by dividing the residual deviance by the residual degrees of freedom. The DI should equal 1 if the model fits well. I found that the Poisson and zero-inflated Poisson regressions were over dispersed (DI > 2), while the negative binomial regression, which accounts for over dispersion, fit the data well (0.9 < DI < 1.4). Thus, I selected the negative binomial regression as my GLM. I used 36 species-specific GLMs to model catch in terms of site with an offset term to account for effort (Catch ~ Site + offset(log(Net_Days))). This effort offset term is not estimated by the model but is rather a known value that is added to the linear predictor so that each predicted response considers effort.

I used the same conceptual model to analyze effect of trophic guild, however for this analysis instead of using negative binomial regression I used a negative binomial mixed-effects model. Using a mixed-effects model allowed me to account for the variation among species within each trophic guild by adding a random effect of species. In this analysis, I modeled catch in terms of trophic guild, site, the interaction between trophic guild and site, species as a random effect and an offset term to account for effort (Catch ~ Trophic_Guild + Site + Trophic_Guild:Site + (1|Species) + offset(log(Net_Days))). In

this analysis, instead of using trophic guild-specific models, all levels were evaluated in one model. Not all levels of trophic guilds had large enough sample sizes to make meaningful conclusions, thus I combined the various insectivorous trophic guilds into two groups: insectivore-ground and insectivore-not ground (lower canopy, bark gleaners, upper canopy, aerial hawkers; Table 1). I ran the model three times, each time releveling the trophic guilds such that each of the three guilds was run once as the intercept. From each run, I recorded the intercept and main site effects along with their associated standard errors. I used these estimates to calculate the catch ratios and 95% confidence intervals for the corresponding trophic guild. I conducted a nonparametric dispersion test on this model to evaluate fit using the *DHARMa* package in R (Hartig 2019). This test calculates a dispersion ratio of fitted residuals versus simulated residuals. If the model fits well it has a dispersion ratio of one.

I estimated catch ratios using the site effects (species analysis) or trophic guild-site interaction effects (trophic guild analysis) of each model. I natural antilog-transformed these estimates and calculated their respective transformed 95% confidence intervals (CI) for each catch ratio. For the species analysis, I performed pairwise comparisons for each combination of species to determine if their catch ratios were significantly different. This was done using pair-specific GLMs (i.e., the data was filtered to include the two species of interest, rather than a single species, and species and the interaction between species and site were added to the model; Catch ~ Species + Site + Species:Site + offset(log(Net_Days))). The p-value for the effect of species at each site was evaluated using a significance level set to $\alpha = 0.05$. Since the trophic guild analysis uses a generalized linear mixed-effects model (GLMM) p-values cannot be reliably determined due to correlations between observations as a result of using random effects (Bates et al. 2019). Thus, in place of p-values 95% CIs were used to determine if trophic guild catch ratios were significantly different from each other. All modelling and calculations were performed in R version 3.4.1 (R Core Team 2017).

2.4 Age analysis

2.4.1 Spatial extent

The spatial extent used in the previous catch analysis was not large enough to provide meaningful sample sizes for a variety of species. Thus, I decided to expand the spatial extent for this analysis. I filtered the 2017 FLAP data for complete data (data with both an address and a date) and then plotted these data on a map using ***ggmap*** in R (Kahle & Wickham 2013). I selected the area between the latitudes 43.64123 and 43.76346 and the longitudes -79.41287 and -79.32006 as the spatial extent, since it included the majority of the data in the Toronto, Ontario area. I then filtered the data for individuals found within this spatial extent.

2.4.2 Species selection

After filtering the 2017 FLAP data for fall and spatial extent, I calculated the total count for each species and only included species that had a count of at least 20. From this list of species, I selected eight species (Brown Creeper, Nashville Warbler, Ovenbird, Black-throated Blue Warbler, Dark-eyed Junco, White-throated Sparrow, Golden-crowned Kinglet and Swainson's Thrush) such that I had a variety of families and included species of interest. This selection of eight then became seven, as I eliminated the Brown Creeper due to a lack of age data at TTP.

2.4.3 Age data collection

The age data for the banding programs were collected and recorded by volunteers at the stations. I filtered the banding data for individuals of the seven study species caught by mist nets in the fall for 2017 and 2018. These programs had a third age class "Unknown", for when the individual could not be aged. Individuals from this age class were excluded from the analysis. The FLAP volunteers do not age the birds they collect. To collect this data for the FLAP data, I acquired the carcasses from FLAP and brought them back to the laboratory to age via skulling. Skulling is one way to age birds in the fall, since hatch year (HY) birds migrate before their skull is fully pneumatized. To age birds this way, one examines the skull and checks if it is fully pneumatized, as seen in

after-hatch year (AHY) birds, or partially pneumatized, as seen in HY birds. The carcasses were stored in the freezer at -20°C until aging, at which point they were thawed before skulling. As these were carcasses, I was able to expose the entire skull for observation. Birds that had fully pneumatized skulls, characterized by uniform, white speckling over the entire skull, were classified as AHY. Birds that had partially pneumatized skulls, characterized by patches of white speckling or no white speckling on the skull, were classified as HY. In cases where the speckling pattern of the pneumatization was difficult to see, as a result of internal bleeding, a piece of the skull was removed, cleaned and examined. All carcasses collected within the spatial and temporal extents were obtained for each species to a maximum of 50 carcasses. When a species had more than 50 carcasses, 50 carcasses were chosen at random to age. Random selection was done by assigning a random number to each individual in Microsoft Excel using the **RAND()** function and then selecting the 50 individuals with the lowest numbers. The actual sample sizes used for some species were less than anticipated, due to inability to locate all carcasses at FLAP's headquarters.

2.4.4 Statistical analysis of age

For this objective, I analyzed the data using species-specific logistic mixed-effect models that modeled age in terms of site and year as a random effect (Age ~ Site + (1|Year)). I conducted a nonparametric dispersion test on this model to evaluate fit using the *DHARMa* package in R (Hartig 2019). I estimated the change in log odds ratios (Δ ln(odds of HY: odds of AHY)) using the site effects for each species-specific model. I inverse logit-transformed these estimated changes (now Δ odds) and calculated their respective transformed 95% confidence intervals. Since this analysis also uses a GLMM, 95% CIs were used to determine if the mist net (TTP and LPBO) probabilities were significantly different from FLAP. If there was no change in log odds ratio from FLAP to TTP or LPBO, then the Δ odds would equal one. Thus, probabilities were deemed significantly different from FLAP if their 95% CI did not include one. Species were determined to have lower odds of catching a HY bird at TTP or LPBO than FLAP, if the Δ odds was significantly less than one. Alternatively, species with Δ odds significantly

greater than one were determined to have higher odds of catching a HY bird at TTP or LPBO than FLAP. All tests were completed using R version 3.4.1 (R Core Team 2017).

Results

3.1   Catch analysis

3.1.1   Tommy Thompson Park species catch ratio

Based on the TTP data, catch ratios differed among species (Figure 5). This suggests that there is differential vulnerability to colliding with windows among migratory songbird species. The six species with the highest catch ratios, and therefore the lowest vulnerability, from highest catch ratio to lowest were: Blue-headed Vireo (TTP Catch Ratio = 204.24, 95% CI [27.88, 1496.07]), Yellow-rumped Warbler (TTP Catch Ratio = 134.13, 95% CI [74.97, 240.00]), Ruby-crowned Kinglet (TTP Catch Ratio = 107.91, 95% CI [73.09, 159.33]), Eastern Phoebe (TTP Catch Ratio = 74.17, 95% CI [26.19, 210.04]), Golden-crowned Kinglet (TTP Catch Ratio = 55.20, 95% CI [36.71, 83.01]) and Veery (TTP Catch Ratio = 45.88, 95% CI [14.02, 150.10]). The six species with the lowest catch ratios, and therefore the highest vulnerability, from lowest catch ratio to highest were: Ovenbird (TTP Catch Ratio = 0.72, 95% CI [0.51, 1.01]), Common Yellowthroat (TTP Catch Ratio = 1.73, 95% CI [1.27, 2.37]), Fox Sparrow (TTP Catch Ratio = 2.23, 95% CI [1.36, 3.67]), Bay-breasted Warbler (TTP Catch Ratio = 2.26, 95% CI [1.13, 4.50]), Red-breasted Nuthatch (TTP Catch Ratio = 2.75, 95% CI [1.30, 5.81]) and Black-throated Blue Warbler (TTP Catch Ratio = 3.52, 95% CI [2.37, 5.23]; see Table 2 for the estimates, standard errors, z-statistics and p-values from all the species-specific models). The p-values for the pairwise comparisons of catch ratios for all species combinations are displayed in Figure 6. Evidence of a site effect can clearly be seen in boxplots of the six least vulnerable species (Figure 7) and is less noticeable in the boxplots of the six most vulnerable species (Figure 8). The effect of site for each species-specific model is recorded in Table 3.
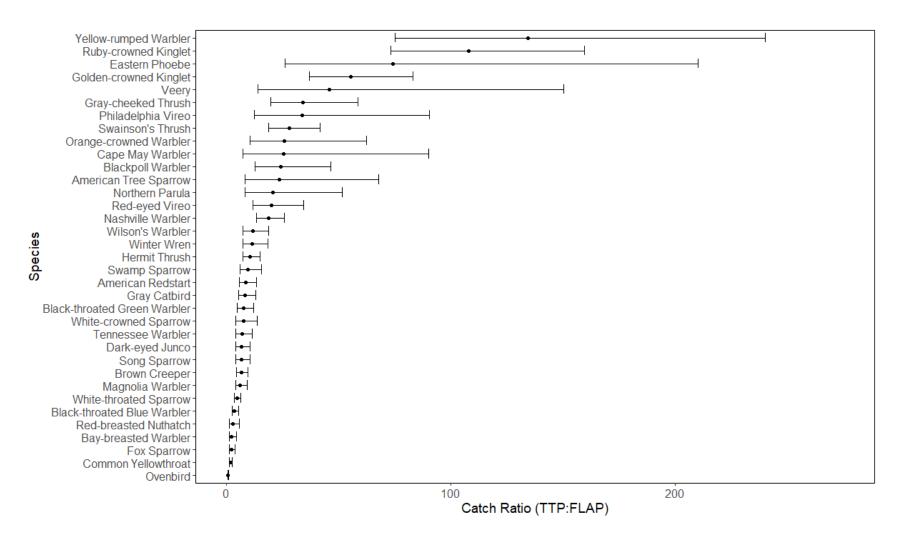
Figure 5. Transformed catch ratios between Tommy Thompson Park (TTP) and the Fatal Light Awareness Program (FLAP) for 35 songbird species organized from largest to smallest catch ratio. The natural antilog-transformed catch ratios are represented by the points and error bars are 95% confidence intervals. Catch ratios were estimated using species-specific negative binomial regressions (Catch ~ Site + offset(Net_Days))). A large catch ratio means that relatively more of that species was caught at TTP than FLAP, which suggests lower vulnerability to colliding with windows than mist nets. Alternatively, a small catch ratio means that relatively more of that species was caught at FLAP than TTP, which suggests higher vulnerability to colliding with windows than mist nets. Species whose 95% confidence intervals overlap are not significantly different from each other (p-values are provided in Figure 6). The Blue-headed Vireo catch ratio (204.24, 95% CI [27.88, 1496.07]) was removed from plot due to its extremely large error bars impeding the ability to discern the smaller catch ratios.

