Window collisions by migratory bird species: urban geographical patterns and habitat associations

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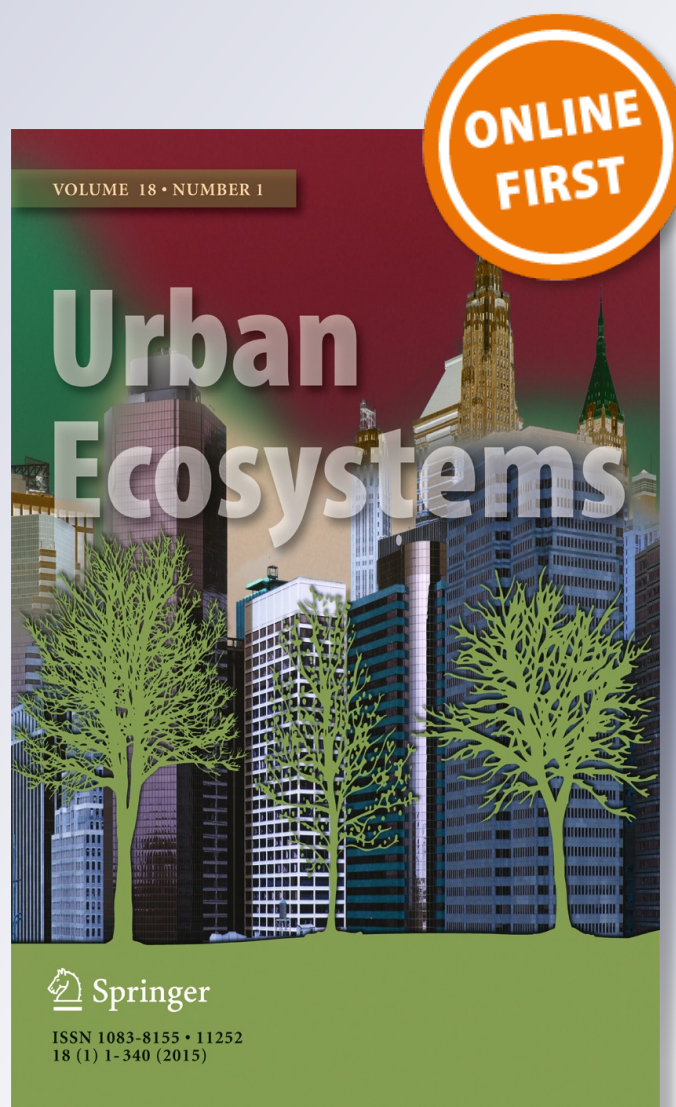# Window collisions by migratory bird species: urban geographical patterns and habitat associations

Marine Cusa[1] · **Donald A. Jackson**[1] · **Michael Mesure**[2]

Abstract Bird collisions with buildings are an increasing concern and yet understanding the factors contributing to collisions at the species level remains largely unknown. This gap in our knowledge of species-specific strike patterns hinders the development of accurate estimates for the impact of death-by-collision on bird populations and impedes on our ability to minimize its effects. Our study offers the first examination of the impact of environmental variables on bird-window collisions at the species level. The Fatal Light Awareness Program Canada collected bird-window collision data in three distinct regions of Toronto, Canada during the migratory season of the years 2009 and 2010. Our results indicated that building percent window cover, exposed habitat cover, and cover of built structures significantly affect bird-window collisions. Multivariate analyses showed that the bird species that collided with buildings surrounded by a high level of urban greenery are species that typically occur in forested habitats and are foliage gleaners. In contrast, species that collided with buildings surrounded by a higher level of urbanization are species that typically occur in open woodland and are ground foragers. These results suggest that the composition of bird species colliding with buildings across various regions of the Greater Toronto Area is influenced by the local bird species community composition, by the configuration of the surrounding landscape, and by the levels of greenery around the buildings.

✉ Marine Cusa
marine.cusa@mail.utoronto.ca

Donald A. Jackson
don.jackson@utoronto.ca

Michael Mesure
mesuremichael@gmail.com

[1] Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2, Canada

[2] Fatal Light Awareness Program Canada (FLAP Canada), 123 Queen St. West, Box 199, Toronto, Ontario M5H 3M9, Canada

Introduction

The urban matrix of major North American cities holds a variety of natural and altered green habitats that provide important ecological functions for both resident and migratory bird species. Although it may be impossible for natural organized environmental systems to subsist in various urban environments (Sattler et al. 2010), response to this urbanization phenomenon varies greatly across species. While some birds are described as "urban-positive" synanthropic species and can readily adapt to habitat degradation and high levels of urbanization (Stracey 2011; Stracey and Robinson 2012a), others are at a disadvantage in the face of such anthropogenic activities. The level of urbanization can be an important predictor of species richness and diversity (Clergeau et al. 1998, 2006) and a high degree of urbanization can lead to biotic homogenization, i.e., an increased similarity in species composition among sites (Blair 2004; Chase and Walsh 2006; MacGregor-Fors and Schondube 2011). Despite providing foraging opportunities and creating potential habitat structures for birds (Clergeau et al. 1998; Evans et al. 2009), cities also present a number of hazards to resident and migratory species (Calvert et al. 2013). Some threats to birds found in cities include collision with vehicles (Mumme et al. 2000; Bishop and Brogan 2013), predation by cats (Lepczyk et al. 2003; Balogh et al. 2011; Blancher 2013), and disorientation due to "ecological traps" and sink habitats (Robertson and Hutto 2006; Robinson and Hoover 2011). Among these threats, migratory bird collisions with human-built structures and the ensuing impact on bird populations have become a growing concern over the past decades (Klem 1990a; Borden et al. 2010; Hager et al. 2013; Machtans et al. 2013; Loss et al. 2014).

