Research Paper

Migratory songbirds and urban window collision mortality: vulnerability depends on species, diel timing of migration, and age class

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ABSTRACT. Hundreds of millions of birds are estimated to die annually in North America by colliding with windows, and understanding the species-level correlates of collision mortality is an important step towards mitigation. We used a 16-year window collision dataset for 35 migratory songbird species from Toronto's (Canada) Fatal Light Awareness Program (FLAP) to quantify species differences in vulnerability to urban window collision mortality and potential correlates during the autumn period by applying generalized linear models. To control for annual abundance, we used migration monitoring data from two stations. Our index of vulnerability was the catch ratio, defined as the ratio of annual catch-per-unit effort in each station's mist net program to annual catch-per-unit effort in FLAP. Catch ratios varied among species with Ovenbird (*Seiurus aurocapilla*), Common Yellowthroat (*Geothlypis trichas*), and Lincoln's Sparrow (*Melospiza lincolnii*) being most vulnerable to window collision mortality and Blue-headed Vireo (*Vireo solitarius*), Yellow-rumped Warbler (*Setophaga coronata*), and Ruby-crowned Kinglet (*Regulus calendula*) being least vulnerable. Foraging guild had a minor effect on the catch ratio, but species with a propensity for nocturnal migration had lower catch ratios (greater vulnerability) than those that did not. Based on a subset of species (n = 4) and years (n = 2), hatch-year birds were overrepresented relative to after-hatch-year birds in FLAP compared to the nearby migration monitoring station in 3 of 4 species. This study provides the first ranked list of species vulnerability to urban window collision mortality for songbirds migrating through downtown Toronto, provides evidence that juveniles are more vulnerable to window collision mortality than adults in some species, and highlights the need for more comparative studies of migratory movement behavior to investigate why some species are more vulnerable to urban window collision mortality than others.

Passereaux migrateurs et mortalité par collision avec les fenêtres en milieu urbain : la vulnérabilité dépend de l'espèce, du moment de la migration et de la classe d'âge

RÉSUMÉ. On estime que des centaines de millions d'oiseaux meurent chaque année en Amérique du Nord en heurtant des fenêtres, et la compréhension des corrélats au niveau des espèces de la mortalité par collision représente une étape importante vers l'atténuation. Nous avons utilisé un jeu de données relatives aux collisions avec les fenêtres sur une période de 16 ans pour 35 espèces de passereaux migrateurs provenant du Fatal Light Awareness Program (FLAP) de Toronto (Canada) pour quantifier les différences de vulnérabilité des espèces à la mortalité par collision avec les fenêtres en milieu urbain et déterminer les corrélats possibles pendant la période automnale au moyen de modèles linéaires généralisés. Pour contrôler l'abondance annuelle, nous avons utilisé les données de suivi de la migration provenant de deux stations. Notre indice de vulnérabilité était le ratio de capture, défini comme le rapport entre la capture annuelle par unité d'effort dans le programme de capture par filets japonais de chaque station et la capture annuelle par unité d'effort dans le programme FLAP. Les ratios de capture ont varié selon les espèces, la Paruline couronnée (*Seiurus aurocapilla*), la Paruline masquée (*Geothlypis trichas*) et le Bruant de Lincoln (*Melospiza lincolnii*) étant les plus vulnérables à la mortalité par collision avec les fenêtres, tandis que le Viréo à tête bleue (*Vireo solitarius*), la Paruline à croupion jaune (Setophaga coronata) et le Roitelet à couronne rubis (*Regulus calendula*) étant les moins vulnérables. La guilde relative à l'alimentation a eu un effet mineur sur le ratio de capture, mais les espèces ayant une propension à migrer la nuit ont eu des ratios de capture plus faibles (plus grande vulnérabilité) que celles qui n'en avaient pas. Sur la base d'un sous-ensemble d'espèces (n = 4) et d'années (n = 2), les oiseaux nés dans l'année étaient surreprésentés par rapport aux oiseaux plus vieux dans le programme FLAP, comparativement à la station de suivi de la migration située à proximité pour 3 des 4 espèces. Cette étude fournit la première liste de la vulnérabilité des espèces à la mortalité par collision avec les fenêtres en milieu urbain pour les passereaux qui migrent par le centre-ville de Toronto, révèle que les jeunes sont plus vulnérables à ce type de mortalité que les adultes chez certaines espèces, et souligne le besoin de mener davantage d'études comparatives sur le comportement lors des déplacements migratoires afin de déterminer pourquoi certaines espèces sont plus vulnérables que d'autres à la mortalité par collision avec les fenêtres en milieu urbain.

Key Words: *anthropogenic mortality; avian migration; bird-window collisions; citizen science; stopover ecology; urban environments*

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INTRODUCTION

Migration is a dangerous part of the annual cycle of migratory songbirds, when individuals are exposed to multiple mortality risks, many of which are naturally occurring threats such as predation, disease, and poor weather (Sillett and Holmes 2002, Newton 2007). The most significant anthropogenic threats to migrating songbirds in North America include predation by cats and collisions with windows, power lines, vehicles, and wind turbines (Calvert et al. 2013, Loss et al. 2015). Anthropogenic threats are largely an issue when birds stop to rest and refuel in urban centers, but they can also affect individuals in less developed suburban and rural areas (Klem 2008, Machtans et al. 2013, Hager et al. 2017). Window collisions, which can occur year-round at any time of day, kill an estimated 16-42 million birds per year in Canada (Machtans et al. 2013) and 365-988 million birds per year in the United States (Loss et al. 2014), making this a significant conservation concern. The current understanding is that artificial light at night attracts and disorients nocturnal migrants, bringing them into the vicinity of buildings where their probability of collision is increased (Drewitt and Langston 2008, Van Doren et al. 2017, Van Doren et al. 2021, Winger et al. 2019, Lao et al. 2020, Zhao et al. 2020). Disoriented birds may hit windows while in flight or on descent to ground level, but most window collisions appear to occur after grounding and during regular daytime activities (Gelb and Delacretaz 2009, Kahle et al. 2016, Aymí et al. 2017). In daylight, birds behave as if they do not perceive windows as barriers, and instead, perceive attractive habitat through clear glass, or as reflected vegetation and sky (Klem 2008, Gelb and Delacretaz 2009). Following window collision, the leading cause of death appears to be internal brain injuries (Veltri and Klem 2005). Our study aimed to better understand differential vulnerability to window collision mortality among migratory songbirds and between age classes in the highly urbanized city of Toronto, Canada.

To rank species on their vulnerability to window collision mortality, studies begin with carcass count data which then must be compared to indices of species abundance (Loss et al. 2014, Kahle et al. 2016, Aymí et al. 2017, Wittig et al. 2017, Nichols et al. 2018, Winger et al. 2019, De Groot et al. 2021, Elmore et al. 2021). These studies differ in their spatial scales (e.g., building, city, region, campus, or continental) and timing, leading to the use of different data sources for species abundance (point counts, mist net surveys, breeding bird surveys, or eBird citizen science data), different types of abundance indices (cumulative counts or occurrence days), and also statistical approaches (e.g., linear models of catch, tests of goodness-of-fit). Studies also differ in whether and how survey effort is controlled, and how uncertainty is quantified. These methodological differences highlight some of the challenges with evaluating species differences in their vulnerability to window collision mortality and applying the results to different contexts.

Prior studies during migration periods typically find that some species are overrepresented in carcass surveys relative to their local or population abundance, suggesting that intrinsic factors play a role (Arnold and Zink 2011, Kahle et al. 2016, Wittig et al. 2017, Nichols et al. 2018, Winger et al. 2019, Elmore et al. 2021). Differential vulnerability to window collision mortality among feeding guilds has been suggested, with higher risk in canopy-foraging insectivores than in ground-foraging birds (Wittig et al.

2017), or in insectivores than in non-insectivores (Elmore et al. 2021). Such differences are thought to be due to behavioral differences in foraging (darting flights vs. hopping; Wittig et al. 2017). There is also evidence that migrants have a higher collision risk than residents (Borden et al. 2010, Arnold and Zink 2011, Kahle et al. 2016, Sabo et al. 2016, Wittig et al. 2017, Elmore et al. 2021). This difference has been attributed to the degree of familiarity with the area, as migrants travel through many unfamiliar areas while residents generally stay within familiar territories (Hager and Craig 2014, Kahle et al. 2016, Sabo et al. 2016, Wittig et al. 2017). Nocturnal migrants also are overrepresented in carcass surveys relative to diurnal migrants (Arnold and Zink 2011, Nichols et al. 2018). Nocturnal flight calling, considered to be a proxy for sociality in movement, is another species-level factor that is positively associated with window collision vulnerability (Winger et al. 2019).