Table 2. Estimated coefficients (β) for each site (FLAP: Fatal Light Awareness Program, TTP: Tommy Thompson Park, LPBO: Long Point Bird Observatory) with respective standard errors (SE), z-values (z) and p-values (p) from each species-specific negative binomial regression (Catch ~ Site + offset(log(Net_Days))). Species are sorted by decreasing catch ratio according to the TTP estimates. The catch ratios comparing TTP and LPBO (TTP:LPBO) are provided for each species. Asterisks indicate significant differences ($p < 0.05$) between the catch at TTP and LPBO.

	FLAP				TTP				LPBO				
Species	β	SE	z	p	β	SE	z	p	β	SE	z	p	TTP:LPBO
Blue-headed Vireo	-6.28	1.01	-6.23	<0.005	5.32	1.02	5.24	<0.005	5.76	1.01	5.68	<0.005	0.44*
Yellow-rumped Warbler	-3.25	0.25	-12.90	<0.005	4.90	0.30	16.5	<0.005	5.65	0.29	19.2	<0.005	0.75*
Ruby-crowned Kinglet	-2.44	0.17	-14.43	<0.005	4.68	0.20	23.5	<0.005	4.94	0.20	25.1	<0.005	0.26
Eastern Phoebe	-4.69	0.51	-9.13	<0.005	4.31	0.53	8.11	<0.005	3.60	0.53	6.76	<0.005	-0.71*
Golden-crowned Kinglet	-1.12	0.16	-7.20	<0.005	4.01	0.21	19.2	<0.005	3.49	0.21	16.9	<0.005	-0.53*
Veery	-4.65	0.59	-7.91	<0.005	3.83	0.60	6.33	<0.005	4.43	0.60	7.37	<0.005	0.60*
Gray-cheeked Thrush	-3.21	0.25	-12.69	<0.005	3.52	0.28	12.6	<0.005	3.89	0.27	14.1	<0.005	0.36*
Philadelphia Vireo	-4.32	0.48	-9.03	<0.005	3.51	0.51	6.94	<0.005	3.85	0.50	7.67	<0.005	0.34
Swainson's Thrush	-2.35	0.17	-13.80	<0.005	3.33	0.20	16.3	<0.005	3.79	0.20	18.9	<0.005	0.46*
Orange-crowned Warbler	-4.26	0.43	-9.98	<0.005	3.25	0.45	7.16	<0.005	3.34	0.45	7.42	<0.005	0.09
Cape May Warbler	-4.50	0.57	-7.86	<0.005	3.24	0.64	5.02	<0.005	4.16	0.63	6.56	<0.005	0.92*
Blackpoll Warbler	-3.35	0.29	-11.69	<0.005	3.19	0.33	9.62	<0.005	4.21	0.33	12.9	<0.005	1.02*
American Tree Sparrow	-2.88	0.47	-6.13	<0.005	3.15	0.54	5.81	<0.005	2.65	0.54	4.88	<0.005	-0.50
Northern Parula	-3.71	0.41	-9.04	<0.005	3.02	0.47	6.48	<0.005	1.96	0.47	4.14	<0.005	-1.06*
Red-eyed Vireo	-3.19	0.24	-13.32	<0.005	3.00	0.27	11.1	<0.005	3.67	0.27	13.8	<0.005	0.67*
Nashville Warbler	-2.08	0.14	-15.04	<0.005	2.92	0.16	17.7	<0.005	2.46	0.16	15.0	<0.005	-0.46*
Wilson's Warbler	-2.58	0.21	-12.46	<0.005	2.46	0.24	10.4	<0.005	2.19	0.23	9.38	<0.005	-0.27
Winter Wren	-2.54	0.20	-12.65	<0.005	2.44	0.24	10.1	<0.005	2.43	0.24	10.2	<0.005	-0.01

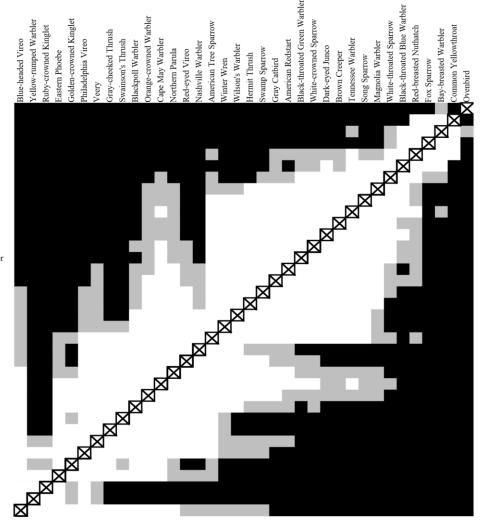| Species	FLAP				TTP				LPBO				TTP:LPBO
	β	SE	z	p	β	SE	z	p	β	SE	z	p	
Hermit Thrush	-0.92	0.13	-6.83	<0.005	2.34	0.18	12.8	<0.005	2.31	0.18	12.9	<0.005	-0.02
Swamp Sparrow	-3.01	0.21	-14.30	<0.005	2.26	0.24	9.25	<0.005	2.85	0.24	11.9	<0.005	0.58*
American Redstart	-2.27	0.18	-12.67	<0.005	2.16	0.22	9.86	<0.005	3.09	0.21	14.4	<0.005	0.93*
Gray Catbird	-3.13	0.21	-15.10	<0.005	2.12	0.23	9.13	<0.005	3.73	0.22	16.8	<0.005	1.61*
Black-throated Green Warbler	-2.47	0.19	-12.94	<0.005	2.02	0.23	8.73	<0.005	1.27	0.23	5.44	<0.005	-0.75*
White-crowned Sparrow	-2.55	0.24	-10.41	<0.005	2.00	0.30	6.60	<0.005	2.24	0.30	7.53	<0.005	0.24
Tennessee Warbler	-2.66	0.21	-12.49	<0.005	1.92	0.26	7.38	<0.005	2.01	0.26	7.85	<0.005	0.09
Dark-eyed Junco	-0.93	0.17	-5.40	<0.005	1.89	0.24	7.94	<0.005	1.90	0.23	8.11	<0.005	0.01
Song Sparrow	-2.54	0.18	-13.85	<0.005	1.89	0.23	8.21	<0.005	2.43	0.22	10.8	<0.005	0.54*
Brown Creeper	-1.21	0.14	-8.47	<0.005	1.87	0.19	9.74	<0.005	2.22	0.19	11.7	<0.005	0.34
Magnolia Warbler	-0.97	0.15	-6.45	<0.005	1.81	0.21	8.80	<0.005	2.21	0.20	10.9	<0.005	0.40*
White-throated Sparrow	0.10	0.11	0.88	0.376	1.54	0.15	10.0	<0.005	1.76	0.15	11.7	<0.005	0.22
Black-throated Blue Warbler	-1.29	0.15	-8.65	<0.005	1.26	0.20	6.23	<0.005	1.84	0.20	9.34	<0.005	0.58*
Red-breasted Nuthatch	-2.97	0.29	-10.37	<0.005	1.01	0.38	2.65	0.008	2.04	0.36	5.63	<0.005	1.02*
Bay-breasted Warbler	-2.02	0.26	-7.74	<0.005	0.81	0.35	2.31	0.021	0.89	0.34	2.59	0.010	0.08
Fox Sparrow	-1.48	0.19	-7.89	<0.005	0.80	0.25	3.17	<0.005	0.84	0.25	3.40	<0.005	0.03
Common Yellowthroat	-0.94	0.12	-8.16	<0.005	0.55	0.16	3.45	<0.005	1.19	0.15	7.79	<0.005	0.64*
Ovenbird	-0.24	0.12	-1.99	0.047	-0.33	0.17	-1.90	0.057	-0.21	0.17	-1.26	0.209	0.12