Annual bird-window collision (BWC, see Hager et al. 2013) fatalities have been suggested to account for 0.5 to 5 % of the total autumn bird population in the United States of America (Klem 1990a; Dunn 1993). Although these estimations are alarming, they remain largely speculative. Recent estimates suggest that about 25 million birds die from window collisions annually in Canada (Machtans et al. 2013) or 0.5 % of the total number of birds in the country; and 365–988 million birds die annually from window collisions in the United States of America (Loss et al. 2014). The effect of those mortalities on bird populations is unknown, as is the relative impact on different species due to interspecific differences. Anthropogenic structures responsible for migratory bird strikes are quite diverse and can range from tall communication towers and glass high-rise buildings to urban and rural homes (Gauthreaux and Belser 2006; Machtans et al. 2013). Toronto is likely to have some of the highest numbers of mid-rise and high-rise building BWCs in Canada due to its location adjacent to Lake Ontario and to the fact that it contains one-third of all tall buildings in Canada (Machtans et al. 2013). Although it appears that mid-rise and high-rise buildings are responsible for only a fraction of the total number of BWCs across the country, bird mortality is disproportionately higher at these types of building than at smaller structures, such as single family dwellings and low rise commercial buildings (Hager et al. 2013; Machtans et al. 2013; Loss et al. 2014). Given that bird species are attracted differently to a variety of habitat features and differ in their abundances, it is likely that species are not equally affected by mid-rise and high-rise building collisions. Additionally, the expansion of urban areas and the growing number of large building structures further suggests that understanding the way these buildings affect individual species is critical in order to reduce BWCs.

Ecologists have predominantly focused on the types of environmental factors that affect total number of BWCs, rather than on factors related to individual species. Many have stated the adverse effects of light pollution on birds during nighttime migration (Herbert 1970;

Verheijen 1981; Ogden 1996). These types of collisions seem to be particularly problematic for nighttime migrants (Crawford 1981) and during bad weather (Newton 2008; Longcore et al. 2012). Glass structures have also been suggested to cause a significant number of bird-building collisions during the daytime (Klem et al. 2009; Borden et al. 2010; Bayne and Rawson-Clark 2012; Hager et al. 2013). There are a number of factors that have been associated with increased frequency of daytime bird strikes. The importance of these factors can be assessed on a small geographical scale by measuring architectural characteristics such as building glass surface area (Klem et al. 2009; Borden et al. 2010; Bayne and Rawson-Clark 2012) or proximate landscape configurations (Hager et al. 2008; Gelb and Delacretaz 2009; Klem et al. 2009), or they can be assessed on a larger geographical scale by measuring neighboring landscape features over a broader geographical extent. The latter landscape features have largely been ignored in BWC studies.

Investigations incorporating small geographical scale features have observed a marked increase in the effect of reflective glass surface area in the presence of adjacent vegetation (Hager et al. 2008; Gelb and Delacretaz 2009; Klem et al. 2009; Borden et al. 2010). Thus, it is not uncommon for a single building to contain both facades with low-strike frequencies and facades with high-strike frequencies. This phenomenon can occur when birds are deceived by the reflection of the vegetation into the reflective pane (Banks 1976). If a window appears to be transparent as opposed to reflective, birds may collide with the pane in an attempt to fly through it (Klem 1989). Some areas form "migrant traps" with a particularly high number of fatalities and these hot-spots are often characterized by the presence of trees over five meters tall, high ground cover, and large areas of reflective glass windows (Klem et al. 2009; Borden et al. 2010). BWC studies that noted the effect of larger geographical scale features are rare (but see Hager et al. 2013) and some studies concluded that environmental variables in a building's immediate vicinity explain more of the BWC variation than large-scale environmental variables (Hager et al. 2013). However, studies on bird species distribution (i.e., non-BWC studies) often include large geographical scale variables (Riffell et al. 2003; Stratford and Robinson 2005; Pennington et al. 2008; Suarez-Rubio and Thomlinson 2009). Therefore, because collisions occur where overall bird abundance or diversity is higher (Klem 1989; Hager et al. 2008, 2013; Bayne and Rawson-Clark 2012), collision patterns are possibly linked to bird distributions across a heterogeneous urban landscape, and large geographical scale features are likely to affect collisions. Declines in the diversity of bird species occur with higher levels of urbanization (Lancaster and Rees 1979; Edgar and Kershaw 1994; Melles et al. 2003) and their richness within urban environments will, in some cases, be positively related to an increase in tree cover and to the presence of coniferous trees (Fontana et al. 2011) in urban areas. This is particularly true for migratory birds seeking stopover habitats to forage and build fat reserves in order to meet the energetic requirements of migration (Moore et al. 1995; Petit 2000; Seewagen and Slayton 2008). Although the distribution of migratory bird species in urban landscapes can be attributed, in part, to the availability of stopover habitats, it also depends on a wide range of variables in the environment or specific to individual birds (e.g., weather patterns, travel distance, migratory route, exhaustion) (Gauthreaux 1980; Diehl et al. 2003). Thus, the patterns of collisions across migratory bird species in urban areas may be influenced by characteristics specific to the individual, species, and the various environmental variables that affect their distribution.

Although the effects of environmental variables on aggregate BWCs have been well studied, focus at the species level lacks this consideration. Hager and Craig (2014) noted that collision risks are dependent on bird age and migratory guild. They observed that adult long-

distant migrants were more prone to collision at the beginning of the breeding season whereas juveniles from all migratory guilds were prone to collision throughout the season. Furthermore, they observed that adults from least abundant species and juveniles from most abundant species had the highest risk of window collisions. Results from this study illustrate the need to adopt a species-specific or group-specific (i.e., guilds, age, etc.…) approach when attempting to assess the effects of BWCs. The objective of our study is to understand the collision signature of individual migratory bird species in Toronto, Canada, by focusing on the spatial distribution of sites and on urban landscape features. Specifically, the following urban landscape features are considered: percent glass cover on a building façade, percent cover of road, canopy, exposed habitat, building structures, and pavement within a given distance of building clusters. First, we predict that increased glass surface on a building, greater canopy cover, and open habitats in the landscape will be positively correlated with BWCs. These predictions are based on the environmental resources hypothesis according to which bird collisions will tend to occur more frequently where bird abundance is high (Hager et al. 2013) and the associated habitat features in these areas will tend to enhance overall bird abundance. Second, we predict that the bird species affected will differ in distribution and abundance across sites, due to the differing ecological characteristics of the species, and that they will form distinct family and guild clusters about an urban gradient. We also provide recommendations for the management of urban landscapes and building features if BWCs are to be mitigated.

Methods

Study area

We used data collected by the Fatal Light Awareness Program (FLAP) Canada in Toronto, Ontario, Canada. Toronto is located on the convergence of the Atlantic and Mississippi migratory flyways. A migratory flyway is a simplified illustration of the most common routes followed by a majority of migrants. Due to the nature of its location with regards to the migratory flyways and to the Lake Ontario, Toronto provides critical stopover habitats for migrants (Dougan and Associates 2009). Lake Ontario can represent a barrier for many migrants (Diehl et al. 2003) forcing them to follow the shore, thereby crossing the city of Toronto. Toronto is the largest urban centre in Canada with various clusters of tall glass towers that are a threat for migratory birds (Ogden 1996). For this study, we selected sites sampled by FLAP Canada volunteers in three distinct regions of Toronto: (1) Scarborough (100, 200, 300 Consilium Place), (2) York Mills (4100, 4110, 4120 Yonge Corporate Centre), and (3) the downtown financial district. These areas were chosen based on the regularity at which they were sampled for bird collisions and on the diversity of the surrounding landscape features.