The addition of hatch year (HY) birds to a population should result in an increase in window collision tallies in autumn, and disproportionately so if HY birds are at greater risk due to their lack of familiarity with buildings and windows. The degree of cranial pneumatization may also contribute to differential window collision mortality between HY and after hatch year (AHY) birds, as HY skulls are not fully pneumatized in the autumn (Pyle 1997), and subadults show more severe injuries than adults among window collision fatalities (Veltri and Klem 2005). Among the few studies that have evaluated window collision vulnerability between age classes, one study showed an overrepresentation of HY vs. AHY birds in window collision tallies compared to birds from nearby mist-netting surveys (Kahle et al. 2016), but two studies did not (Sabo et al. 2016, Aymí et al. 2017).

In this study, we had four objectives: (1) present a novel approach to the analysis of carcass count data for Toronto, Canada, while controlling for species abundance using migration monitoring data, (2) rank migratory songbird species according to their differential vulnerability to urban window collision mortality during fall migration, (3) compare vulnerability among species, trophic guilds, and species with or without nocturnal flight calls, and (4) test for differential vulnerability by age class. Regarding objectives (3) and (4), we hypothesized that species and age classes of individuals would differ in their vulnerability to urban window collision mortality. Based on prior empirical evidence as described above, we predicted that non-ground foraging insectivorous migrants would be more vulnerable than granivorous or ground-foraging insectivorous migrants, that species using nocturnal flight calls would be more vulnerable than those that do not, and that HY birds would be more vulnerable than AHY birds.

METHODS

We tested for differential vulnerability to urban window collision mortality among species using data from 3 temporally overlapping datasets spanning the years 2003-2018: an urban window collision dataset from Toronto, Canada, and two migration monitoring datasets. We focused on the autumn period when AHY birds would be joined by HY birds on their first migration south. Our general statistical approach was to estimate annual catch for each dataset and species within the autumn migration period, and then for each species, estimate the ratio of annual catch between each migration monitoring dataset and the

Fig. 1. (A) The locations of the three bird sampling programs in Ontario with an inset showing the location of Toronto (magenta square) relative to North America; (B) the location of the Fatal Light Awareness Program (FLAP) in relation to Tommy Thompson Park Bird Research Station (TTP) in Toronto; (C) the spatial extent of FLAP's core area; (D) a bird's eye view of Long Point Bird Observatory (LPBO). Maps were made using layers from Google maps or rnaturalearth. The inset of North America is shown with a Lambert Conformal Conic projection.
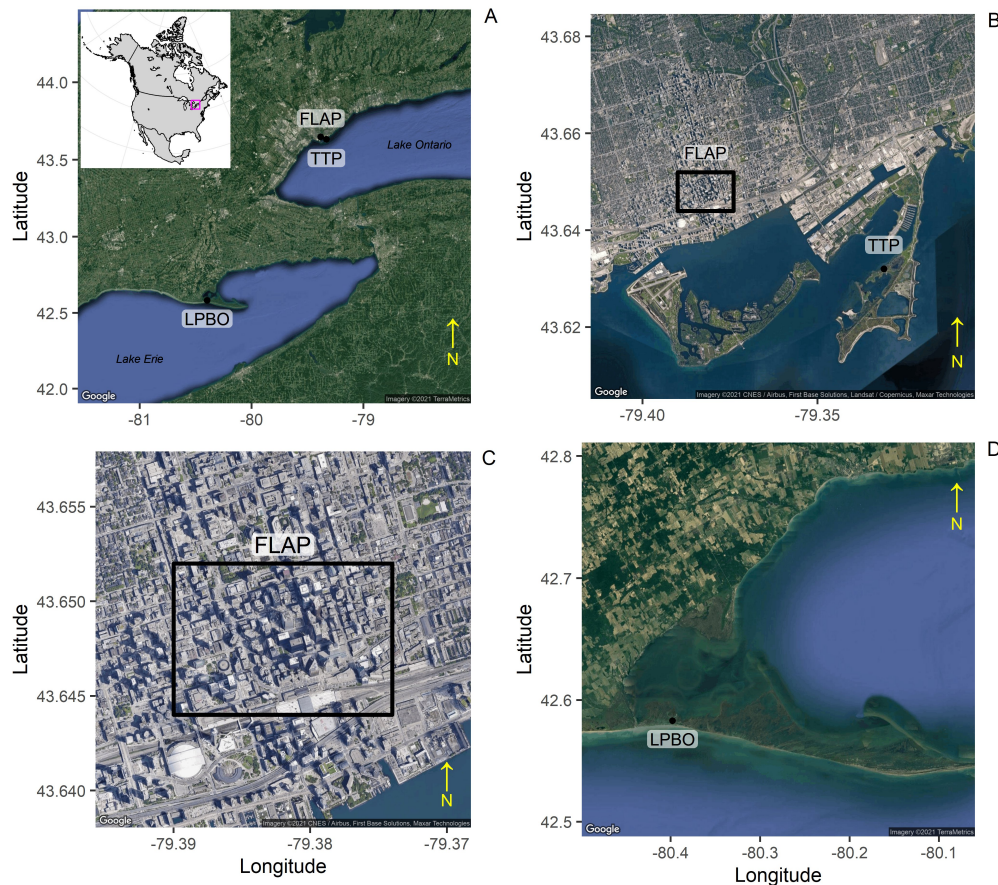
window collision dataset while controlling for annual effort in a generalized linear model. The "catch ratio" was then used as an index of vulnerability to window collision mortality. In a separate analysis using a subset of data with known-aged birds, we tested if HY birds were overrepresented in carcass counts relative to each migration monitoring dataset using a different type of generalized linear model. The availability of carcasses for aging limited this analysis to 2017 and 2018.

Datasets

The Fatal Light Awareness Program (FLAP; www.flap.org) is a citizen science program that monitors window collision mortality in Toronto, Canada. Each autumn during the 2003-2018 period, volunteers completed daily window collision surveys in the Toronto area (Fig. 1A). Volunteers walked the sidewalks and recorded the address where a bird was found, the day and time it

was found, the species (if possible to identify), and the bird's status (dead, alive, scavenged, or sent to a rehabilitation center). Carcasses were brought to FLAP headquarters or the Royal Ontario Museum for storage at -20°C and later identified to species. Birds were not aged as part of the FLAP program. Because the daily number and effort of volunteers were not standardized and carcasses may have been removed by scavengers, carcass counts should be considered as minimum counts.

We filtered the FLAP dataset to only include entries of intact carcasses with address and date information. Addresses were standardized and then assigned geographical coordinates using Google Maps geocoding in the ggmap R package (Kahle and Wickham 2013). Since the FLAP survey area increased across years as the program increased in popularity, we limited the spatial extent to a 1.14 km² core area in Toronto where surveying was

consistent across the time series (43.644°N-43.652°N, 79.374° W-79.39°W; Fig. 1B). This core area was within the highly urbanized downtown core of Toronto, where there is a concentration of tall buildings (Fig. 1C). We set the temporal extent of our study to September 1 to October 31 each year to cover the majority of the autumn migration period.

The two migration monitoring datasets differed in their proximity to the FLAP survey area (i.e., local vs. regional). The local migration monitoring dataset— best representing local species abundance—came from the Tommy Thompson Park (TTP) Bird Research Station (43.627°N, 79.331°W; Tommy Thompson Park Bird Research Station 2018), located 4.7 km southeast of the main FLAP survey area on the naturalized area of Leslie Street Spit, a reclaimed and partially wooded headland which extends into Lake Ontario (Fig. 1A and 1B). The year 2008 was excluded from our TTP analyses as data were not available that year. The regional migration monitoring dataset came from the Old Cut site of the Long Point Bird Observatory (LPBO) banding program, Long Point, Ontario (42.583°N, 80.398°W; Long Point Bird Observatory 2018), which is 144 km southwest of the FLAP site. The Old Cut site is within a naturalized woodlot situated near the base of Long Point Peninsula, which extends into Lake Erie (Fig. 1D). The inclusion of LPBO data allowed us to test for differences at a broader spatial scale, which may be attributable to spatial heterogeneity in species abundance.