Figure 6. Matrix displaying the p-values from pairwise comparisons of the catch ratios between Tommy Thompson Park (TTP) and the Fatal Light Awareness Program (FLAP) for 36 songbird species. Each row in the matrix reflects one species' (labeled to the left) comparisons with each of the 36 species that are labeled across the top. Each column in the row is colour-coded based on significance level: black: p-value < 0.005, gray: p-value < 0.05 and white: p-value > 0.05. The "X" is placed in the column that corresponds to the species that the row belongs to, since a species cannot be compared against itself. Comparisons were completed using negative binomial regressions that were specific to each pairing of species (Catch ~ Site + Species + Site:Species + offset(log(Net_Days))).
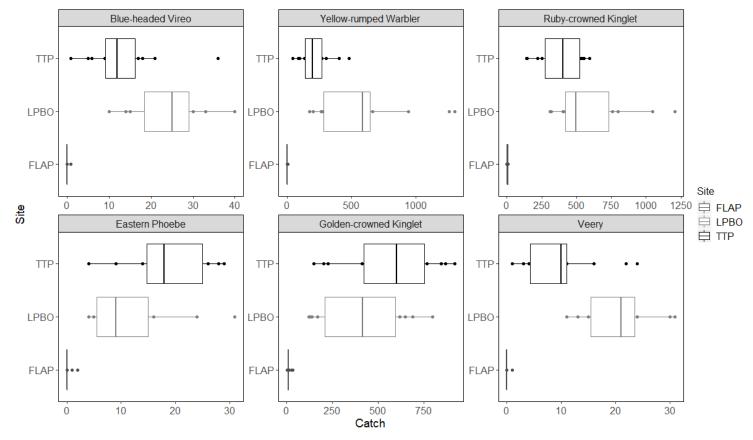
Figure 7. Catch at Tommy Thompson Park (TTP), Long Point Bird Observatory (LPBO) and the Fatal Light Awareness Program (FLAP) for the six songbird species with the highest catch ratios (based on TTP:FLAP) from 2003-2017. Each boxplot represents the distribution of data for that species at the different sites. Each box represents the inter-quartile range with the median marked by a vertical line. All six species show a clear difference between the mist net catch (TTP and LPBO) and the window catch (FLAP), with mist net catch being greater than window catch. The species-specific site effect values are provided in Table 3.
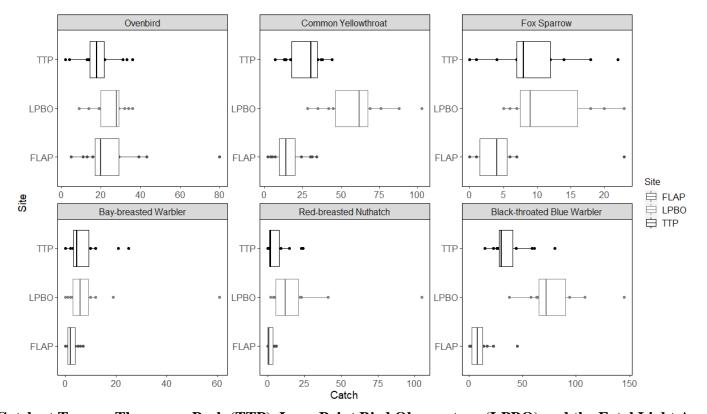
Figure 8. Catch at Tommy Thompson Park (TTP), Long Point Bird Observatory (LPBO) and the Fatal Light Awareness Program (FLAP) for the six songbird species with the lowest catch ratios (based on TTP:FLAP) from 2003-2017. Each boxplot represents the distribution of data for that species at the different sites. Each site's box represents the inter-quartile range with the median marked by a vertical line. The five lowest species (first row, bottom-left and bottom-center) show minimal differences between the mist net catch (TTP and LPBO) and the window catch (FLAP), with the difference increasing in Black-throated Blue Warblers. The species-specific site effect values are provided in Table 3.
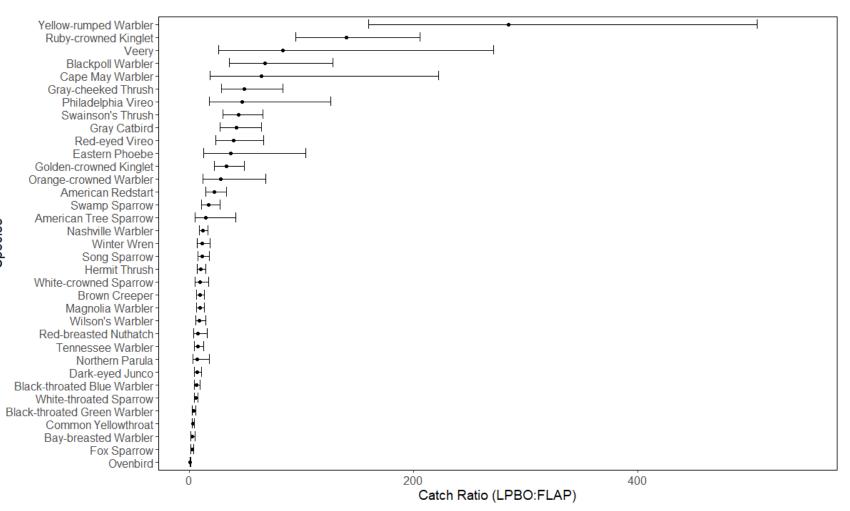
Table 3. Residual deviance due to site (X^2) for the species-specific negative binomial regressions (Catch ~ Site + offset(log(Net_Days))) with their respective degrees of freedom (df) and p-values (p). The dispersion index (DI) of each model is also included as a measure of fit.

Species	X^2	df	p	DI
Blue-headed Vireo	36.60	41	<0.005	0.9
Yellow-rumped Warbler	50.99	41	<0.005	1.2
Ruby-crowned Kinglet	47.51	41	<0.005	1.2
Eastern Phoebe	42.08	41	<0.005	1.0
Golden-crowned Kinglet	44.96	41	<0.005	1.1
Veery	41.56	41	<0.005	1.0
Gray-cheeked Thrush	49.55	41	<0.005	1.2
Philadelphia Vireo	43.70	41	<0.005	1.1
Swainson's Thrush	43.78	41	<0.005	1.1
Orange-crowned Warbler	39.31	41	<0.005	1.0
Cape May Warbler	42.34	41	<0.005	1.0
Blackpoll Warbler	44.50	41	<0.005	1.1
American Tree Sparrow	46.94	41	<0.005	1.1
Northern Parula	43.89	41	<0.005	1.1
Red-eyed Vireo	43.17	41	<0.005	1.1
Nashville Warbler	48.13	41	<0.005	1.2
Wilson's Warbler	57.29	41	<0.005	1.4
Winter Wren	45.50	41	<0.005	1.1
Hermit Thrush	45.59	41	<0.005	1.1
Swamp Sparrow	41.81	41	<0.005	1.0
American Redstart	44.61	41	<0.005	1.1
Gray Catbird	44.10	41	<0.005	1.1
Black-throated Green Warbler	58.40	41	<0.005	1.4
White-crowned Sparrow	46.22	41	<0.005	1.1
Tennessee Warbler	45.73	41	<0.005	1.1
Dark-eyed Junco	45.06	41	<0.005	1.1
Song Sparrow	47.19	41	<0.005	1.2
Brown Creeper	43.11	41	<0.005	1.1
Magnolia Warbler	47.60	41	<0.005	1.2
White-throated Sparrow	47.28	41	<0.005	1.2
Black-throated Blue Warbler	49.54	41	<0.005	1.2
Red-breasted Nuthatch	46.80	41	<0.005	1.1
Bay-breasted Warbler	47.08	41	0.026	1.1
Fox Sparrow	51.63	41	<0.005	1.3
Common Yellowthroat	47.90	41	<0.005	1.2
Ovenbird	46.44	41	0.148	1.1

3.1.2 Long Point Bird Observatory species catch ratio

Catch ratios differed among species based on the LPBO data (Figure 9). This further supports that there is differential vulnerability to colliding with windows among migratory songbird species. The six species with the highest catch ratios, and therefore the lowest vulnerability, from highest catch ratio to lowest at LPBO were: Blue-headed Vireo (LPBO Catch Ratio = 318.67, 95% CI [43.66, 2326.17]), Yellow-rumped Warbler (LPBO Catch Ratio = 284.39, 95% CI [159.91, 505.76]), Ruby-crowned Kinglet (LPBO Catch Ratio = 139.71, 95% CI [95.00, 205.46]), Veery (LPBO Catch Ratio = 83.57, 95% CI [25.77, 271.08]), Blackpoll Warbler (LPBO Catch Ratio = 67.37, 95% CI [35.56, 127.63]) and Cape May Warbler (LPBO Catch Ratio = 64.09, 95% CI [18.50, 221.99]). The six species with the lowest catch ratios, and therefore the highest vulnerability, from lowest catch ratio to highest were: Ovenbird (LPBO Catch Ratio = 0.81, 95% CI [0.58, 1.13]), Fox Sparrow (LPBO Catch Ratio = 2.31, 95% CI [1.42, 3.73]), Bay-breasted Warbler (LPBO Catch Ratio = 2.44, 95% CI [1.24, 4.81]), Common Yellowthroat (LPBO Catch Ratio = 3.27, 95% CI [2.43, 4.41]), Black-throated Green Warbler (LPBO Catch Ratio = 3.57, 95% CI [2.26, 5.65]) and White-throated Sparrow (LPBO Catch Ratio = 5.79, 95% CI [4.32, 7.77]; see Table 2 for the estimates, standard errors, z-statistics and p-values from all the species-specific models, as well as catch ratios comparing the catch at TTP and LPBO). The p-values for the pairwise comparisons of catch ratios for all species combinations are displayed in Figure 10. The rankings of the species by vulnerability were slightly different between TTP and LPBO but were strongly correlated (Spearman's rho = 0.88, p-value < 0.001; Figure 11). The three least vulnerable species and four most vulnerable species (with a slightly different order) were the same at both sites. However, when looking at each species independently, the majority of species had TTP:LPBO catch ratios significantly greater than zero (Table 3). This suggests that regional-scale abundance data is adequate for broad ranking of relative vulnerability, however local-scale abundance data is required for accuracy in catch ratio size. The clear site effect of LPBO is also shown in the boxplots of the six least vulnerable species for TTP (Figure 7) and is, again, less noticeable in the boxplots of the

six most vulnerable species for TTP (Figure 8). The effect of site from all species-specific models are recorded in Table 3.