Data source, sampling process

The Fatal Light Awareness Program has been collecting dead and injured migratory birds in Toronto since 1993 (Ogden 1996). One of FLAP Canada's goals is to expand awareness on BWCs in order to prevent migratory bird collisions with building windows. During migratory season (April, May, September, and October), FLAP Canada volunteers sample a set of commercial buildings on a daily basis in Scarborough, York Mills, and in the financial district.

FLAP Canada does not follow a standardized sampling regime but rather its sampling protocol is to collect as many dead and injured birds as possible within the time of each collection. Given the extensive sampling and its regularity in particular locations, it results in data well suited to examine questions about bird collisions, their association with particular habitat features, and the relative numbers of collisions amongst species.

We used data that were collected by FLAP Canada and selected records for the fall and spring of the year 2009 and 2010. In the first data set (A) we pooled the migratory bird collision data for all species during the migratory months of 2009 and 2010 thereby creating a total BWC category. In the second data set (B) we pooled data for the year 2009 and 2010 but kept the species and the season separate thereby summarizing fall and spring data for each individual species. Here, we did not discriminate between birds collected pre-dawn or post-dawn because FLAP volunteers concentrated their patrolling efforts during post-dawn hours and over 90 % of the patrols for which time was recorded in the selected records occurred post-dawn.

Building and landscape variables

For all three sites (1), (2), and (3), we estimated percent landscape area covered by canopy (C), exposed habitat and grass land (E), structures and buildings (S), roads (R), and pavement (P). Pavement excluded roads but included all additional paved surfaces such as parking lots, sidewalks, and concrete covered grounds. These features were chosen based on earlier studies of the distribution of bird species across the urban landscape (Melles et al. 2003; Minor and Urban 2010) and the impact of certain environmental variables on BWCs (Klem et al. 2009; Hager et al. 2013). We excluded areas covered by water due to the small dimension of the water bodies (totaling <0.5 % land cover). The percentages of canopy, exposed habitats, structures, roads, and pavement were measured within a 500 m radius circle from building clusters thereby allowing us to measure large-scale landscape variables. As some adjacent buildings may be located within 200 m of each other, some buildings may have overlapping circles of influence given common habitat features. To measure percentages of these landscape features, we used several resources including infrared aerial orthorectified images taken during 2012 from Airborne Sensing Corporation and from the City of Toronto's Geospatial Competency Centre. In addition we used orthorectified colour air photographs of 2011, and a high resolution colour-coded land-cover data map from the Urban Forestry Services, both from the City of Toronto. The colour-coded land-cover map was produced in 2007 and summarizes land cover of tree canopy, grass/shrub, bare earth, water, buildings, roads, other paved surfaces, and agriculture over the Greater Toronto Area. The photographs and map were imported into ArcMap 10 and landscape features measured using these resources, along with photographs taken at each individual site in 2013 by the first author. We used the high-resolution colour-coded land-cover map as a template and corrected it for C, E, P, R, and S cover by comparing the map with aerial and site photographs. Once the high-resolution map was rectified, we measured 500 m radius circles and measured landscape feature percentages using pixel counts in Adobe Photoshop CS5. Percentages for window cover were measured by using photographs taken on site. The images were imported into Adobe Photoshop CS5 and percentages were estimated using pixel counts. Furthermore, we assessed the effect of other building variables on BWC to identify whether these building metrics would affect our ability to compare the effect of percent glass cover on BWCs from buildings of different size. We

measured building height, façade base length, façade surface area, and roof-top surface area for each building and building façade analyzed in the study.

Statistical analysis

As many variables and relationship did not meet assumptions of parametric statistical methods, we used the non-parametric Kendall's tau correlation coefficient to test for associations between our hypothesized predictors and response variables. We used dataset (A) to assess the effect of landscape features and building attributes on the total number of BWCs in 2009 and 2010. Kendall's tau enabled us to quantify the association between total BWCs and percent glass cover (PGlass) and attributes of building size as well as individual landscape features within a 500 m radius of a building (C, E, P, R, and S). Additionally, regressions were performed to assess the effect of building size on BWCs (see supplemental material).

We used dataset (B) to calculate the relationship between environmental variables and individual species. We first removed all species with less than 5 % occurrence in order to focus on the general community relationships (Jackson and Harvey 1989). In order to measure the relationship between our species collision data and the associated environmental variables, we used Canonical Correspondence Analysis (CCA). The CCA is a direct gradient analysis that can be used to determine how patterns in species composition are related to the environmental variables. Given inherent problems associated with the use of compositional data (e.g., lack of independence, negative bias in variable correlations, Jackson 1997), we used Correspondence Analysis (CA) of the percentage environmental data to generate summary axes that were then used as predictive variables in the CCA. The CA Axis I was used to summarize the variation in habitat composition and to examine associations between environmental variables and the distribution of bird species that collided across the GTA.

All statistical analyses were performed in R (R Core Team 2013). The CA was performed using the "ca" package (Nenadic and Greenacre 2007) and the CCA was performed using the "vegan" package (Oksanen et al. 2013).

Results

The FLAP Canada volunteers collected and recorded a total of 3034 bird collisions in 2009 and 4934 bird collisions in 2010. The total number of BWCs retained for the analysis was of 3924 (1719 for 2009 and 2205 for 2010) after selecting data for the three regions of interest (1), (2), and (3) and for the months of April, May, September, and October of 2009 and 2010. Over the course of the fall and spring migratory seasons during 2009 and 2010, the species with the greatest number of collisions were the Golden-crowned Kinglet ($n=808$), the White-throated Sparrow ($n=551$), the Dark-eyed Junco ($n=262$), and the Ovenbird ($n=248$). When considering all buildings, the majority of the collisions were recorded at the Consilium Place (CP) in eastern Toronto, and in the Financial District (FD) in the city downtown core.

Data set A   Total number of BWCs (all species combined) pooled for the fall and the spring, and for the years 2009 and 2010.