At both migration monitoring sites, we used their mist net survey data to provide an index of local abundance. Mist nets are lightweight, have a fine mesh, and are effective at intercepting and "trapping" birds through entanglement. In the mist net survey, staff and volunteers aimed to survey birds daily during spring and autumn migration for 6 hr starting 30 min before sunrise. In practice, the daily net hours deviated from this target because poor weather conditions sometimes forced the closure of all or a subset of nets. Volunteers were trained on-site to capture and band birds and to record measurements. Standard bird banding measurements were taken for each individual, including variables such as species, date, time captured, age (by plumage), and mass.

Alternatives to the mist net survey data were considered to be less suitable for the purposes of our study. This includes data from the daily route census of all birds seen and heard, which cannot distinguish previously counted birds, and is more sensitive to the identification skills of observers. For the same reason, we also did not use the daily "estimated total", which combines the daily counts from mist nets and from the fixed route census. Another source of potential data was eBird, but this citizen science project was far less structured than the mist net monitoring program, and was subject to a strongly increasing trend in annual survey effort over the period of our study (Fink et al. 2020). In general, the limitation and biases associated with different survey methods are well understood (Remsen and Good 1996) and have implications for how monitoring programs are designed to address specific data needs (Hussell and Ralph 1998, Dunn et al. 2004).

We analyzed data for all migratory species from the Order Passeriformes with total catches of more than 100 birds at both TTP and LPBO across the study period. This ensured that all species in the analysis were catchable by mist nets, which partially accounted for the problem of species differences in catchability

in mist nets (e.g., Remsen and Good 1996). Thirty-five species were selected, and all were confirmed to be regular migrants with minimal stopovers at TTP and LPBO based on information from the Canadian Migration Monitoring Network (Birds Canada 2021). The 35 species were classified by taxonomic family and trophic guild (i.e., diet and foraging height) based on González-Salazar et al. (2014). Trophic guild was then simplified into three levels: granivore, ground foraging insectivore, and non-ground foraging insectivore (Table S1). In our set of species, all but the "Near Threatened" Blackpoll Warbler (*Setophaga striata*) were classified as "Least Concern" by IUCN criteria (Billerman et al. 2020). We assigned to each species the presence or absence of nocturnal flight calls based on Winger et al. (2019). We also assigned the index of diel timing of migration from Ralph (1981). This continuous metric was calculated as the log of catch at the Long Point lighthouse —located at the tip of Long Point— divided by the log of catch in nets and traps. Birds were assumed to be attracted to the artificial light at night so higher values of the index indicated species with a greater propensity to migrate at night.

Annual survey effort

Both mist net datasets were filtered with the same within-year temporal extent as the FLAP data (September 1 to October 31), and only first captures were included. For TTP and LPBO, we calculated annual survey effort as the number of days the mist nets were open with at least one individual caught during the September 1 to October 31 period. For FLAP, annual survey effort was calculated as the number of days with at least one carcass retrieved from September 1 to October 31. Among years, annual survey efforts ranged from 29 to 57 days for TTP (48-93%), 54-61 days for LPBO (89-100%), and 29-52 days for FLAP (48-85%). Across the three data sets, days without effort were distributed uniformly within the autumn catch periods, resulting in empirical cumulative distribution functions that conformed to straight lines. Finer resolution information on survey effort (i.e., mist net hours per day or survey hours per day) either was not reported (FLAP) or was not consistently reported (TTP and LPBO). Imprecise estimates of survey effort were expected to account for some of the error in statistical models.

Assignment of age

Carcasses from the FLAP collections were made available for aging, but only for 2017 and 2018. Because carcass recovery locations were similar between 2017 and 2018 (Fig. A1), we let the spatial extent of the analysis cover the complete 101 km² survey area in Toronto. The availability of carcasses permitted decent sample sizes for 4 species: Nashville Warbler (*Oreothlypis ruficapilla*), Ovenbird (*Seiurus aurocapilla*), White-throated Sparrow (*Zonotrichia albicollis*), and Swainson's Thrush (*Catharus ustulatus*). For comparison to TTP and LPBO, we used the 2017 and 2018 age information from the migration monitoring datasets.

Carcasses were thawed, then aged by plumage and skulling. Birds that had fully pneumatized skulls were classified as AHY, whereas birds that had partially pneumatized skulls were classified as HY (Pyle 1997). In cases where the degree of pneumatization was difficult to see, possibly as a result of internal bleeding, a piece of the skull was removed, cleaned, and examined. Because the

process of skull pneumatization is gradual and varies among species, there are cutoff dates when age data become unreliable. We retained age data for carcasses prior to the cutoff dates indicated in McKinney (2004): before October 1 for Swainson's Thrush, before October 15 for Nashville Warbler and Ovenbird, and before November 1 for White-throated Sparrow. Individuals with unknown age (n = 5) were excluded from analyses.

Statistical analyses

In our approach, we first explored the data so that we could understand the statistical properties of the data and determine if we could fit a single global model; these and all additional analyses were performed in R 4.0.0 (R Core Team 2020). Exploratory analysis of the catch data by species suggested overdispersion relative to a Poisson distribution, even after accounting for the fixed effects of program and year, with the degree of overdispersion varying by species. We formally tested for differences in overdispersion among species to determine if all species could be included in a single model. To do so, we fit a double generalized linear model (dGLM) to the catch data. The class of dGLM extends standard GLM by allowing for both the mean and the dispersion parameter of the negative binomial distribution to be modeled as linear functions of covariates (Dunn and Smyth 2019). In our case, we fit an overdispersed Poisson model in which the mean depended on site (FLAP, TTP, and LPBO), year, the site-by-year interaction, species, and the species-by-site interaction. The dispersion was modeled either as a function of species or as a single parameter. The inclusion of an offset term for log(effort) in the mean model would account for variable effort among years and sites, but the dGLM function could not accommodate this formulation, and so effort was not included as a predictor in these models. The model with a single dispersion parameter was compared to a model with species-specific dispersion parameters with a likelihood ratio test (LRT).

Next, we analyzed catch as a function of site, year, and log(effort) as an offset term using species-specific negative binomial models implemented with the function glm.nb in package MASS (Venables and Ripley 2002), which allows for overdispersion through the estimation of the dispersion parameter θ, which factors into the calculation of variance. The Poisson model is the limit of the negative binomial model as θ tends to infinity, so in cases in which θ could not be estimated because of this limit, we instead fit Poisson GLMs using function glm. For well-fitting models, the dispersion index (residual deviance/residual degrees of freedom) should be < 2 (Beckerman et al. 2017). In the species-specific models, expected catch (μ_{ijk}) for observation i at site j and year k was assumed to follow this functional form:

$$\log(\mu_{ijk}) = \beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \sum_{k=1} \gamma_k z_{ik} + \log(u_{ijk}) \quad (1)$$

where x_{1ij} indicates whether or not an observation came from TTP (i.e., x_{1ij}=1 if j=TTP and 0 otherwise), x_{2ij} indicates whether or not an observation came from LPBO (i.e., x_{2ij}=1 if j=LPBO and 0 otherwise), and the z_{ik} represents dummy variables coding for the factor year. The β and γ terms represent the fitted coefficients. The term u_{ijk} represents survey effort, which was included as an offset term. Catch ratios (CR) between each mist netting site and FLAP with 95% confidence limits were calculated from model

coefficients, with catch ratio = 1 indicating that the mean catch per unit effort was the same at the two programs:

$$CR_{TTP} = e^{\beta_1} \quad (2)$$
$$CR_{LPBO} = e^{\beta_2} \quad (3)$$

Among species, non-overlapping confidence intervals would be indicative of differences in the catch-per-unit effort between sites that may be attributable to species differences in their probability of window collision given their presence in the FLAP survey area (i.e., conditional risk), catchability by mist nets, and/or abundance at the two sites.