Figure 9. Transformed catch ratios between Long Point Bird Observatory (LPBO) and the Fatal Light Awareness Program (FLAP) for 35 songbird species organized from largest to smallest catch ratio. The natural antilog-transformed catch ratios are represented by the points and the error bars are 95% confidence intervals. Catch ratios were estimated using species-specific negative binomial regressions (Catch ~ Site + offset(log(Net_Days))). A large catch ratio means that relatively more of that species was caught at LPBO than FLAP, which suggests lower vulnerability to colliding with windows than mist nets. Alternatively, a small catch ratio means that relatively more of that species was caught at FLAP than LPBO, which suggests higher vulnerability to colliding with windows than mist nets. Species whose 95% confidence intervals overlap are not significantly different from each other (p-values are provided in Figure 10). The Blue-headed Vireo catch ratio (318.67, 95% CI [43.66, 2326.17]) was removed from plot due to its extremely large error bars impeding the ability to discern the smaller catch ratios.
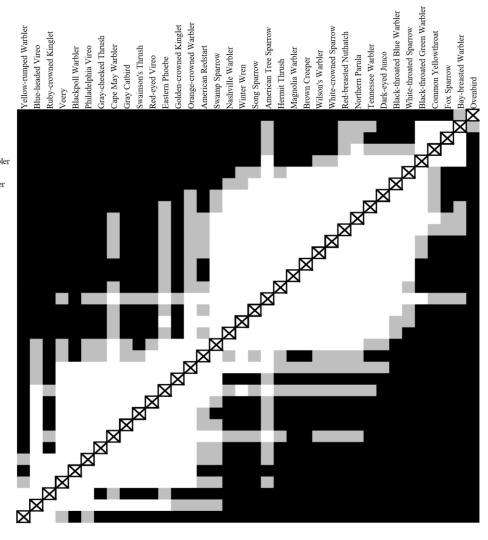
Figure 10. Matrix displaying the p-values from pairwise comparisons of the catch ratios between Long Point Bird Observatory (LPBO) and the Fatal Light Awareness Program (FLAP) for 36 songbird species. Each row in the matrix reflects one species' (labeled to the left) comparisons with each of the 36 species that are labeled across the top. Each column in the row is colour-coded based on significance level: black: p-value < 0.005, gray: p-value < 0.05 and white: p-value > 0.05. The "X" is placed in the column that corresponds to the species that the row belongs to, since a species cannot be compared against itself. Comparisons were completed using negative binomial regressions that were specific to each pairing of species (Catch ~ Site + Species + Site:Species + offset(log(Net_Days))).
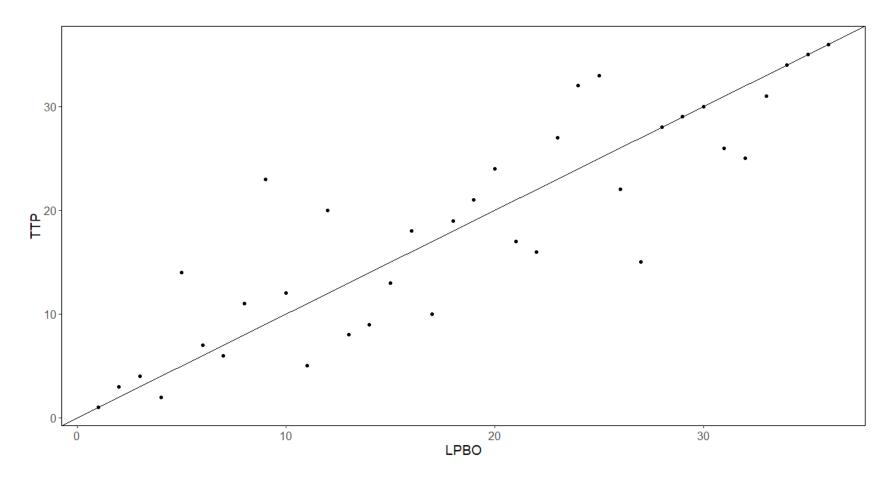
Figure 11. Correlation between the rank orders of species at TTP and LPBO for the catch analysis. The rank order of the species at TTP was significantly correlated with the rank order at LPBO (Spearman's rho = 0.88, p-value < 0.001). This suggests that regional-scale abundance data can be used for broad ranking of relative vulnerability among species.

3.1.3   Trophic guild catch ratio

There were significant differences between the catch ratios of the granivore trophic guild and the insectivore-not ground trophic guild at both TTP (Figure 12; granivore = 5.70, 95% CI [4.45, 7.31], insectivore-not ground = 12.29, 95% CI [10.73, 14.09]) and LPBO (Figure 13; granivore = 6.36, 95% CI [4.99, 8.10], insectivore-not ground = 15.46, 95% CI [13.53, 17.67]). At both sites granivores had smaller catch ratios than insectivores that do not forage on the ground, suggesting that granivores are more vulnerable to dying from window collisions than this guild of insectivores. At TTP there was a significant difference between the insectivore-ground trophic guild (6.42, 95% CI [4.91, 8.38]) and the insectivore-not ground trophic guild, suggesting that insectivores that forage at the ground level are more vulnerable to dying from window collisions than insectivores that forage above the ground level. At TTP there was not a significant difference between granivores and ground foraging insectivores, suggesting that these guilds have equal vulnerability. At LPBO there was not a significant difference between insectivore trophic guilds (insectivore-ground = 11.66, 95% CI [8.92, 15.24]), however at this site the catch ratio of ground foraging insectivores was significantly greater than the granivore catch ratio, suggesting ground foraging insectivores are less vulnerable than granivores. The estimates, standard errors, z-statistics and p-values, as well as catch ratios comparing the catch at TTP and LPBO from the trophic guild model are provided in Table 4. A small site effect can be seen between mist net catch (TTP and LPBO) and FLAP in the boxplots of these three guilds (Figure 14).

3.1.4   Validation of models

The dispersion indices for all the species-specific models ranged between 0.9 and 1.4, indicating good model fit based on the general rule that the dispersion index should be less than two. The dispersion indices for each of the species-specific models are provided in Table 3. The dispersion ratio for the trophic guild model was not significantly different from one, indicating good fit (dispersion ratio = 1.3, p-value = 0.352).
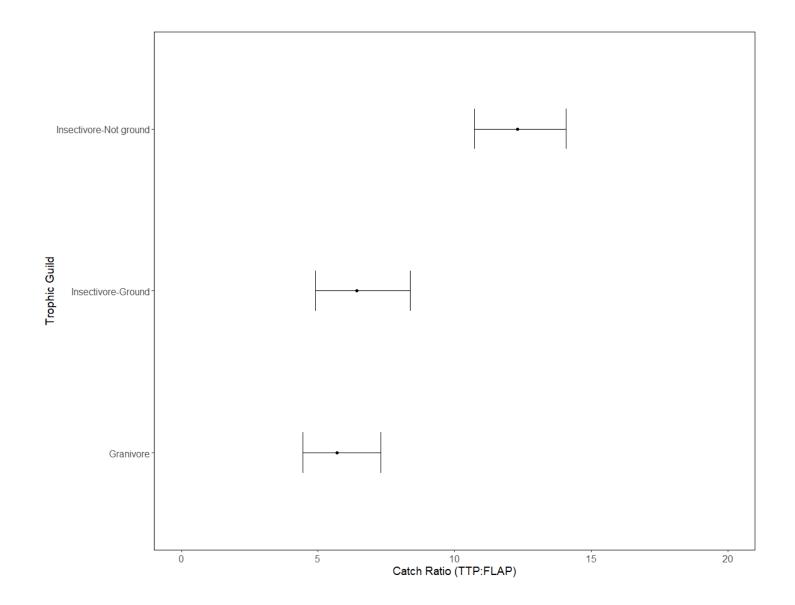
Figure 12. Transformed catch ratios between Tommy Thompson Park (TTP) and the Fatal Light Awareness Program (FLAP) for three trophic guilds (granivore, insectivore-not ground and insectivore-ground) organized from largest to smallest catch ratio. The natural antilog-transformed catch ratios are represented by the points and the error bars are 95% confidence intervals. Catch ratios were estimated using a negative binomial mixed-effects model (Catch ~ Trophic_Guild + Site + Trophic_Guild:Site + (1|Species) + offset(log(Net_Days))). A large catch ratio means that relatively more of that trophic guild was caught at TTP than FLAP, which suggests lower vulnerability to colliding with windows than mist nets. Alternatively, a small catch ratio means that relatively more of that trophic guild was caught at FLAP than TTP, which suggests higher vulnerability to colliding with windows than mist nets. The 95% confidence intervals of the two insectivore guilds are distinct, indicating that they are significantly different. This suggests that foraging height influences vulnerability, with ground foragers being more vulnerable. Diet is partially supported as an influence of vulnerability with granivorous species being more vulnerable than insectivorous species that do not forage on the ground, as the granivorous guild's 95% CI does not overlap with the insectivorous–not ground guild. However, granivorous species were not significantly different from ground foraging insectivores, as these two guilds had overlapping 95% CIs.
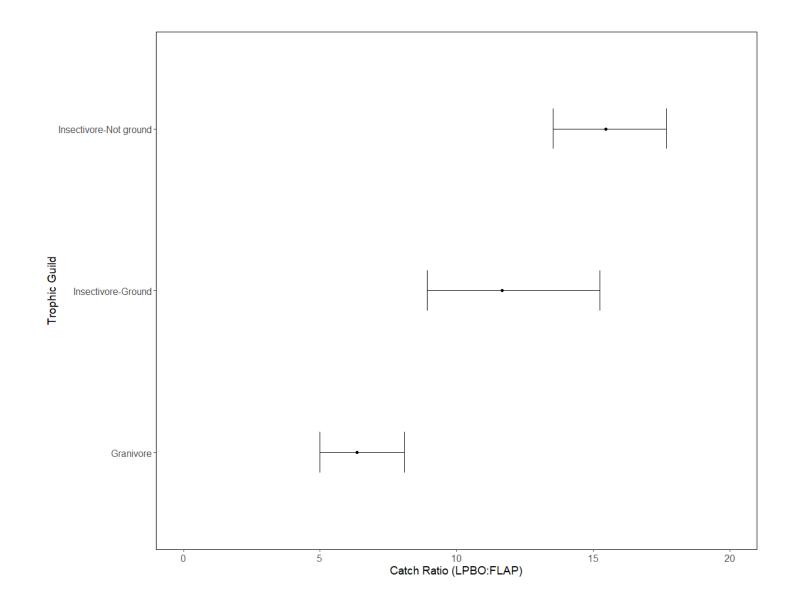
Figure 13. Transformed catch ratios between Long Point Bird Observatory (LPBO) and the Fatal Light Awareness Program (FLAP) for three trophic guilds (granivore, insectivore-not ground and insectivore-ground) organized from largest to smallest catch ratio. The natural antilog-transformed catch ratios are represented by the points and the error bars are 95% confidence intervals. Catch ratios were estimated using a negative binomial mixed-effects model (Catch ~ Trophic_Guild + Site + Trophic_Guild:Site + (1|Species) + offset(log(Net_Days))). A large catch ratio means that relatively more of that trophic guild was caught at LPBO than FLAP, which suggests lower vulnerability to colliding with windows than mist nets. Alternatively, a small catch ratio means that relatively more of that trophic guild was caught at FLAP than LPBO, which suggests higher vulnerability to colliding with windows than mist nets. The 95% confidence intervals of the two insectivore guilds overlap, indicating that they are not significantly different. This suggests that foraging height does not influence vulnerability. Diet is supported as an influence of vulnerability with granivorous species being more vulnerable than insectivorous species, as the granivorous guild's 95% CI does not overlap with either insectivorous guild.

Table 4. Estimated coefficients (*β*) for each site (FLAP: Fatal Light Awareness Program, TTP: Tommy Thompson Park, LPBO: Long Point Bird Observatory) with respective standard errors (SE), z-values (*z*) and p-values (*p*) from the trophic guild negative binomial mixed-effects model (Catch ~ Trophic_Guild + Site + Trophic_Guild:Site + (1|Species) + offset(log(Net_Days))). Trophic guilds are sorted by decreasing catch ratio according to the TTP estimates. The catch ratios comparing TTP and LPBO (TTP:LPBO) are provided for each trophic guild. Asterisks indicate significant differences (*p* < 0.05) between the catch at TTP and LPBO.