As expected, there was a significant relationship between BWCs per building and percentage of glass (PGlass). In the pooled collision data for each building façade, BWC was

positively correlated with the percentage of glass cover ($r_\tau=0.67$, $p<0.001$; Fig. 1a). Increased amounts of exposed habitats and decreased cover of building structures were significantly related to BWCs ($r_\tau=0.41$, $p<0.005$, Fig. 1b; and $r_\tau=-0.41$, $p<0.005$, Fig. 1d respectively). The percent cover of road showed a trend towards decreased numbers of BWCs ($r_\tau=-0.27$, $p=0.054$; Fig. 1e). Percent canopy cover ($r_\tau=0.2$, $p=0.160$; Fig. 1c) and percent pavement cover ($r_\tau=-0.1$, $p=0.476$; Fig. 1f) were not significantly related to BWCs. The resulting regressions and Kendall tau rank correlation tests showed no significant effect due to building height, façade surface width or overall surface area on the number of BWCs (see supplemental material section for additional figures). Thus, we concluded that our measurements of percent glass cover on BWC were not affected by these additional building variables and could be used independently of building size.

Data set B   Number of collisions per species per site pooled for the years 2009 and 2010.
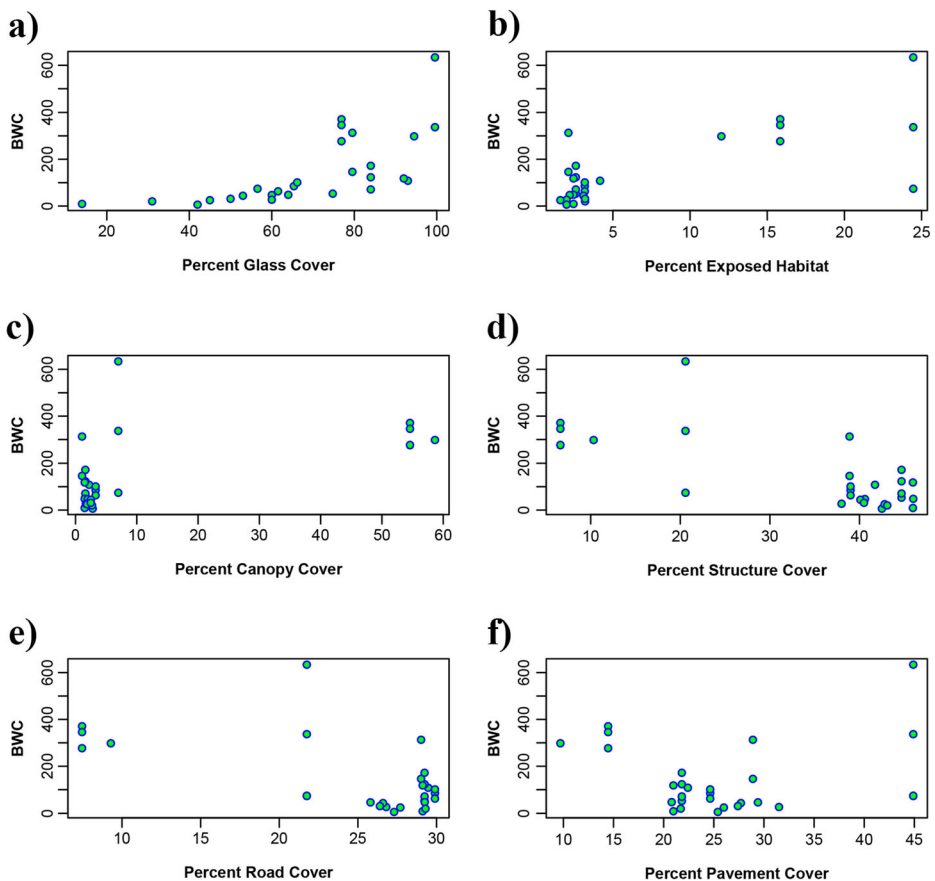
Fig. 1 Kendall's tau rank correlations for environmental variables and Bird-Window Collisions (BWCs). Three relationships are significant: **a** PGlass with $r_\tau=0.67$, $p<0.001$; **b** E500 with $r_\tau=0.41$, $p<0.005$; and **d** S500 with $r_\tau=-0.41$, $p<0.005$. Three relationships are not significant: **c** C500 with $r_\tau=0.2$, $p<0.160$; **e** R500 with $r_\tau=-0.27$, $p=0.054$; and **f** P500 with $r_\tau=-0.1$, $p=0.476$

Sites with high positive values for CA Axis I scores were sites with generally more greenery such as tree canopy (C) and exposed habitats (E), and a relatively low to medium cover of built structures such as buildings (S), roads (R), and pavement (P). Sites at the negative end of the first axis score were sites that tend to have very little greenery (<5 % cover of C or E) and a large portion of their landscape was covered by built hard structures (S, R, and P). Thus, there was a strong association between site scores and environmental variables, and Axis I clearly captured this gradient from greener urban environments to urban environments with little to no vegetative cover. Therefore, the resulting data from CA Axis I was interpreted as a measure of vegetative cover, henceforth referred to as 'GreenLevels', and used as a summary environmental variable in a canonical correspondence analysis.