We tested if TTP:FLAP and LPBO:FLAP catch ratios differed among the three main trophic guilds (granivore, ground insectivore, and non-ground insectivore) and between species with and without nocturnal flight calls using non-parametric Kruskal-Wallis tests. We also tested if catch ratios were correlated with the index of diel timing using Spearman rank-order correlation tests. Non-parametric tests were used because our dGLM analyses supported the use of species-specific GLMs rather than a global GLM that included species as a factor. For this reason, we did not attempt to control for phylogenetic relatedness when testing for an effect of trophic guild and nocturnal calling.

To test if HY and AHY birds differed in their vulnerability to window collision mortality vs. mist net capture at TTP and LPBO, we analyzed the probability of a bird being HY using species-specific generalized linear models (GLMs) with binomial error distributions using package glm. The model included site and year as fixed effects. A nonparametric dispersion test, which used simulated residuals within years, was used to evaluate model fit and was implemented using functions in package DHARMa (Hartig 2020). The fitted coefficients associated with site indicate the difference in the log odds ratio (Δ ln[odds of HY: odds of AHY]) between each mist net program and FLAP. We inverse logit-transformed the Δ log odds ratios (now Δ odds) and calculated their respective transformed 95% confidence intervals. A Δ odds = 1 indicates no difference between sites in the odds of being a HY bird.

Consistent rankings in indices of collision risk among species would indicate a role for intrinsic, species-specific factors. We tested whether the ordered rank of TTP:FLAP catch ratios was correlated with the ordered rank of LPBO:FLAP catch ratios with a Spearman rank-order correlation test. To supplement our case study, we compared our rank order of species vulnerability to species ranks from two long-term studies of window collision mortality that also controlled for local abundance using citizen science data, but in different ways. Nichols et al. (2018) studied window collision mortality over 4 years in Minneapolis-St. Paul, Minnesota. They fit a global negative binomial model to the annual carcass count data and included local abundance from point counts as a fixed effect and random intercepts for species. The species intercepts were used as indices of vulnerability. We extracted the rank order of these values for our analysis. Winger et al. (2019) used a 39 year window collision mortality dataset for Chicago, Illinois. They used a χ² goodness-of-fit test to compare occurrence days in FLAP to occurrence days in eBird checklists, summed across years, and used the species-specific χ² residuals as indices of vulnerability. We extracted the rank order of these

values from their figure 2. We used Spearman rank correlation tests to compare our ranked lists to those of Nichols et al. (2018) and Winger et al. (2019).

Fig. 2. Catch ratios between Tommy Thompson Park Bird Research Station (TTP) and the Fatal Light Awareness Program (FLAP) for 35 songbird species sorted from largest to smallest catch ratio. Catch ratios ± 95% confidence intervals were log-transformed to facilitate plotting on the same axis. A large catch ratio means that relatively more of that species was caught at TTP than FLAP. Trophic guild is indicated by orange triangles and dotted lines (granivore), blue circles and solid lines (ground insectivore), and green circles and solid lines (non-ground insectivore). The music notes indicate the use of nocturnal flight calls.
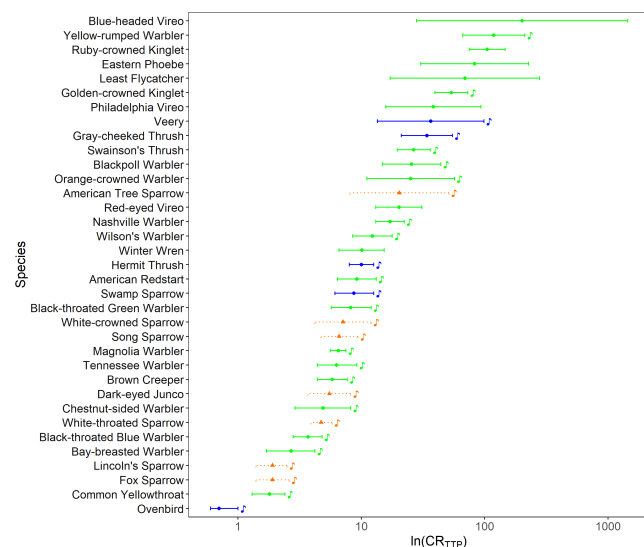

RESULTS

In the comparison of dGLM models with single vs. species-specific dispersion parameters, the more complex, species-specific dispersion model fit better (LRT: $\chi^2 = 865.0$, df = 35, $P < 0.001$), justifying the use of species-specific models. Among all the species-specific models, 6 were fit with Poisson models and 29 were fit with negative binomial models, and dispersion indices varied from 1.04 to 2.56 (Table 1). The TTP:FLAP catch ratios showed substantial variation among species, with many cases of non-overlapping 95% confidence intervals (Fig. 2, Table 1). This indicates differential vulnerability to window collision mortality among some subsets of migratory songbird species. Those species with the lowest CR_{TTP} values represent those with the greatest vulnerability to window collision mortality compared to mist net capture. A similar ranking of species was found for the LPBO: FLAP catch ratios (Fig. A2 and Table A2). The Ovenbird stood out as being distinctly different from all other species in both ranked lists.

Species-specific catch ratios showed weak evidence of being different among trophic guilds, and differences were not sufficiently robust for statistical significance at the 0.05 α-level (CR_{TTP}: Kruskal-Wallis $\chi^2 = 4.99$, df = 2, $P = 0.083$, Fig. 2;

CR_{LPBO}: Kruskal-Wallis $\chi^2 = 4.69$, df = 2, $P = 0.096$; Fig. A2). Granivores and ground insectivores tended towards greater vulnerability to window collision mortality than non-ground insectivores. Species-specific catch ratios were higher for species without nocturnal flight calls ($n = 7$) than for species with nocturnal flight calls ($n = 28$; CR_{TTP}: Kruskal-Wallis $\chi^2 = 9.57$, df = 1, $P = 0.002$, Fig. 2; CR_{LPBO}: Kruskal-Wallis $\chi^2 = 8.22$, df = 1, $P = 0.004$, Fig. A2). In addition, catch ratios were negatively correlated with the index of diel timing ($n = 30$; CR_{TTP}: $r_s = -0.469$, $P = 0.009$; CR_{LPBO}: $r_s = -0.414$, $P = 0.023$).

In 2017 and 2018 we aged 85 Nashville Warblers, 35 Ovenbirds, 54 Swainson's Thrushes, and 80 White-throated Sparrows. Comparable age data were available for 128 Nashville Warblers, 25 Ovenbirds, 223 Swainson's Thrushes, and 296 White-throated Sparrows at TTP and 123 Nashville Warblers, 47 Ovenbirds, 448 Swainson's Thrushes, and 815 White-throated Sparrows at LPBO. Age ratios (proportion HY) were variable among species, sites, and years (Fig. 3). When comparing TTP to FLAP, Nashville Warblers, Ovenbirds, and Swainson's Thrushes had significantly lower odds (Δ odds < 1) of being HY than AHY (Fig. 4). When comparing LPBO to FLAP, only the Swainson's Thrushes had significantly lower odds (Δ odds < 1) of being HY (Fig. A3). Adequate model fit was supported by nonsignificant dispersion tests ($Ps > 0.088$).