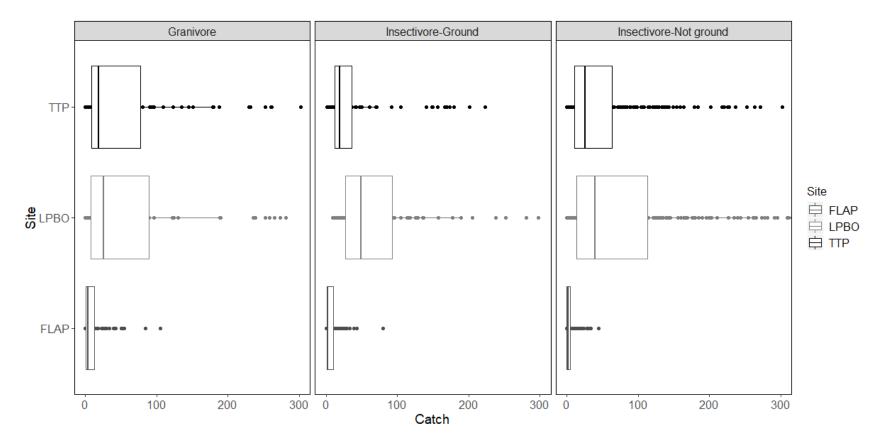| Trophic Guild	FLAP				TTP				LPBO				TTP:LPBO
	β	SE	*z*	*p*	*β*	SE	*z*	*p*	*β*	SE	*z*	*p*	
Granivore	-1.57	0.40	-3.95	<0.005	1.74	0.13	13.7	<0.005	1.85	0.12	15.0	<0.005	0.11
Insectivore-not ground	-0.88	0.44	-1.99	0.05	0.77	0.14	5.32	<0.005	0.89	0.14	6.30	<0.005	0.12
Insectivore-ground	-0.41	0.56	-0.72	0.47	0.12	0.19	0.63	0.53	0.61	0.18	3.29	<0.005	0.49*

Figure 14. Catch at Tommy Thompson Park (TTP), Long Point Bird Observatory (LPBO) and the Fatal Light Awareness Program (FLAP) for three trophic guilds from 2003-2017. Each boxplot represents the distribution of data for that trophic guild at the different sites. Each site's box represents the inter-quartile range with the median marked by a vertical line. Site effects are seen between the mist net catch (TTP and LPBO) and the window catch (FLAP). Larger outliers were excluded from the plots to allow a better comparison of the distributions.

3.2   Age analysis

3.2.1   The odds of catching a hatch year bird

The change in the odds of catching a hatch year (HY) bird from FLAP to TTP was significant for five of the seven species included in the analysis (Figure 15). Nashville Warbler (Δ odds = 0.42, 95% CI [0.22, 0.80]), Golden-crowned Kinglet (Δ odds = 0.33, 95% CI [0.21, 0.53]), Ovenbird (Δ odds = 0.21, 95% CI [0.06, 0.76]), Dark-eyed Junco (Δ odds = 0.18, 95% CI [0.04, 0.79]) and Swainson's Thrush (Δ odds = 0.07, 95% CI [0.02, 0.25]) all had significantly lower odds (Δ odds < 1) of catching a HY bird at TTP compared to FLAP suggesting that for these species HY birds are more vulnerable to dying from window collisions than after-hatch year (AHY) birds. The change in odds of catching a HY from FLAP to LPBO was inconsistent with the results based on TTP. Only three of the seven species were significantly different from FLAP at LPBO (Figure 16). White-throated Sparrow (Δ odds = 2.21, 95% CI [1.05, 4.63]) and Golden-crowned Kinglet (Δ odds = 1.92, 95% CI [1.20, 3.09]) had significantly higher odds (Δ odds > 1) of catching a HY bird at LPBO compared to FLAP suggesting that for these species HY birds are less vulnerable to dying from window collisions than AHY birds. Swainson's Thrush (Δ odds = 0.25, 95% CI [0.08, 0.81]) had significantly lower odds (Δ odds < 1) of catching a HY bird at LPBO compared to FLAP suggesting that for this species HY birds are more vulnerable to dying from window collisions than AHY birds. The rankings of the species by the odds of catching a HY bird were not significantly correlated between TTP and LPBO (Spearman's rho = 0.71, p-value = 0.09; Figure 17) and the majority of species had TTP:LPBO catch ratios significantly greater than zero (Table 5). This could explain the inconsistencies between the two sites. The estimates, standard errors, z-statistics and p-values, as well as catch ratios comparing the catch at TTP and LPBO from all the species-specific models are provided in Table 5. A clear site effect can be seen in Figure 18 with TTP's AHY proportions being distinctly greater than FLAP's for the majority of species in both years. LPBO's AHY proportions compared to FLAP's have a less clear and consistent pattern across species and years, which is reflective of the majority of species not being significantly different from FLAP, and the variable

direction of the significant effects. The dispersion ratios for all the species-specific models ranged between 0.98 and 1.02 and were not significantly different from one, indicating good model fit (all p-values > 0.05). The dispersion ratios and associated p-values for each species-specific model are provided in Table 5.
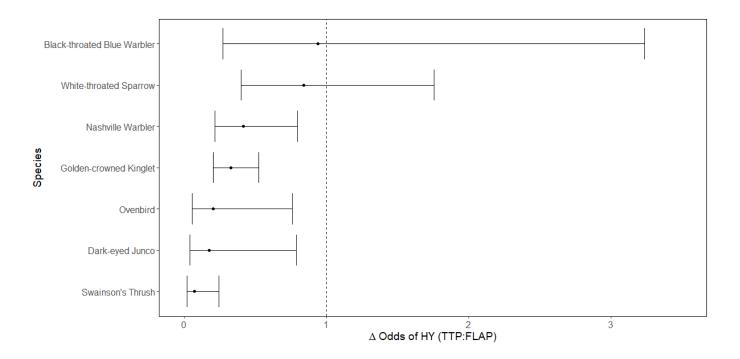
Figure 15. Comparison of the Tommy Thompson Park (TTP) to the Fatal Light Awareness Program (FLAP) changes in odds of catching hatch year (HY) birds for the seven aged songbird species. Estimated changes in odds are represented by the points and the error bars are 95% confidence intervals. Log odds ratios were estimated using species-specific logistic mixed-effects models (Age ~ Site + (1|Year)). The vertical dashed line represents the null hypothesis where the HY log odds at TTP is equal to the HY log odds at FLAP, and therefore the change in log odds is equal to zero. Species with 95% confidence intervals that do not cross the vertical line have significantly different odds at TTP and FLAP. Species to the left of the dashed line have lower odds of catching a HY bird at TTP than at FLAP. This means that the proportion of HY birds caught at FLAP is greater than at TTP. This suggests that in these species HY birds have higher vulnerability to window collisions than after-hatch year birds.
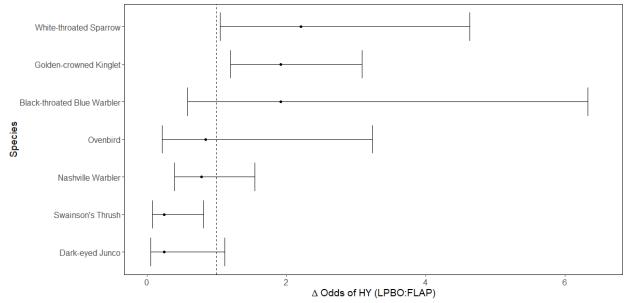
Figure 16. Comparison of the Long Point Bird Observatory (LPBO) to the Fatal Light Awareness Program (FLAP) changes in odds of catching hatch year (HY) birds for the seven aged songbird species. Estimated changes in odds are represented by the points and the error bars are 95% confidence intervals. Log odds ratios were estimated using species-specific logistic mixed-effects models (Age ~ Site + (1|Year)). The vertical dashed line represents the null hypothesis where the HY log odds ratios at LPBO and FLAP are equal, and therefore the change in log odds ratios is zero. Species with 95% confidence intervals that do not cross the vertical line have significantly different odds at LPBO and FLAP. Species to the left of the dashed line have lower odds of catching a HY bird at LPBO than at FLAP. This means that the proportion of HY birds caught at FLAP is greater than at LPBO, suggesting that in these species HY birds have higher vulnerability to window collisions than after-hatch year (AHY) birds. Species to the right of the dashed line have higher odds of catching a HY bird at LPBO than at FLAP, meaning that the proportion of HY birds caught at FLAP is less than at LPBO. This suggests that in these species HY birds have lower vulnerability to window collisions than AHY birds.
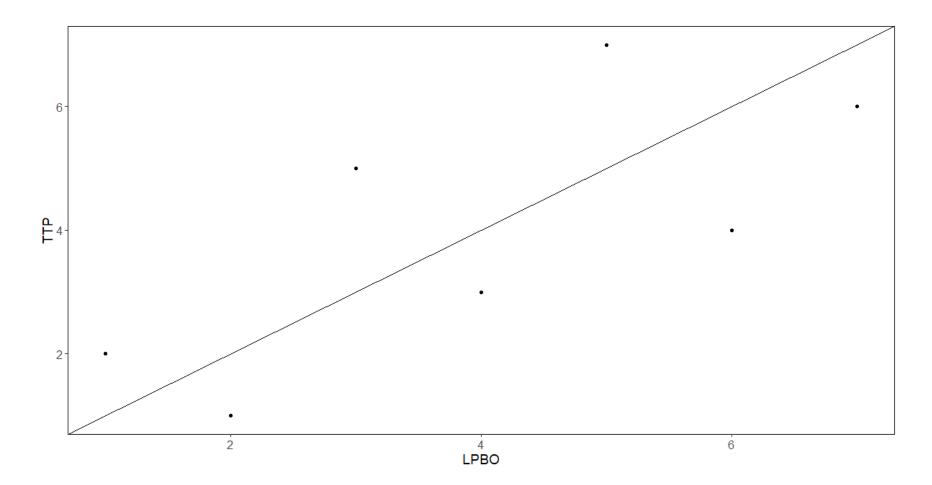
Figure 17. Correlation between the rank orders of species at TTP and LPBO for the age analysis. The rank order of the species at TTP was not significantly correlated with the rank order at LPBO (Spearman's rho = 0.71, p-value = 0.09). This suggests that regional-scale abundance data should not be used when analyzing relative vulnerability between age classes.