Results of the Canonical Correspondence Analysis (CCA; Fig. 2) using the environmental variables (C, E, S, R, P summarized as GreenLevels; and PGlass) to constrain bird-window collision data, showed most financial district sites (FD) positioned at the opposite end of GreenLevels and associated with higher percent land cover of pavement, structure, and road cover. CP and YM sites tended to be distributed closer to higher GreenLevels and therefore were associated with higher percent land cover of tree canopy and exposed habitats. PGlass provided a strong contrast in the summary gradient and was positioned at right angles to the GreenLevels variable. As expected, the gradient from more heavily urbanized sites (FD) to urban sites with more vegetation (CP and YM) was seen along the vector for the GreenLevels summary variable.
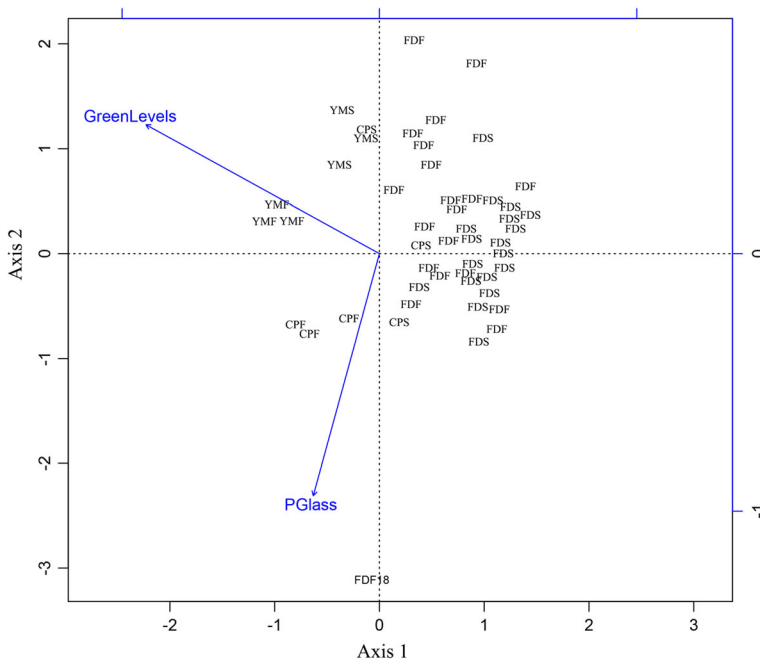
Fig. 2 Canonical correspondence ordination plot of urban sites in which birds collided with glass structures. A total of 26 sites are included and independently analyzed for the spring and the fall. 20 of those sites were found in the financial district (FD), 3 of them were in Scarborough (CP), and 3 of them were in the York Mills region (YM). Eigenvalues (Axis I = 0.27, Axis II = 0.03) indicate that CCA axis I explains 88.33 % of the explained variance. 'GreenLevels' is the resulting data from CA Axis I and is a measure of vegetative cover summarizing canopy cover, exposed habitat, structures and buildings, roadways, and pavement

Table 1 shows the bird species included in the CCA, their family, guild, and code names. Bird species were distributed in the CCA ordination plot based on the sites in which the collisions occurred and in association with the environmental variables at the sampling sites. The relationship between bird species collisions and environmental variables (Fig. 3) contrasts the species most commonly found resulting from collisions at buildings with higher amounts of vegetation to those from locations with greater amounts of hardened surfaces. Bird species that were associated with higher percent amounts of canopy cover and exposed habitat (i.e., GreenLevels) were those species that typically occur in forested habitats and that are considered foliage gleaners (FF) such as the Golden-crowned Kinglet (GCKI), the Blackpoll Warbler (BLPW), and the Blue-headed Vireo (BHVI) (Fig. 4). Bird species that were associated with higher percent cover of pavement (P), buildings (S), and roads (R) (i.e., the opposite end of GreenLevels) were composed of both species that typically occur in forested habitats and species that typically occur in open woodland. A majority of the forest habitat species found on the opposite end of GreenLevels were ground foragers (FG) such as the Ovenbird (OVEN), the White-throated Sparrow (WTSP), and the Winter Wren (WIWR) (Fig. 4).

As mentioned above, GreenLevels illustrate a strong gradient in the level of urbanization and bird species were distributed along the length of this gradient. Of the most abundant species (≥100 individuals), both the Black-capped Chickadee (BCCH) and the Magnolia Warbler (MAWA) were close to the origin of the vector line of GreenLevels which is consistent with the fact that they occur somewhat evenly in all sites or have no strong association with this environmental condition. Bay-breasted Warbler (BBWA), Mourning Dove (MODO), Philadelphia Vireo (PHVI), and Eastern Phoebe (EAPH) occurred at the extremes of the graph and occurred relatively rarely in the dataset (≤10 individuals). Considering the family level of birds in the CCA, we noted that members of the Parulidae were more strongly associated with higher GreenLevels (high tree canopy and exposed habitats; Fig. 5). This pattern was also true for the members of the Vireonidae, Paridae, Turdidae, and Regulidae. On the other hand, members of the Emberizidae were found either on the opposite end of GreenLevels or close to the origin of the vector line of GreenLevels. Members of the Paridae (BCCH) were relatively close to the origin (Fig. 5). Thus, the Paridae family was associated with both greenery and heavy urbanization which is consistent with the aforementioned observation on their distribution across sites. Species associated with PGlass seem to be species that collided more frequently whereas species associated with the opposite end of PGlass were generally recorded in lower numbers.

Discussion

Studies that have incorporated glass percentage of buildings as a predictor variable in BWCs have typically noted an increase in collisions with increased glass surface area (Klem 1990a; Klem et al. 2009; Borden et al. 2010; Hager et al. 2013). Our results are consistent with those findings as we observed that BWCs increased significantly with increased building façades covered by reflective glass. The glass surface area of a building is part of what Hager et al. (2013) called the building mortality signature and not surprisingly, is one of the most important predictor of BWCs (Klem et al. 2009; Borden et al. 2010). In our study, we did not discriminate between the type of glass (reflective versus transparent) considering that practically all of our data originated from collisions on reflective glass panels and that the characteristics of glass can vary depending on the orientation relative to light source (e.g.,