Fig. 3. Proportion of birds that were HY in the Fatal Light Awareness Program (FLAP), Tommy Thompson Park Bird Research Station (TTP), and Long Point Bird Observatory (LPBO) for four songbird species in 2017 and 2018. NAWA = Nashville Warbler; OVEN = Ovenbird; SWTH = Swainson's Thrush; WTSP = White-throated Sparrow.
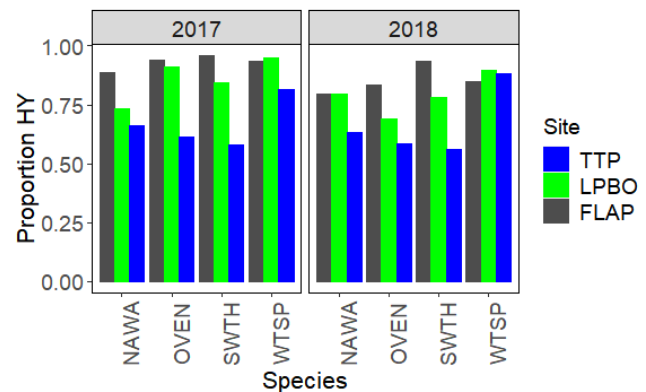
Between the two migration monitoring sites, the rank orders of CR_{TTP} and CR_{LPBO} were highly correlated ($r_s = 0.948$, $P < 0.001$). The 5 most vulnerable species were shared between the TTP and LPBO ranked lists: Ovenbird, Lincoln's Sparrow (*Melospiza lincolnii*), Fox Sparrow (*Passerella iliaca*), Bay-breasted Warbler (*Setophaga castanea*), and Common Yellowthroat (*Geothlypis trichas*). Four of the 5 least vulnerable species were shared between the TTP and LPBO ranked lists: Blue-headed Vireo (*Vireo solitarius*), Yellow-rumped Warbler (*Setophaga coronata*), Ruby-crowned Kinglet (*Regulus calendula*), and Least Flycatcher (*Empidonax minimus*). Our dataset had 30 species in common with the Nichols et al. (2018) dataset. The rankings of species

Table 1. Comparison of catches between Tommy Thompson Park Bird Research Station (TTP) and the Fatal Light Awareness Program (FLAP). Shown are the total catches across all years by program (TTP:FLAP), the catch ratio (CR_{TTP}), and 95% confidence interval from specific-specific negative binomial or Poisson generalized linear models, $\theta \pm SE$ (for negative binomial generalized linear models; NA for Poisson models), and the dispersion index. Species are sorted by CR_{TTP}. Binomial nomenclature given in Table A1.

Species	TTP:FLAP	CR_{TTP}	95% CI	θ	Dispersion Index
Blue-headed Vireo	212:1	201.3	28.1-1444.5	27.6 ± 18.1	1.42
Yellow-rumped Warbler	3046:27	118.5	66.3-211.8	2.9 ± 0.8	1.91
Ruby-crowned Kinglet	5788:55	104.9	75.1-146.5	13.0 ± 3.4	1.93
Eastern Phoebe	320:4	83.0	30.3-227.4	14.4 ± 6.8	1.51
Least Flycatcher	138:2	69.2	17.1-279.4	NA	2.19
Golden-crowned Kinglet	8360:168	53.7	39.5-73.0	7.5 ± 1.7	1.60
Philadelphia Vireo	192:5	38.3	15.8-93.2	NA	1.34
Veery	142:4	36.5	13.5-98.6	NA	1.70
Gray-cheeked Thrush	645:19	34.0	21.1-54.7	32.4 ± 13.4	1.87
Swainson's Thrush	1569:57	26.6	19.5-36.3	19.0 ± 5.8	1.80
Blackpoll Warbler	442:20	25.6	14.8-44.1	6.2 ± 1.7	1.56
Orange-crowned Warbler	148:6	25.1	11.1-56.9	127.5 ± 301.5	1.28
American Tree Sparrow	125:6	20.3	8.1-51.3	3.6 ± 1.8	1.83
Red-eyed Vireo	467:23	20.2	13.1-31.0	52.7 ± 30.7	1.74
Nashville Warbler	1480:87	17.1	13.1-22.3	21.6 ± 7.1	1.77
Wilson's Warbler	368:30	12.3	8.5-17.8	NA	2.31
Winter Wren	440:41	10.1	6.6-15.3	7.6 ± 2.7	1.99
Hermit Thrush	2177:223	10.0	8.0-12.6	16.7 ± 4.6	1.67
American Redstart	490:52	9.2	6.4-13.2	10.9 ± 3.6	1.93
Swamp Sparrow	281:32	8.7	6.1-12.6	NA	2.56
Black-throated Green Warbler	341:44	8.2	5.7-12.0	13.9 ± 6.8	2.06
White-crowned Sparrow	202:33	7.1	4.2-12.0	4.6 ± 1.5	1.73
Song Sparrow	370:56	6.6	4.7-9.4	12.9 ± 4.7	1.88
Magnolia Warbler	1255:197	6.4	4.7-8.7	7.5 ± 2.1	1.87
Tennessee Warbler	267:41	6.3	4.4-9.2	21.2 ± 11.2	1.63
Brown Creeper	1087:175	5.8	4.4-7.7	10.7 ± 2.8	1.68
Dark-eyed Junco	1126:203	5.5	3.7-8.2	3.9 ± 0.9	1.80
Chestnut-sided Warbler	141:30	4.9	2.9-8.2	5.3 ± 2.2	1.88
White-throated Sparrow	3094:692	4.7	3.9-5.8	16.3 ± 4.1	1.78
Black-throated Blue Warbler	541:165	3.7	2.8-4.8	14.2 ± 4.9	1.92
Bay-breasted Warbler	151:42	2.7	1.7-4.2	6.5 ± 3.0	1.81
Fox Sparrow	136:73	1.9	1.4-2.6	28.8 ± 25.0	1.91
Lincoln's Sparrow	160:84	1.9	1.4-2.5	NA	1.04
Common Yellowthroat	407:236	1.8	1.3-2.4	9.2 ± 3.0	1.96
Ovenbird	277:401	0.7	0.6-1.0	11.8 ± 4.0	1.75

vulnerability were positively associated between TTP and Minneapolis-St. Paul ($r_s = 0.443$, $P = 0.015$), but not between LPBO and Minneapolis-St. Paul ($r_s = 0.283$, $P = 0.130$). All of the species in our analyses were present in the Winger et al. (2019) dataset, and the rankings of species vulnerability between both sites and Chicago were positively associated (TTP: $r_s = 0.599$, $P = 0.0002$; LPBO: $r_s = 0.508$, $P = 0.002$).

DISCUSSION

We found evidence that songbird species differ in their vulnerability to urban window collision mortality vs. mist net capture, and present the first ranked list of vulnerability to window collision mortality for Toronto that accounts for an index of local abundance. The finding that not all species collide proportionally to local abundance corroborates previous studies (Kahle et al. 2016, Aymí et al. 2017, Wittig et al. 2017, Nichols et al. 2018, Winger et al. 2019). We also found that the rank order of vulnerability was correlated both between TTP and LPBO and between our study and the Nichols et al. (2018) and Winger et al. (2019) studies in three of the four comparisons. Synthesizing our results with Nichols et al. (2018) and Winger (2019) and using the

"super-collider" vs. "super-avoider" terminology of Arnold and Zink (2011), Ovenbirds, Dark-eyed Juncos (*Junco hyemalis*), and White-throated Sparrows were amongst the 10 most vulnerable, and thus appear to be consistent super-colliders. Blue-headed Vireos, Yellow-rumped Warblers, and Eastern Phoebes, on the other hand, appear to be consistent super-avoiders as they were amongst the 10 least vulnerable species. There were also discrepancies in individual rankings among studies, which could be due to site differences that affect window collision frequency (e.g., building, window, and landscape configuration, lighting, and weather; Borden et al. 2010, Cusa et al. 2015, Kahle et al. 2016, Hager et al. 2017, Lao et al. 2020, Elmore et al. 2021, Van Doren et al. 2021), differences in sampling design (i.e., spatiotemporal extent), or statistical methodology. The observed similarities in species rankings among studies suggest that certain trends are strong enough to be conserved across locations, spatiotemporal scales, local abundance metric, and statistical methodology.