Table 5. Estimated coefficients (*β*) for each site (FLAP: Fatal Light Awareness Program, TTP: Tommy Thompson Park, LPBO: Long Point Bird Observatory) with respective standard errors (SE), z-values (*z*) and p-values (*p*) from each species-specific logistic mixed-effects model (Age ~ Site + (1|Year)). Dispersion ratio (DR) and its associated p-value are also provided for each model as a measure of fit. Species are sorted by decreasing Δ odds according to the TTP estimates. The catch ratios comparing TTP and LPBO (TTP:LPBO) are provided for each species. Asterisks indicate significant differences (*p* < 0.05) between the catch at TTP and LPBO.

| Species	FLAP				TTP				LPBO						
	β	SE	*z*	*p*	*β*	SE	*z*	*p*	*β*	SE	*z*	*p*	DR	*p*	TTP:LPBO
Black-throated Blue Warbler	1.25	0.69	1.82	0.07	-0.06	0.63	-0.09	0.93	0.65	0.61	1.07	0.28	0.98	0.86	0.71
White-throated Sparrow	2.00	0.34	5.94	<0.005	-0.17	0.38	-0.46	0.64	0.79	0.38	2.09	0.04	1.00	0.93	0.97*
Nashville Warbler	1.49	0.28	5.38	<0.005	-0.88	0.33	-2.64	0.01	-0.25	0.35	-0.71	0.48	1.00	0.98	0.63*
Golden-crowned Kinglet	0.99	0.36	2.77	0.01	-1.11	0.24	-4.64	<0.005	0.65	0.24	2.70	0.01	0.98	0.68	1.76*
Ovenbird	2.05	0.53	3.85	<0.005	-1.58	0.67	-2.37	0.02	-0.18	0.69	-0.26	0.80	1.02	0.89	1.40*
Dark-eyed Junco	3.07	0.72	4.24	<0.005	-1.72	0.76	-2.27	0.02	-1.40	0.77	-1.82	0.07	1.01	0.94	0.32
Swainson's Thrush	2.96	0.59	5.00	<0.005	-2.59	0.61	-4.28	<0.005	-1.39	0.61	-2.30	0.02	1.00	0.91	1.20*
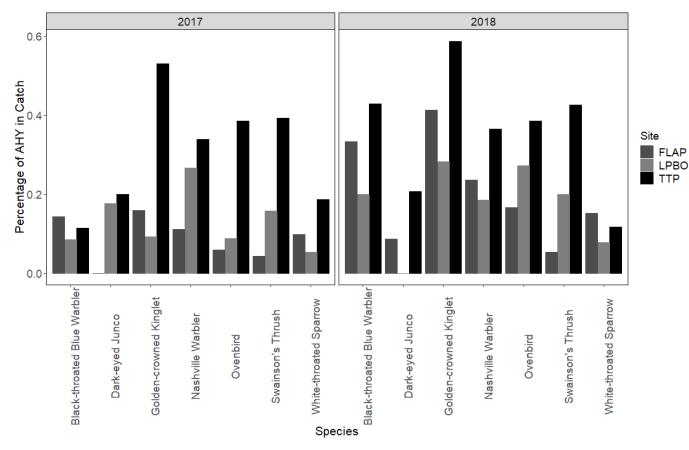
Figure 18. After-hatch year (AHY) proportion of species-specific catch at Tommy Thompson Park (TTP; black), Long Point Bird Observatory (LPBO; light gray) and the Fatal Light Awareness Program (FLAP; dark gray) for the seven aged songbird species from 2017 and 2018. A distinct site effect is seen in the majority of species for both years. TTP clearly shows a greater proportion of AHY in these species' catches, and therefore a lower proportion of hatch years in the catches, compared to FLAP. The effect of LPBO is less clear and consistent across species and years compared to FLAP.

Discussion

Bird-window collisions are a serious concern in cities and residential areas. As such it is important to determine factors that influence the vulnerability to dying from window collisions. We can then prioritize high-risk species and direct preventive measures and research to these species. A new approach to studying differential vulnerability to window collisions in birds that accounts for local abundance of species has been initiated by a handful of researchers (Nichols et al. 2018, Wittig et al. 2017, Kahle et al. 2016, Sabo et al. 2016, Aymí et al. 2017, Winger et al. 2019). These researchers have found evidence supporting differential vulnerability to window collisions across bird species, as well as various groupings of species (e.g., feeding guilds). I provide further support of differential vulnerability among and within bird species using long-term migratory songbird window collision and local abundance data from Southern Ontario. More specifically, I found that (1) there is differential vulnerability among migratory songbird species, (2) that trophic guild contributes to window collision mortality vulnerability and (3) age may contribute to window collision mortality vulnerability, but effects appear to be species-specific.

4.1 Key Findings

4.1.1 Differential vulnerability among migratory songbird species

My results suggest that there is differential vulnerability to window collision mortality present among migratory songbird species. Catch ratios significantly varied across the 36 species studied, suggesting that the species did not collide proportionally to their local abundances estimated by mist net surveys. This finding corroborates previous studies that found differential vulnerability among species after accounting for local abundance (Wittig et al. 2017, Nichols et al. 2018, Winger et al. 2019, Kahle et al. 2016, Sabo et al. 2016, Aymí et al. 2017). I did not test for a taxonomic family effect, however based on the rankings of warblers it is likely that my results agree with what Nichols et al. (2018) observed with Parulidae being more variable than any other family they investigated. Individuals of this family are seen in the most (e.g., Ovenbird) and least vulnerable (e.g.,

Yellow-rumped Warbler) ranks as well as throughout the mid-ranks (e.g., Wilson's Warbler).

Ovenbirds have previously been reported as highly vulnerable to window collisions by researchers (Winger et al. 2019, Nichols et al. 2018, Wittig et al. 2017). I also found this species to have the highest vulnerability. Common Yellowthroats were another species that I found highly vulnerable which supports the findings reported by Nichols et al. (2018) and Winger et al. (2019). Additionally, there were several parallels between my results and the results from Winger et al. (2019). For example, White-throated Sparrows, Fox Sparrows and Brown Creepers were vulnerable in both studies, and Kinglets were less vulnerable in both studies. There were also conflicting results for some species, such as Swainson's Thrush, which I found to be less vulnerable and they found to be more vulnerable, and Black-throated Blue Warbler, which they found to collide as expected and I found to be a species with high vulnerability. The varying results between our studies could stem from Winger et al. (2019) using spring and fall data, whereas I only used fall. Perhaps some species have consistent vulnerability in spring and fall, while others vary depending on the season. Like Nichols et al. (2018) and Winger et al. (2019), I found that Vireos had relatively lower vulnerability, which disagrees with the findings reported by Wittig et al. (2017) who found that Red-eyed Vireos collided more than expected. The results of my study further agree with Winger et al.'s (2019) results that suggest Yellow-rumped Warblers have low vulnerability to window collisions. This opposes the results of Sabo et al. (2016) that suggest Yellow-rumped Warblers have high vulnerability, as well as the results of Kahle et al. (2016) who reported Yellow-rumped Warblers collided as expected based on local abundance. Inconsistencies that arise when comparing the estimates of relative vulnerability for a species from different studies are perhaps due to differences in the locales' building, window and landscape characteristics, all of which have been reported as factors affecting window collisions (Borden et al. 2010, Hager et al. 2013, Cusa et al. 2015, Kahle et al. 2016, Hager et al. 2017). The similarities that are observed among studies, despite site differences, suggest that certain species-specific window collision vulnerabilities are strong enough to be conserved across locations (e.g., high vulnerability in Ovenbirds is observed in Toronto, Ontario, Minneapolis, Minnesota (Nichols et al. 2018), Chicago, Illinois (Winger et al. 2019) and

the Raleigh-Durham-Chapel Hill area, North Carolina (Wittig et al. 2017)). The similarities between the rankings at my two study sites supports that some vulnerability trends are also strong enough to be observed at different scales (i.e., local versus regional).

Many behavioural and physiological differences among species might contribute to the differences that are observed in species' vulnerabilities to colliding with windows. I investigated trophic guild (i.e. diet and foraging height), as a partial explanation for the differential vulnerability among species, however there are many other potential sources of variation that are described in the literature. For example, one common behavioural trait that differential vulnerability is attributed to is migratory status. Nichols et al. (2018) proposed two aspects of nocturnal migration that could increase this group's window collision risk. First, cognitive (e.g. reaction time) and physical deficits during descent at stopover sites could alter normal functions, increasing the propensity for collision. Second, altered stopover site choice due to low lighting during descent in combination with phototaxis to artificial light of lit buildings could increase window exposure and therefore collision risk (Nichols et al. 2018). The majority of the species I used in my study are considered nocturnal migrants, thus this is likely a minor, if present, source of variation across species in my study. Flocking behaviour is another trait that varies species to species and has been considered as a factor with mixed results. There are two main schools of thought when it comes to flocking and window collisions. The first is that flocking reduces window collisions because the group collectively has higher window detection rates as a result of predator vigilance being divided (Kahle et al. 2016). Alternatively, it has been suggested that flocking could increase window collision risk as more conspecifics are drawn to dangerous, high-risk areas increasing local density which has been shown to increase window collision risk (Winger et al. 2019, Sabo et al. 2016). My results show support for both schools of thought, as I found some species that display flocking behaviour to have high vulnerability, while other flocking species have low vulnerability, suggesting that the influence of flocking is complex. For instance, Blue-headed Vireos (low vulnerability) and Bay-breasted Warblers (high vulnerability) are two species that have been observed joining mixed-species flocks during fall migration. Habitat preference (open area vs forested area) is also believed to impact window

collision risk (Winger et al. 2019, Wittig et al. 2017). Physiological features of the eye such as lateral eye placement, fovea area of the retina and visual range have also been proposed as potential factors in power line collision susceptibility which can readily be applied to window collision susceptibility (Bernardino et al. 2018, Martin 2011, Martin 2012, Sillman 1973, Ödeen et al. 2011). Varying maneuverability across species as a result of differences in wing and tail morphology has also been proposed as a contributor to collisions. For example, species that are heavy with small wings (high wing loading with low wing aspect ratio) have been observed as frequent power line collision victims (Rayner 1988, Bernardino et al. 2018). Tail length is also a factor in maneuverability as it has been reported to help with balance, stability and flight control (Hedenström 2002). It is possible that the difference between birds that avoid windows, birds that collide as expected, and birds that collide with windows more than expected could be their ability to escape collision via efficient maneuvering that is defined by their wings and tails. I did not have the necessary data to discover patterns related to these factors in my relative vulnerability rankings. However, further research of habitat preference, eye physiology and maneuverability in a variety of species that show differences in their vulnerabilities could elucidate additional patterns in differential vulnerability among species and improve our understanding of this issue. Overall body size has also been reported in the literature as influencing vulnerability, with smaller-bodied species being more prone to dying from window collisions than larger-bodied species (Kahle et al. 2016). Based on average body sizes reported in the Birds of North America species accounts (https://birdsna.org/Species-Account/bna/species), my results do not appear to support body size having a strong influence on vulnerability, as large and small-bodied species are observed scattered throughout the relative vulnerability ranking at both sites.