Table 1 Bird species included in the canonical correspondence analysis

Common name	Code name	Latin name	Family	Habitat guild	Foraging guild
American Redstart	AMRE	*Setophaga ruticilla*	Parulidae	Forest	Foliage Gleaner
American Robin	AMRO	*Turdus migratorius*	Turdidae	Open Woodland	Ground Forager
American Woodcock	AMWO	*Scolopax minor*	Scolopacidae	Forest	Probing
American Tree Sparrow	ATSP	*Spizella arborea*	Emberizidae	Open Woodland	Ground Forager
Baltimore Oriole	BAOR	*Icterus galbula*	Icteridae	Open Woodland	Foliage Gleaner
Black-and-white Warbler	BAWW	*Mniotilta varia*	Parulidae	Forest	Bark Forager
Bay-breasted Warbler	BBWA	*Setophaga castanea*	Parulidae	Forest	Foliage Gleaner
Black-capped Chickadee	BCCH	*Poecile atricapillus*	Paridae	Forest	Foliage Gleaner
Blue-headed Vireo	BHVI	*Vireo solitarius*	Vireonidae	Forest	Foliage Gleaner
Blackburnian Warbler	BLBW	*Setophaga fusca*	Parulidae	Forest	Foliage Gleaner
Blue Jay	BLJA	*Cyanocitta cristata*	Corvidae	Forest	Ground Forager
Blackpoll Warbler	BLPW	*Setophaga striata*	Parulidae	Forest	Foliage Gleaner
Brown Creeper	BRCR	*Certhia americana*	Certhiidae	Forest	Bark Forager
Black-throated Blue Warbler	BTBW	*Setophaga caerulescens*	Parulidae	Forest	Foliage Gleaner
Black-throated Green Warbler	BTNW	*Setophaga virens*	Parulidae	Forest	Foliage Gleaner
Canada Warbler	CAWA	*Cardellina canadensis*	Parulidae	Forest	Foliage Gleaner
Cedar Waxwing	CEDW	*Bombycilla cedrorum*	Bombycillidae	Open Woodland	Foliage Gleaner
Common Yellowthroat	COYE	*Geothlypis trichas*	Parulidae	Scrub	Foliage Gleaner
Chestnut-sided Warbler	CSWA	*Setophaga pensylvanica*	Parulidae	Open Woodland	Foliage Gleaner
Dark-eyed Junco	DEJU	*Junco hyemalis*	Emberizidae	Forest	Ground Forager
Eastern Phoebe	EAPH	*Sayornis phoebe*	Tyrannidae	Open Woodland	Flycatching
Eastern Wood-Pewee	EAWP	*Contopus virens*	Tyrannidae	Forest	Flycatching
Eastern Whip-poor-will	EWPW	*Antrostomus vociferus*	Caprimulgidae	Open Woodland	Aerial Forager
Fox Sparrow	FOSP	*Passerella iliaca*	Emberizidae	Forest	Ground Forager
Golden-crowned Kinglet	GCKI	*Regulus satrapa*	Regulidae	Forest	Foliage Gleaner
Gray-cheeked Thrush	GCTH	*Catharus minimus*	Turdidae	Forest	Ground Forager

Table 1 (continued)

Common name	Code name	Latin name	Family	Habitat guild	Foraging guild
Gray Catbird	GRCA	*Dumetella carolinensis*	Mimidae	Open Woodland	Ground Forager
Hermit Thrush	HETH	*Catharus guttatus*	Turdidae	Open Woodland	Ground Forager
House Wren	HOWR	*Troglodytes aedon*	Troglodytidae	Open Woodland	Foliage Gleaner
Indigo Bunting	INBU	*Passerina cyanea*	Cardinalidae	Open Woodland	Foliage Gleaner
Least Flycatcher	LEFL	*Empidonax minimus*	Tyrannidae	Forest	Flycatching
Lincoln's Sparrow	LISP	*Melospiza lincolnii*	Emberizidae	Scrub	Ground Forager
Magnolia Warbler	MAWA	*Setophaga magnolia*	Parulidae	Forest	Foliage Gleaner
Mourning Dove	MODO	*Zenaida macroura*	Columbidae	Open Woodland	Ground Forager
Mourning Warbler	MOWA	*Geothlypis philadelphia*	Parulidae	Forest	Foliage Gleaner
Nashville Warbler	NAWA	*Oreothlypis ruficapilla*	Parulidae	Forest	Foliage Gleaner
Northern Flicker	NOFL	*Colaptes auratus*	Picidae	Open Woodland	Ground Forager
Northern Parula	NOPA	*Setophaga americana*	Parulidae	Forest	Foliage Gleaner
Northern Waterthrush	NOWA	*Parkesia noveboracensis*	Parulidae	Forest	Ground Forager
Orange-crowned Warbler	OCWA	*Oreothlypis celata*	Parulidae	Forest	Foliage Gleaner
Ovenbird	OVEN	*Seiurus aurocapilla*	Parulidae	Forest	Ground Forager
Palm Warbler	PAWA	*Setophaga palmarum*	Parulidae	Open Woodland	Ground Forager
Philadelphia Vireo	PHVI	*Vireo philadelphicus*	Vireonidae	Forest	Foliage Gleaner
Pine warbler	PIWA	*Setophaga pinus*	Parulidae	Forest	Bark Forager
Rose-breasted Grosbeak	RBGR	*Pheucticus ludovicianus*	Cardinalidae	Forest	Foliage Gleaner
Red-breasted Nuthatch	RBNU	*Sitta canadensis*	Sittidae	Forest	Bark
Ruby-crowned Kinglet	RCKI	*Regulus calendula*	Regulidae	Forest	Foliage Gleaner
Red-eyed Vireo	REVI	*Vireo olivaceus*	Vireonidae	Forest	Foliage Gleaner
Ruby-throated Hummingbird	RTHU	*Archilochus colubris*	Trochilidae	Open Woodland	Hovering
Song Sparrow	SOSP	*Melospiza melodia*	Emberizidae	Open Woodland	Ground Forager
Swamp Sparrow	SWSP	*Melospiza georgiana*	Emberizidae	Marsh	Ground Forgager
Swainson's Thrush	SWTH	*Catharus ustulatus*	Turdidae	Forest	

Table 1 (continued)

Common name	Code name	Latin name	Family	Habitat guild	Foraging guild
					Foliage Gleaner
Tennessee Warbler	TEWA	*Oreothlypis peregrina*	Parulidae	Forest	Foliage Gleaner
Veery	VEER	*Catharus fuscescens*	Turdidae	Forest	Ground Forager
Virginia Rail	VIRA	*Rallus limicola*	Rallidae	Marsh	Probing
White-breasted Nuthatch	WBNU	*Sitta carolinensis*	Sittidae	Forest	Bark Forager
White-crowned Sparrow	WCSP	*Zonotrichia leucophrys*	Emberizidae	Scrub	Ground Forager
Wilson's Warbler	WIWA	*Cardellina pusilla*	Parulidae	Scrub	Foliage Gleaner
Winter Wren	WIWR	*Troglodytes hiemalis*	Troglodytidae	Forest	Ground Forager
Wood Thrush	WOTH	*Hylocichla mustelina*	Turdidae	Forest	Ground Forager
White-throated Sparrow	WTSP	*Zonotrichia albicollis*	Emberizidae	Forest	Ground Forager
Yellow-bellied Sapsucker	YBSA	*Sphyrapicus varius*	Picidae	Forest	Bark Forager
Yellow-rumped Warbler	YRWA	*Setophaga coronata*	Parulidae	Forest	Foliage Gleaner

All species that occurred in less than 5 % of the samples in a Presence/Absence matrix were removed. The species alpha names were used in the analysis along with their habitat and foraging guild. All species were grouped under the label BWC for the Kendall's tau coefficient

sun versus internal building lights). Ideally, considering glass panels and objects of collisions from a bird's visual perspective would be ideal towards understanding the importance of glass type on BWCs (Martin 2011). However, this type of study requires a minute sensory and physiological approach to birds' visual perception and is outside the realm of the broader issues we address.