Across the vulnerability scale, we suggest that a species with a lower TTP:FLAP or LPBO:FLAP catch ratio is at greater conditional risk of urban window collision mortality than a

Fig. 4. Change in odds of catching HY birds between Tommy Thompson Park Bird Research Station (TTP) and the Fatal Light Awareness Program (FLAP) for four songbird species. Estimated changes in odds are represented by the points and the error bars are 95% confidence intervals. The vertical dashed line represents the null hypothesis where the HY log odds at TTP is equal to the HY log odds at FLAP. Species with 95% confidence intervals that do not cross 1 have significantly different odds at TTP and FLAP. NAWA = Nashville Warbler; OVEN = Ovenbird; SWTH = Swainson's Thrush; WTSP = White-throated Sparrow.
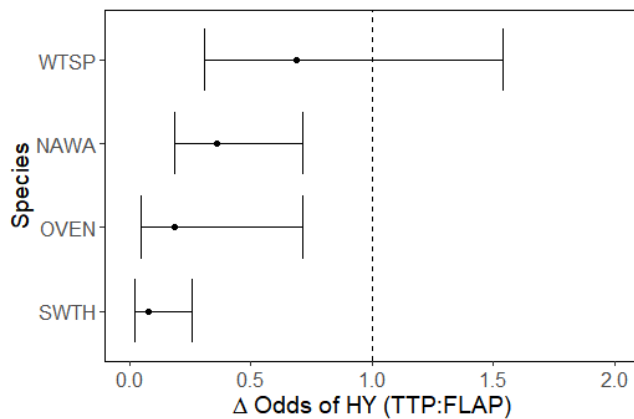
species with a higher catch ratio, as this is parsimonious with the weight of evidence for the existence of super-colliders and super-avoiders. But alternative mechanisms should not be ruled out. Possibly, behavioral differences may have led to some species being more abundant in the FLAP survey area of downtown Toronto, or less catchable by mist nets at TTP. For example, the results suggest that Ovenbirds are particularly prone to window collision mortality compared to other species, but Ovenbirds also may be trapped by urban areas thus increasing their abundance in the downtown core, or they may be less catchable by mist nets. Comparative studies on how super-colliders and super-avoiders perceive and interact with window glass, and how they move about urban vs. forested habitats while on migratory stopover, would help to evaluate the alternatives. For example, recent advances in automated radiotelemetry now make it possible to document the spatial scale and diel timing of stopover movements in small birds (Taylor et al. 2011, Dossman et al. 2016).

Species with nocturnal flight calls and those with a greater propensity to migrate at night were more vulnerable to window collision mortality than species without nocturnal flight calls and those with a lower propensity to migrate at night. These results corroborate results in Winger et al. (2019) and support the hypothesis that nocturnal migrants are attracted to hazardous urban areas with artificial light at night. Under this hypothesis, Ovenbirds, an exemplary nocturnal migrant with the highest index of diel timing of migration (1.02), are predicted to initially alight in downtown Toronto rather than the low-lit area of Tommy Thompson Park. We extend this hypothesis and speculate that some nocturnal migrants may have the behavioral flexibility to continue migration via daytime movements, thus allowing them

to move out of inhospitable and hazardous areas more quickly. Automated radiotelemetry studies could shed light on the understudied aspect of diurnal migration by primarily nocturnal migrants. For example, Yellow-rumped Warblers showed low site tenacity when released at a stopover site and subsequently tracked with automated radiotelemetry, with many individuals leaving the site within hours of release during daylight (Seewagen et al. 2019, Lupi et al. 2022). Such a propensity for diurnal movement may account for the low vulnerability ranking for this otherwise nocturnal migrant. We speculate that the relative collision risk of different species depends not only on their propensity to migrate at night but also on their behavioral plasticity in diurnal movement.

We found weak evidence that trophic guild influences vulnerability to urban window collision mortality, with a tendency for greater vulnerability among granivores and ground insectivores than among non-ground insectivores. This supports the findings of Cusa et al. (2015), who found that ground foraging birds were overrepresented in window collision tallies in more urbanized parts of Toronto. While this suggests that foraging height can play a role in collision risk, previous studies showed higher risk in insectivores than granivores (Wittig et al. 2017, Elmore et al. 2021). In our study, we cannot distinguish whether non-ground insectivores were less prone to collide with windows, more catchable in mist nets, or more abundant in the mist net survey areas. Moreover, species within a single trophic guild were quite variable in their catch ratios, suggesting that foraging behavior and height may not be the dominant factor affecting vulnerability to window collision mortality and that other species-level traits dominate. Differences between our study and previous studies could be due to climatic or habitat variability among sites or years, the lack of replication within some guilds, different statistical methods, or differences in statistical power. One shortcoming of the data is that we were unable to compare species and trophic guilds within a single, parametric statistical model because species models differed in their error distributions.

Additional species-level factors may account for their differential vulnerability to window collision mortality vs. mist net capture, besides the diel timing of migration and foraging height. These include flocking behavior (Kahle et al. 2016, Winger et al. 2019), habitat preferences (open vs. forested; Wittig et al. 2017, Winger et al. 2019), eye morphology and physiology (e.g., eye placement, fovea area of the retina, and visual range; Martin 2011, 2012), and overall body size (Kahle et al. 2016). Stopover movement behavior, including length-of-stay, may also be important to consider. More individual-level studies on these topics across a variety of species are needed to better understand the factors affecting vulnerability to window collision mortality in urban environments.

In our assessment of age class differences in vulnerability to window collision mortality, HY birds were overrepresented in FLAP compared to nearby TTP in 3 species (Swainson's Thrushes, Ovenbirds, and Nashville Warblers) and were equally represented in White-throated Sparrows. In addition to age differences in experience, age differences in stopover duration and migration routes could also influence vulnerability. For example, longer stopovers in HY than in after hatch year (AHY) birds (reviewed in Morbey and Hedenström 2020) could increase their

exposure to windows. Whether HY birds are more likely to traverse urbanized areas than AHY birds is unknown, but avoidance of water barriers, such as the Laurentian Great Lakes, could increase the time HY birds spend along urbanized lakeshores. Age effects were not fully replicated in the FLAP to LPBO comparison, as HY birds were overrepresented only in Swainson's Thrush. This inconsistency may be due, in part, to different migration routes or habitat associations between age classes (e.g., Ralph 1981). In fact, HY:AHY ratios at TTP appeared to be low compared to LPBO in several year-species combinations. Alternatively, perhaps HY birds that alight in downtown Toronto are less likely to move out of the city towards Tommy Thompson Park than AHY birds.

Our study contributes to a growing number of studies of urban window collision mortality that vary in their spatiotemporal extent, type and quality of local abundance data, statistical approach, and how effort is controlled (Kahle et al. 2016, Aymí et al. 2017, Wittig et al. 2017, Nichols et al. 2018, Winger et al. 2019). The ideal study would have high-resolution data over a large spatial and temporal extent, accurate local abundance data, complete and accurate effort data, and catch data that conform in their error distributions. Unfortunately, neither our study nor any prior study had access to data that met this set of idealistic criteria, making it challenging to generalize studies to different contexts. Compared to previous studies, ours was robust in terms of the model selection procedure, the use of years as replicates, and the accounting for annual survey effort. The generalized linear modeling approach to derive "catch ratios" could be applied to address additional questions concerning the FLAP dataset, other collision risk datasets in other cities, and the sensitivity of comparisons to the type of survey data used to estimate local abundance. Such an approach could also help to compare species-specific catchability among mist nets, point counts, fixed-route censuses, eBird occurrence or count data, and other survey methods.

By leveraging long-term citizen science datasets, our study offers a unique source of support for species and age differences in window collision vulnerability that is arguably stronger and more robust than the majority of previous studies that used short-term collision data. Longer periods of observation increase the chance of observing reliable trends by minimizing the effects of spatiotemporal variability, which is inherent in ecological studies. We have identified species and age differences in vulnerability and call for more studies of individual-based movement to help identify the behaviors underlying differential vulnerability. Bird window collisions are a growing concern as urbanization increases, but there is much to learn about the root causes of window collisions, and the impact of window:collisions on avian species and populations. Such information may help to inform and support the mitigation strategies—such as turning off lights at night, bird-safe building design, and the use of bird-safe window markings—that are promoted by charitable organizations like FLAP Canada and NYC Audubon's Project Safe Flight.