There were some deviations in the relative rankings of the 36 species between the two sites (TTP and LPBO), however the most vulnerable and least vulnerable species were consistent at both sites. The species whose ranks varied between the sites were not significantly different from each other, which could explain the discrepancies in ranks from site to site. Perhaps they have equal vulnerability and therefore the exact ordering is irrelevant. While the relative ranking indicates the priority species, it does not show the threshold where the catch ratio should become a matter for greater priority. Further

research is needed using a similar framework to Arnold and Zink (2011) that correlates relative collision vulnerability to annual rate of population change but using a local scale to estimate the impact of window collision mortality on local populations. This research could also provide evidence supporting the classification of urban centers as ecological traps for migratory birds if the impact is significant.

4.1.2   Differential vulnerability among trophic guilds

Trophic guild has previously been reported as a contributing factor of vulnerability (Wittig et al. 2017). My results corroborate that trophic guild influences vulnerability. However, I observed that granivores were at higher risk than insectivores that forage above the ground, which is opposite of previous findings where insectivores were reported as the more vulnerable guild (Wittig et al. 2017). According to the local TTP data, my results suggest that foraging height is a more important factor of vulnerability than diet, as ground foraging insectivores and granivores, which also forage on the ground, were not significantly different, but were both significantly more vulnerable than insectivores foraging above the ground. However, this finding was not supported at LPBO, where my results suggest that diet has greater influence on vulnerability than height, as both insectivore guilds were significantly less vulnerable than the granivore guild, but not significantly different from each other. Differences between the results of the sites, as well as the differences between my study and Wittig et al.'s (2017), could be due to site differences, which suggests that local data is more appropriate for trophic guild analyses, rather than regional data, as proportions may fluctuate across locations. This conclusion is further supported by the catch ratios comparing TTP and LPBO presented in Table 4. The catches for the granivore and insectivore-not ground trophic guilds are not significantly different between TTP and LPBO, and the results for these guilds are consistent. However, the catch for the insectivore-ground trophic guild is significantly between the banding sites, and the results for this guild are inconsistent.

Focusing on the local results from TTP, it appears that ground foragers, despite diet preferences, are more vulnerable. It has previously been suggested that differential vulnerability across trophic guilds is likely attributed to the differences in movement between guilds (Wittig et al. 2017, Aymí et al. 2017). Insectivores typically move in

darting fashions, quickly flying amongst branches, meanwhile granivores generally hop or make short flights between locations (Aymí et al. 2017, Wittig et al. 2017). A similar observation was made by Kahle et al. (2016) who reported that hummingbirds had the highest collision frequency of any other species and this could be connected to their trap-lining flight behaviour. My results do not support these conclusions, as I found granivores to be more vulnerable. Instead of differences in foraging behaviour, perhaps this increased vulnerability in granivores is a result of the greater availability of ground foraging habitat in Toronto than above ground foraging habitat as a result of less vegetation being present. This could potentially increase the density of ground foragers in downtown Toronto, which has been shown to increase vulnerability (Nichols et al. 2018). Thus, differences in the amount of vegetation in the survey areas between my study and previous studies could explain why our results are conflicting. Further differences were observed between my results and those of Wittig et al.'s (2017) regarding the influence of foraging height. I found evidence of ground foragers being more vulnerable, whereas Wittig et al. (2017) reported lower canopy foragers as more vulnerable. It is possible that these differences are due to site differences (e.g. amount of vegetation present) as well as small sample sizes in my study. Since samples for the various heights were limited, different heights were combined into two categories. Perhaps combining the various heights into the broad categories of ground and not ground masked the true effect of foraging height.

4.1.3 Differential vulnerability among age classes

My results were not consistent across sites when it came to an effect of age. It was clear at both sites that the age effect was dependent on the species, however significance and effect direction varied site to site. At TTP, all age effects were either insignificant or less than one (i.e., HY birds are more vulnerable), meanwhile, at LPBO some species had effects that were estimated to be greater than one (i.e., HY birds are less vulnerable). These variable effects of age that are dependent on the species could explain why there is such controversy in the literature regarding the presence of differential vulnerability between age classes. Sabo et al. (2016) investigated the effect of age using 11 different species and found no effect, while Kahle et al. (2016) investigated the effect of age using

37 species and found evidence of an effect. Both studies pooled species together and compared the number of HY to the number of AHY of the entire bird population, which could be the reason these results are at odds. My results suggest that species differ in the effect of age on window collision vulnerability. If this is true then by pooling all species together to investigate age, as these two studies have done, could produce very different results depending on which species are used and their age effect's strength and direction. It is possible that how age class affects window collision vulnerability varies species to species and as a result cannot simply be stated as a general rule, for or against, for all species. Rather, it needs to be investigated separately for each species.

High HY vulnerability is generally attributed to inexperience (Bernardino et al. 2018, Aymí et al. 2017, Kahle et al. 2016, Hager et al. 2013). Behavioural differences in stopover duration as well as differences in migration routes between age classes could also influence vulnerability across age classes. Increased stopover duration for HY birds could increase their exposure to windows which ultimately increases their vulnerability. Increased stopover length has been observed in some studies (Yong et al. 1998, Rguibi-Idrissi et al. 2003, Mackenzie 2010, Dossman et al. 2016, Morbey et al. 2018), but has also been absent in others (Morris et al. 1996, Morris & Glasgow 2001, Morris et al. 2003, Mackenzie 2010, McKinnon et al. 2014). It is likely that the difference in stopover duration between age classes is species-specific which could explain why certain species showed an age effect while others collided proportionally. It is also possible that some HY birds of certain species circumnavigate Lake Ontario and Lake Erie during fall migration. If HY birds are travelling along the coast of Lake Ontario and Lake Erie this could impact the catch at TTP and LPBO. It is possible that by flying around the lake, rather than across it, a portion of the HY birds migrating through Toronto never reaches TTP because this portion stops over further down the coast. This could inflate the perceived vulnerability of species that travel through Toronto and are colliding with windows, but then are caught at TTP in low numbers because they stop over elsewhere. Perhaps, TTP is the stopover site of birds preparing to cross the lake rather than go around it, which skews the data for the species that display this migration tactic.

Other behavioural factors could also result in greater vulnerability for HY birds, such as flying behind parents or at the back of flocks. This following behaviour could mean that HY birds have less time to react to obstacles, increasing collision events (Bernardino et al. 2018). There may also be physiological differences between age classes that affect window collision risk in HY birds, such as incomplete cranial pneumatization, decreased maneuverability and slower reaction time (Bernardino et al. 2018). If decreased maneuverability is paired with the following behaviour in certain species, then collision risk could be amplified in these species. Differences in the number of contributing factors that are present in species could explain why an age effect was observed in some species but not others.

There were differences in my age analysis results between TTP and LPBO. One possible explanation for this is that the city attracts and traps HY birds and acts as a filter that changes the age demographic of the population before the birds arrive at TTP. In the future, it would be interesting to measure the population's age demographic before an urban center and after to see if the population's structure is in fact changing as it moves through the city. Alternatively, these differences could be the result of the assumption that LPBO and TTP sample from the same population not being met. If this is the case, then there may be proportional differences between the two sites that cause the discrepancies seen in my results.

4.2   Assumptions and limitations

Several assumptions were made in the development of the conceptual model (Section 2.3.1). Unfortunately, it is unlikely that many of these assumptions are met, however they are necessary for the analysis given the available data. First, I assumed that the probability of stopping over at one of the programs (P_1) is constant over years and species. This assumption is arguably met as all 36 species stopped over in Toronto and Long Point during fall migration each year. The next assumption I made in the model was that the capture efficiencies for LPBO and TTP (P_t) are constant over years and species. It is very unlikely that this assumption is true, however there is insufficient data to estimate variable capture efficiencies. Thus, this assumption is necessary to complete the analysis. Constant window kill rate for FLAP (ϕ) over the years was also assumed in

the conceptual model. This assumption is reasonably met, however minor fluctuations may be seen year to year due to new building developments or newly implemented window collision deterrents. Constant detection rate for FLAP (ρ) over years and species was assumed, however it is probable that this is wrong for two reasons: differences in species size and colouration, and variable search effort depending on a carcass detection. It is indisputable that some species are easier to detect in carcass surveys than others. Larger-bodied individuals and brightly coloured individuals will both be more readily detected than smaller-bodied or dull coloured individuals. Furthermore, detection rate is likely affected by what the volunteer completing the carcass survey expects. For example, if it is common to find multiple individuals at the same site, then once one carcass is found, the volunteer may increase search effort knowing they are likely to find more. Likewise, if it is uncommon to find additional individuals at the same site, then once one carcass is found, the volunteer may reduce search effort and possibly move onto the next site. All probabilities in this model were assumed to conform to binomial distributions which assume independent trials. Independence among trials may not be achieved due to flocking and/or communication among individuals, via recruitment or alert calls, that encourages or discourages the trapping of following individuals. While many of these assumptions are not met, they are necessary as a replacement for the unavailable data that would be required to make estimates for these variables. In addition to replacing the unavailable data, these assumptions are also needed to make window kill rate (ϕ) the only source of variation contributing to species differences. Without these assumptions, there are too many sources of variation to make reliable conclusions specific to differential vulnerability to window collision mortality.