Amounts of exposed habitats, cover of building structures, and road cover within a 500 m radius from buildings were environmental features that had a strong association with BWCs per building. To our knowledge, it is unusual for BWC studies to incorporate environmental variables from larger geographical scales. Hager et al. (2013) measured distance to potential stopover habitat over 0.5 ha, and, although they noted a significant effect of distance on bird abundance, richness, and diversity, they observed a non-significant effect of this variable on BWCs. Here, it should be noted that their measure of large landscape variable was a distance metric from point A to point B as opposed to a metric considering the proportional composition of various landscape variables. In this study, we focused primarily on large-scale environmental features as proportional variables and noted a strong association between these landscape conditions and the composition of species colliding in buildings. Large-scale variables, such as those measured within 500 m, possibly influence or account for the effect of local variables (variables within the vicinity of the building) and bird density on BWC frequencies. Indeed, most studies on bird distribution in the urban landscape (i.e., studies not focused on collision issues) do include large-scale variables (e.g., a 500 m radius circle from
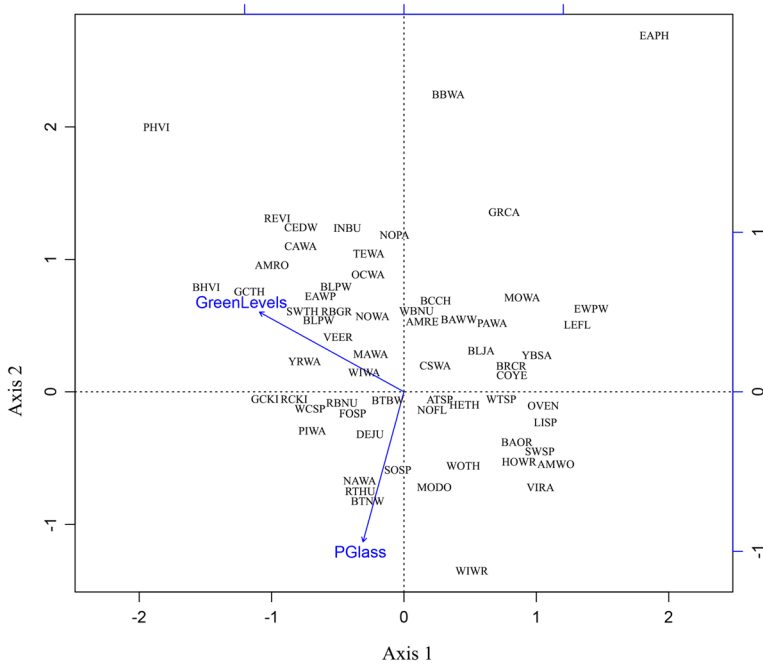
Fig. 3 Canonical correspondence ordination plot of a total of 63 bird species showing the association between species distribution across urban sites and their likelihood to collide based on given environmental variables. 'GreenLevels' is the resulting data from CA Axis I and is a measure of vegetative cover summarizing canopy cover, exposed habitats, structures and building cover, road cover, and paved surfaces

survey sites in Melles et al. 2003) and recognize the effect of those variables on bird abundance, distribution, and species composition (Flather and Sauer 1996; Melles et al. 2003; Suarez-Rubio and Thomlinson 2009; Minor and Urban 2010). Therefore, if landscape characteristics influence the overall numbers of birds and the relative numbers of species, then large-scale variables are expected to affect collision patterns (Klem 1989; Dunn 1993; Bayne and Rawson-Clark 2012). Following these assumptions, the impact of exposed habitats, structures, and roads within 500 m of buildings on BWC supports the hypothesis in which bird collisions will increase with increased numbers of birds present in the area. The exposed habitat variable was positively related with BWCs whereas the structure and the roads variables were negatively related with BWCs. Based on these findings we suggest that BWCs will decrease with more intensified levels of urbanization, and associated lack of green space, a conclusion which is consistently found in other BWC studies focusing on small geographical scale environmental variables (Borden et al. 2010; Hager et al. 2013). While most studies on bird distributions acknowledge that severe levels of urbanization decrease bird species diversity (Edgar and Kershaw 1994; Melles et al. 2003), others have noted variable effects of the levels of urbanization on bird diversity and abundance (Blair 1996). Therefore, the non-significant results from the canopy cover and the paved surfaces variables in explaining overall numbers of collisions, does not detract from their potential influence on the types of species involved in the collisions. Some species that have sometimes been observed in high abundance near collision sites, did not collide with windows (Dunn 1993; Hager et al. 2013). As a consequence, the environmental resource hypothesis cannot be evenly
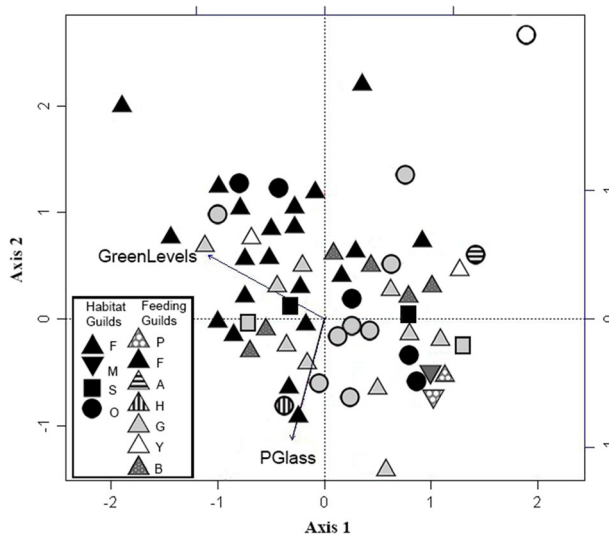
Fig. 4 Canonical correspondence ordination plot of a total of 63 bird species arranged in guilds showing the association between guild distribution across urban sites and their likelihood to collide based on given environmental variables. Habitat guilds are indicated by the shape of the data point and the legend indicates this relationship with F standing for forest habitat guild, O for open woodland habitat guild, S for scrub habitat guild, and M for Marsh habitat guild. Foraging behavior guilds are indicated by the fill of the symbol and the legend indicates this relationship with P standing for probing foraging behavior, F standing for foliage gleaning foraging behavior, A standing for aerial foraging behavior, H standing for hovering foraging behavior, G for ground dwelling foraging behavior, Y for flycatching foraging behavior, and B for bark foraging behavior. 'GreenLevels' is the resulting data from CA Axis I and is a measure of vegetative cover summarizing canopy cover, exposed habitats, structures and building cover, road cover, and paved surfaces

applied for all bird species and collision studies must acknowledge the fact that collision patterns are species specific with differential impacts on different species. A few recent studies have pointed out the necessity to measure the impact of collisions on bird populations by adopting a species-specific approach (Schaub et al. 2011; Loss et al. 2012; Longcore and Smith 2013; Machtans et al. 2013).