Responses to this article can be read online at:
https://www.ace-eco.org/issues/responses.php/2107

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Appendix

Table A1. Summary information for 35 songbird species used in the analysis of window collision mortalities from the Fatal Light Awareness Program. Guild refers to the diet of the species and foraging height refers to the canopy height at which the species generally forages. Initial guild assignments from González and Salazar (2014) were simplified into three levels. Species are arranged alphabetically by Family and common name.

| Species	Family	Species	Guild
Brown Creeper	Certhiidae	*Certhia americana*	Non-ground insectivore
American Redstart	Parulidae	*Setophaga ruticilla*	Non-ground insectivore
Bay-breasted Warbler	Parulidae	*Setophaga castanea*	Non-ground insectivore
Blackpoll Warbler	Parulidae	*Setophaga striata*	Non-ground insectivore
Black-throated Blue Warbler	Parulidae	*Setophaga caerulescens*	Non-ground insectivore
Black-throated Green Warbler	Parulidae	*Setophaga virens*	Non-ground insectivore
Chestnut-sided Warbler	Parulidae	*Setophaga pensylvanica*	Non-ground insectivore
Common Yellowthroat	Parulidae	*Geothlypis trichas*	Non-ground insectivore
Magnolia Warbler	Parulidae	*Setophaga magnolia*	Non-ground insectivore
Nashville Warbler	Parulidae	*Oreothlypis ruficapilla*	Non-ground insectivore
Orange-crowned Warbler	Parulidae	*Oreothlypis celata*	Non-ground insectivore
Ovenbird	Parulidae	*Seiurus aurocapilla*	Ground insectivore
Tennessee Warbler	Parulidae	*Oreothlypis peregrina*	Non-ground insectivore
Wilson's Warbler	Parulidae	*Cardellina pusilla*	Non-ground insectivore
Yellow-rumped Warbler	Parulidae	*Setophaga coronata*	Non-ground insectivore
American Tree Sparrow	Passerellidae	*Spizelloides arborea*	Granivore
Dark-eyed Junco	Passerellidae	*Junco hyemalis*	Granivore
Fox Sparrow	Passerellidae	*Passerella iliaca*	Granivore
Lincoln's Sparrow	Passerellidae	*Melospiza lincolnii*	Granivore
Song Sparrow	Passerellidae	*Melospiza melodia*	Granivore
Swamp Sparrow	Passerellidae	*Melospiza georgiana*	Ground insectivore
White-crowned Sparrow	Passerellidae	*Zonotrichia leucophrys*	Granivore
White-throated Sparrow	Passerellidae	*Zonotrichia albicollis*	Granivore
Golden-crowned Kinglet	Regulidae	*Regulus satrapa*	Non-ground insectivore
Ruby-crowned Kinglet	Regulidae	*Regulus calendula*	Non-ground insectivore
Winter Wren	Troglodytidae	*Troglodytes hiemalis*	Non-ground insectivore
Gray-cheeked Thrush	Turdidae	*Catharus minimus*	Ground insectivore
Hermit Thrush	Turdidae	*Catharus guttatus*	Ground insectivore
Swainson's Thrush	Turdidae	*Catharus ustulatus*	Non-ground insectivore
Veery	Turdidae	*Catharus fuscescens*	Ground insectivore
Eastern Phoebe	Tyrannidae	*Sayornis phoebe*	Non-ground insectivore
Least Flycatcher	Tyrannidae	*Empidonax minimus*	Non-ground insectivore
Blue-headed Vireo	Vireonidae	*Vireo solitarius*	Non-ground insectivore
Philadelphia Vireo	Vireonidae	*Vireo philadelphicus*	Non-ground insectivore
Red-eyed Vireo	Vireonidae	*Vireo olivaceus*	Non-ground insectivore
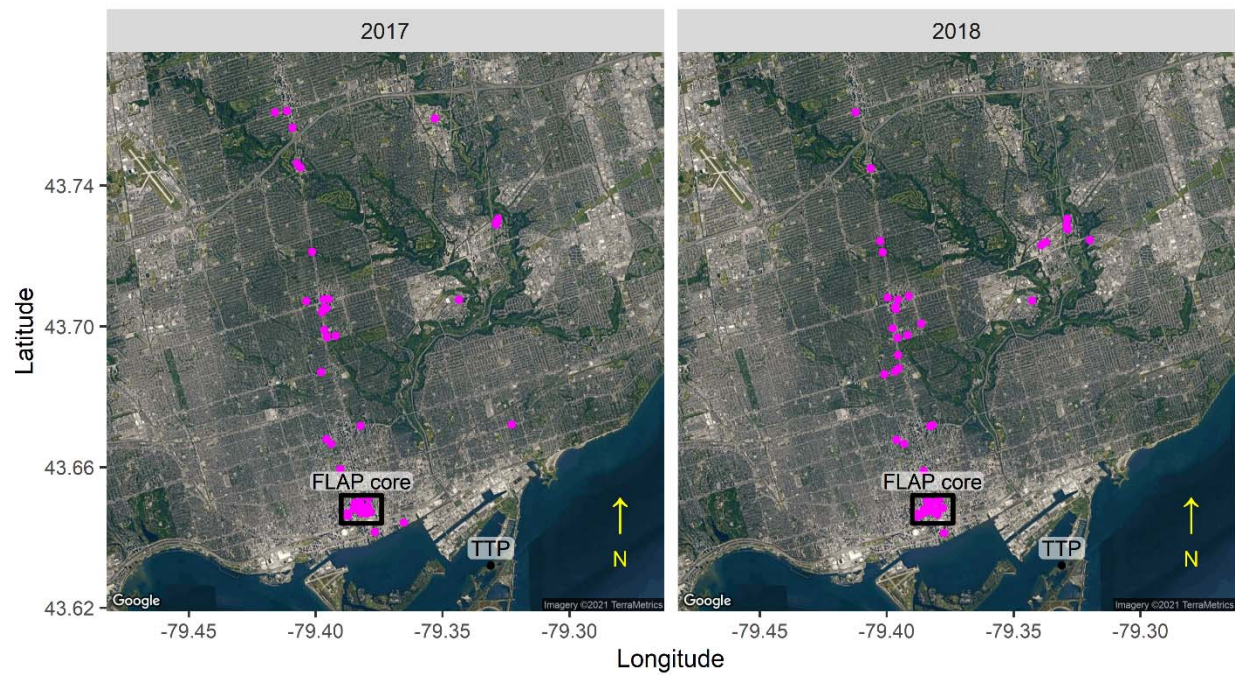
Figure A1. Location of aged carcasses from the Fatal Light Awareness Program in 2017 and 2018, Toronto, Canada.
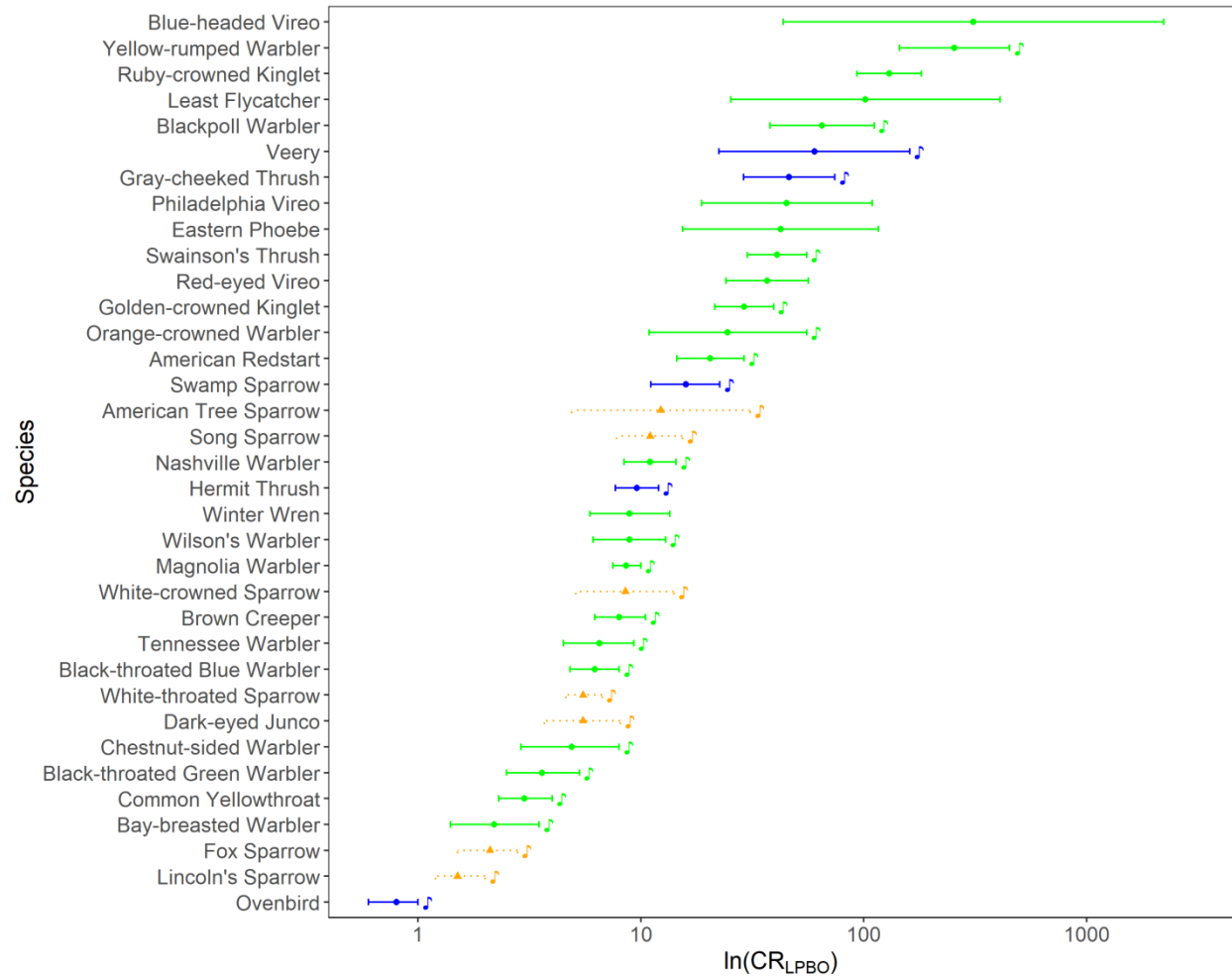
Figure A2. Catch ratios between Long Point Bird Observatory (LPBO) and the Fatal Light Awareness Program (FLAP) for 35 songbird species sorted from largest to smallest catch ratio. Catch ratios ± 95% confidence intervals were log-transformed to facilitate plotting on the same axis. A large catch ratio means that relatively more of that species was caught at LPBO than FLAP. Trophic guild is indicated by orange triangles and dotted lines (granivore), blue circles and solid lines (ground insectivore), and green circles and solid lines (non-ground insectivore). Music notes indicate the use of nocturnal flight calls.