Beyond these model assumptions, I also assumed that FLAP's subset was representative of the window collisions in downtown Toronto. However, it is possible that this assumption was not met as there is generally volunteer biases introduced during collection in these types of citizen science programs. A common bias is volunteers targeting areas with high mortality more than areas with low or none (Johnston et al. 2019). In order to meet this assumption, I narrowed my survey extent to one area of Toronto that seemed to be evenly surveyed, however even within this area it is probable that some areas received more survey effort than others. Although, this likely has little

impact on my conclusions due to the size and general uniformity of the survey extent used. It is also possible that the window collision counts were underestimated due to the lack of parallel scavenging surveys conducted alongside the carcass survey. Some studies have estimated that anywhere from 13-65% of carcasses could be removed by scavengers (Klem et al. 2004, Kahle et al. 2016, Hager et al. 2012). Nevertheless, Hager et al. (2012) reported that scavenger activity was highest at buildings with little pavement and high canopy cover, while scavenger activity was lowest at buildings with larger areas of pavement and little canopy cover. Thus, if this description of scavenger activity is accurate in downtown Toronto where there is mostly pavement and little canopy cover, then it is possible that scavenging has a minimal effect on FLAP's carcass surveys and therefore minimal effect on my conclusions.

I further assumed that both TTP and LPBO mist net surveys provided accurate indices of the local abundances of the 36 species studied. However, there could be underestimation in the local abundance count data for certain species due to mist net biases. While mist net surveys offer an excellent method for estimating local abundance and also provide an opportunity to age and sex birds in the hand, which allows estimations of population demographics that would otherwise be impossible to accomplish, they are limited to the lower canopy region. Thus, upper canopy species are likely to be underrepresented in the surveys. It is also possible that trapped birds influence the survey results by drawing individuals into the area via recruitment calls. Alternatively, they could also alert conspecifics of the mist net via alarm calls, movement or simply their presence in the net.

These potential biases in the mist net surveys limited my study as I was unable to distinguish between high vulnerability to window collision mortality and low vulnerability to being caught by a mist net. Each estimated catch ratio had two components: (1) window catch and (2) mist net catch, and I assumed that the mist net catch was reflective of local abundance and therefore interpreted low catch ratios as high vulnerability to window collision mortality. However, low catch ratios could be the result of relatively low mist net vulnerability rather than high window collision mortality vulnerability.

4.3   Future directions

4.3.1   Future research

While there is some controversy regarding the causes of differential window collision vulnerability, the conclusion that window collision vulnerability is a complex phenomenon with complex interactions among a variety of physiological and behavioural traits is fairly unanimous. As such, future studies should aim to make more comprehensive models that include a variety of traits to account for the various complex combinations of factors that could be additively contributing to a single species' vulnerability. Some of the factors that should be considered when developing future models are body size, maneuverability, eye placement, visual range, flocking behaviour, migratory status, migratory distance, aggressiveness, bone fragility, minimum flight speed, foraging height, diet and all the resulting interactions. Furthermore, by focusing on previously reported high-risk and low-risk species in future comparative studies, it may be possible to pinpoint why certain species are colliding more than others and what features are associated with this increased window collision risk. As previous studies have observed high percentages (13-65%) of carcass removal by scavengers that vary by location and time of year, future studies should also use parallel scavenging data to ensure that carcass survey results can be corrected to accurate detection rates (Klem et al. 2004, Kahle et al. 2016, Hager et al. 2012). Additionally, future studies should use local abundance data, rather than regional abundance data, when possible to maximize the accuracy of estimated vulnerabilities. As seen in my results, regional abundance data is not always an accurate representation of local abundance.

It is evident that there are certain species being affected by this aspect of urbanization more than others. Future research should utilize this rapidly growing collection of results to develop effective innovations and solutions that cater to the reported high-risk species in order to minimize bird-window collisions. There are many preventive measures being produced, however the effectiveness of these deterrents is still in question. Further research to determine which deterrents are effective is needed, but testing the effectiveness of these products directly can be unethical. Therefore, future work should

monitor building collisions before and after window treatments are implemented to determine the effectiveness of these products (e.g., Kahle et al. 2016).

4.3.2   Citizen science recommendations

Based on my experience working with citizen science datasets in this thesis, I have three recommendations for citizen science programs to consider regarding record keeping and unbiased surveying. The range of questions that citizen science datasets could be successfully applied to could be vastly increased by recording GPS coordinates. This not only improves location accuracy but also data cleanliness. By recording location as GPS coordinates the data are in an easily usable format and there is less opportunity for submission errors (i.e., typographical errors) and inconsistent formatting that need to be addressed before the data can be utilized. The record keeping of effort is also an important aspect of the data collection that should receive more consideration where possible. Effort data is essential for the standardization of count data that allows comparisons to be made across sites and time. Without recorded survey effort it is difficult to accurately extrapolate beyond the original dataset. Citizen science programs could also minimize survey bias by expanding survey routes beyond known hotspots and ensuring that sites with fewer or no collisions are regularly included in sampling and records. If survey protocols are amended to include this change, it is important that program coordinators inform and educate volunteers on the importance of recording zeroes in their surveys.

Improving the rigidity of citizen science programs can be difficult. It can be easy to discourage and bore citizen scientists who may simply be looking to casually participate in a program that has minimal protocol and requires little detail during their data collection. Some citizen scientists will also be less informed on the importance of their work, and perhaps be more inclined to cut corners without realizing the overall effect of this (Dickinson et al. 2010). To avoid these situations communication and encouragement are of utmost importance to ensure strong understanding of the importance of their contributions and to ensure a reliable level of dedication. There is a trade-off between participation and quality of data that results in a delicate balancing act performed by citizen science program coordinators who have varying levels of scientific

training (Johnston et al. 2019, Dickinson et al. 2010). Loss et al. (2015) suggest that the best way to ensure high quality data with high participation and enthusiasm is collaboration between professional scientists and citizen science program coordinators to find the best way to implement the most effective and useful sampling techniques for citizen science programs on a case by case basis.

4.4   Conclusions

Bird-window collisions are a growing concern as populations grow and urbanization increases. Much is still unknown when it comes to the extent and impact of window collisions on avian species. How vulnerability to window collisions varies across species is an important area of research to advance as we begin to develop and implement preventive measures to protect birds. In this thesis, I investigated two hypotheses: (1) there is differential vulnerability to dying from window collisions among migratory songbird species, and trophic guild contributes to these differences and (2) age contributes to differential vulnerability. My results support both hypotheses as there was evidence of differential vulnerability among the species studied, as well as among the trophic guilds investigated, and various species-dependent age effects were observed, indicating that there is an age effect in some, but not all species.

My results contribute to the rapidly growing literature on this topic, lending support to previous findings in other locales. Furthermore, the temporal extent of my study offers a unique source of support that is arguably stronger and more robust as, to my knowledge, the majority of previous studies focus on short-term, snapshots of collision data based on one to four years of observations, while my study used 15 years of data. By using such a long period of observation, there is a better chance of observing reliable trends as the effects of outlying years, that are possibly influenced by external factors affecting stopover duration, such as weather or resource abundance, are diluted by the many other years of observation also considered in the model. However, the similarities between my results and the results of previous studies support the credibility of short-term studies as well as studies monitoring fewer buildings. Although, the differences among reported results could also indicate that there are site differences, and perhaps year differences, that create diversity in the conclusions of these short-term studies that are only observing

part of the overall trend. If this is the case, then long-term studies should reduce the variation that is observed across studies. In conclusion, it is possible that coarse trends can be observed in short-term studies, however longer observational periods are ideal for finer, more consistent conclusions. These long-term studies are also required to investigate year-to-year fluctuations in vulnerability. Long-term studies that are able to elucidate species-specific trends, as well as show if and how vulnerability is evolving or improving, are imperative in developing solutions that will allow society to continue to use the desired large glass panes during development, while protecting the unaware, innocent birds as they traverse the continents.

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Appendix 1. Total net days for each site from 1 September to 31 October from 2003 to 2017.

Site	Year	Total net days
FLAP	2003	50
LPBO		56
TTP		57
FLAP	2004	50
LPBO		54
TTP		56
FLAP	2005	54
LPBO		58
TTP		51
FLAP	2006	54
LPBO		55
TTP		45
FLAP	2007	49
LPBO		61
TTP		54
FLAP	2008	49
LPBO		61
TTP		*NA*
FLAP	2009	54
LPBO		58
TTP		36
FLAP	2010	55
LPBO		58
TTP		44
FLAP	2011	45
LPBO		61
TTP		41
FLAP	2012	52
LPBO		58
TTP		45
FLAP	2013	44
LPBO		59
TTP		47
FLAP	2014	44
LPBO		60
TTP		48
FLAP	2015	39
LPBO		59
TTP		52

Site	Year	Total net days
FLAP	2016	42
LPBO		61
TTP		47
FLAP	2017	35
LPBO		61
TTP		40

Curriculum Vitae

Olivia Colling

Education

Master of Science Biology (Anticipated 2019), University of Western Ontario,
London, Ontario, Canada

Bachelor of Science Zoology (Honours), (2017), University of Guelph,
Guelph, Ontario, Canada

Honours and Awards

Western Graduate Research Scholarship   September 2017 – May 2019

University of Guelph – Dean's Honours List   December 2013 – April 2017

Entrance Scholarship to University of Guelph   September 2013
High School average above 90%

Related Work Experience

Teaching Assistant, 2017-2019, University of Western Ontario,
London, Ontario, Canada

Research Assistant, May 2017 – August 2017, Fryxell Lab, University of Guelph,
Guelph, Ontario, Canada

Research Assistant, September 2016 – April 2017, Wootton Lab, University of Guelph,
Guelph, Ontario, Canada

Research Assistant, April 2016 – August 2016, Subramanian Lab, University of Guelph,
Vineland, Ontario, Canada

Other Related Experience

Guest Speaker, May 2018, The 25th Annual Fatal Light Awareness Program Layout,
Toronto, Ontario, Canada

Student Moderator, November 2018, Latornell Conservation Symposium,
Alliston, Ontario, Canada

Conference Presentations

Colling, O., Morbey, Y.E. & Guglielmo, C.G. (2018) Differential Vulnerability to Window Collision Mortality Among Songbird Species. Ontario Ecology, Ethology and Evolution Colloquium. London, ON, Canada. [Poster]

Colling, O., Morbey, Y.E. & Guglielmo, C.G. (2018) Differential Vulnerability to Window Collision Mortality Among Songbird Species. Biology Graduate Research Forum. London, ON, Canada. [Standard Talk]

Colling, O., Morbey, Y.E. & Guglielmo, C.G. (2019) Differential Vulnerability to Window Collision Mortality Among Songbird Species. Comparative Physiology and Biochemistry Workshop. Rice Lake, ON, Canada. [Poster]

Outreach and Service

Society of Biology Graduate Students, Seminar Committee, 2017 – 2018

Biology Graduate Research Forum, Outreach Committee, 2018

Society of Biology Graduate Students, SOGS Representative, 2018 – 2019