Table A2. Comparison of catches between Long Point Bird Observatory (LPBO) and the Fatal Light Awareness Program (FLAP). Shown are the total catches across all years by program (LPBO:FLAP), the catch ratio (CR_{LPBO}), and 95% confidence interval from the specific-specific generalized linear models. Species are sorted by CR_{LPBO}.

| Species	LPBO:FLAP	CR_{LPBO}	95% CI
Blue-headed Vireo	434:1	311.0	43.5–2225.3
Yellow-rumped Warbler	8880:27	255.6	144.5–452.2
Ruby-crowned Kinglet	9805:55	130.0	93.4–181.1
Least Flycatcher	288:2	101.8	25.3–408.8
Blackpoll Warbler	2133:20	65.1	38.0–111.5
Veery	333:4	60.1	22.4–161.0
Gray-cheeked Thrush	1196:19	46.3	28.9–74.2
Philadelphia Vireo	325:5	45.1	18.7–109.2
Eastern Phoebe	267:4	42.4	15.4–116.3
Swainson's Thrush	3240:57	40.8	30.0–55.4
Red-eyed Vireo	1209:23	36.9	24.1–56.4
Golden-crowned Kinglet	6555:168	29.1	21.5–39.4
Orange-crowned Warbler	202:6	24.5	10.9–55.5
American Redstart	1526:52	20.5	14.5–29.1
Swamp Sparrow	705:32	15.9	11.1–22.6
American Tree Sparrow	108:6	12.3	4.9–31.0
Nashville Warbler	1278:87	11.0	8.4–14.4
Song Sparrow	883:56	11.0	7.8–15.4
Hermit Thrush	2882:223	9.6	7.7–12.0
Magnolia Warbler	2395:197	9.0	6.7–12.0
Winter Wren	523:41	8.9	5.9–13.5
Wilson's Warbler	368:30	8.9	6.1–12.9
White-crowned Sparrow	434:33	8.5	5.1–14.1
Brown Creeper	2078:175	8.0	6.2–10.5
Tennessee Warbler	381:41	6.5	4.5–9.3
Black-throated Blue Warbler	1259:165	6.2	4.8–8.0
White-throated Sparrow	4970:692	5.5	4.6–6.7
Dark-eyed Junco	1579:203	5.5	3.7–8.1
Chestnut-sided Warbler	193:30	4.9	2.9–8.0
Black-throated Green Warbler	220:44	3.6	2.5–5.3
Common Yellowthroat	963:236	3.0	2.3–4.0
Bay-breasted Warbler	199:42	2.2	1.4–3.5
Fox Sparrow	188:73	2.1	1.5–2.8
Lincoln's Sparrow	177:84	1.5	1.2–2.0
Ovenbird	390:401	0.8	0.6–1.0
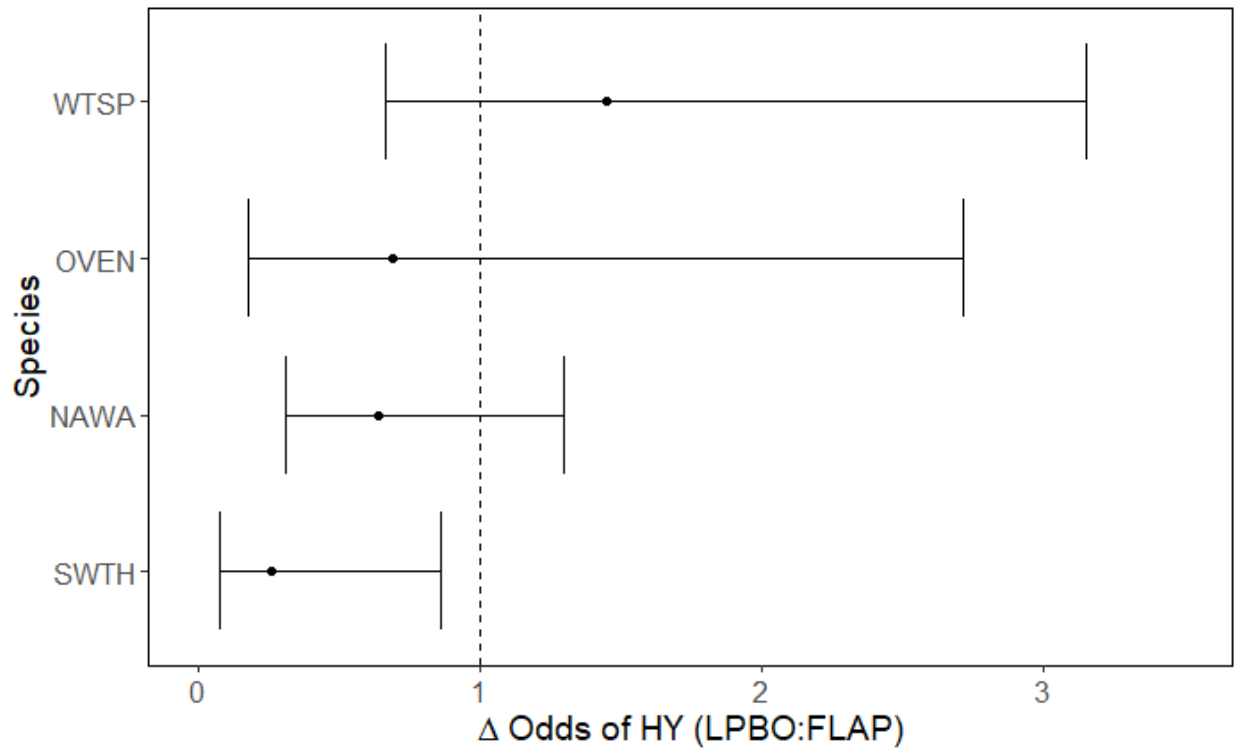
Figure S3. Change in odds of catching HY birds between Long Point Bird Observatory (LPBO) and the Fatal Light Awareness Program (FLAP) for four songbird species. Estimated changes in odds are represented by the points and the error bars are 95% confidence intervals. The vertical dashed line represents the null hypothesis where the HY log odds at LPBO is equal to the HY log odds at FLAP. Species with 95% confidence intervals that do not cross 1 have significantly different odds at LPBO and FLAP. NAWA = Nashville Warbler; OVEN = Ovenbird; SWTH = Swainson's Thrush; WTSP = White-throated Sparrow.

LITERATURE CITED

González-Salazar, C., E. Martínez-Meyer, and G. López-Santiago. 2014. A hierarchical classification of trophic guilds for North American birds and mammals. Revista Mexicana de Biodiversidad 85:931–941.