Our results indicate that the variation in BWCs follows a gradient of urbanization intensity but collisions in the city of Toronto do occur even if the landscape is heavily urbanized. This suggests that not all species respond similarly to urbanization. "Urban adapted" species have been noted to thrive and have a high survival rate in urban centers (Stracey and Robinson 2012b) whereas sensitive species will often be associated with the greener end of the urbanization spectrum (Melles et al. 2003). We focused on migratory species that are likely to be more sensitive to urban development, rather than urban resident species, although some migratory species adapt quite well to urbanization. Additionally, it is important to note that we did not discriminate between dead and injured birds as injured birds may survive or may die off from injuries subsequently (Klem 1990b) and neither the state of injury nor the post-collision survival rate were monitored by FLAP. This inevitably adds a crippling bias to our study which may have lead us to underestimate overall BWCs (Loss et al. 2014) or species specific collisions. As expected, the CCA indicated that species that collided with buildings in the financial district of the urban core were generally different in terms of guilds and families from species that collided with buildings in the other two regions, areas less intensely

Fig. 5 Canonical correspondence ordination plot of a total of 20 bird families showing the association between bird family distribution across urban sites and their likelihood to collide based on given environmental variables. 'GreenLevels' is the resulting data from CA Axis I and is a measure of vegetative cover summarizing canopy cover, exposed habitats, structures and building cover, road cover, and paved surfaces. The abbreviations correspond to the following bird families: *PA* Parulidae, *TU* Turdidae, *SC* Scolopacidae, *EM* Emberizidae, *PR* Paridae, *VI* Vireo, *CO* Corvidae, *CE* Certhiidae, *BO* Bombycillidae, *TY* Tyrannidae, *CA* Caprimulgidae, *RE* Regulidae, *MI* Mimidae, *TR* Troglodytidae, *CD* Cardinalidae, *CU* Columbidae, *PI* Picidae, *ST* Sittidae, *TC* Trochilidae, *RL* Rallidae

developed. New World Warblers, Vireos, Chickadees, Thrushes, and Kinglets were more strongly associated with higher levels of canopy cover and exposed habitats. American Sparrows were associated more strongly with higher levels of urban development. Some New World Warbler and Thrush species also seemed to occur in more urbanized areas, but most species belonging to these families were associated with higher levels of greenery. As an example, the Northern Parula, a member of the Parulidae family, was strongly associated with higher levels of vegetation. This is consistent with the observation from Minor and Urban (2010) who noted that the Northern Parula was strictly associated with rural environments and absent from urban regions. On the other hand, the Black-capped Chickadee was associated with both greenery and heavy levels of urbanization. Melles et al. (2003) observed a similar trend and described the Black-capped Chickadee as being an "urban-adapted" species. The Ruby-Crowned Kinglet and the Golden-Crowned Kinglet are both members of the Regulidae family and tended to collide more regularly in less urbanized sites suggesting that those species are sensitive to urban development. This observation is consistent with findings by Kalinowski and Johnson (2010) who reported that the Ruby-crowned Kinglet was associated with vegetative cover and were negatively related to road and structure cover. Although trends are observable at a species and genus level, using families in a gradient analysis further helped

us determine that bird species collisions tended to show distinct family clusters. Within a single bird family, species will tend to share common features and will often belong to the same foraging or habitat guild. The results from this direct gradient analysis suggest that distinct and predictable clusters of bird families will collide within given geographical regions that hold a set of particular environmental and building variables. Studies on bird diversity and distribution associated with landscape features have been conducted elsewhere (Melles et al. 2003; Kalinowski and Johnson 2010; Minor and Urban 2010), but remain difficult to compare with a study performed in the Toronto area as some of the bird species are different or adopt different life-history strategies and as the landscape itself may differ in characteristics.

The distribution of species colliding across the urban landscape of Toronto and the factors that may affect these collisions, can be further understood when considering bird guilds. For this study we selected both species habitat guilds and species foraging guilds and excluded nesting guilds from the analysis because some migratory birds are only transient in Toronto. Our observations indicate that bird species typically found in forest habitats collide both in heavily urbanized areas and areas with higher levels of vegetation. However, among those species, a majority of foliage gleaners (such as the Blue-headed Vireo, the Canada Warbler, and the Golden-crowned Kinglet) were associated with higher levels of canopy cover and exposed habitats, whereas a majority of ground foragers (such as the Ovenbird, the White-throated Sparrow, and the Blue Jay) were associated with higher levels of structure and building cover, roads, and paved surfaces. The same is true for species that usually occur in open woodland habitats. Among the species that typically occur in open woodland, a majority of foliage gleaners collided in sites with greater cover of exposed habitats and canopy whereas a majority of ground foragers collided in sites with greater cover of structures and buildings, roads, and paved surfaces. These results are consistent with observations from Beissinger and Osborne (1982) who found that birds in an urban site were dominated by ground gleaners whereas birds in a forest site were dominated by foliage gleaners. Those authors attributed these patterns to vegetation type, habitat patchiness, and foliage volume, e.g., suburban grass patch can offer a rich food source for ground dwellers.

Close examination of these results and their interpretation demonstrate the need to focus on individual species when attempting to assess the impact of BWCs on bird populations. Based on our results from the bird family gradient analysis and the guild gradient analysis we conclude that buildings with high glass cover in both highly urbanized areas and areas with more greenery will represent a greater threat to a wide range of bird species. Blair (1996) suggested that suburban areas are often comprised of a great diversity of birds due to the heterogeneous nature of the vegetation present. In our study, two suburban areas are relatively close (<300 m for Consilium Place) and very close (<5 m for York Mills) to ravines and patches of natural habitats including strips of closed canopy woods, rivers, riparian habitats, and more importantly channels of natural habitats. These channels, such as abandoned railway corridors, are often bordered with dense vegetation and extend in a capillary fashion across the city leading from parks and ravines to gardens and building clusters. As such, the York Mills and Scarborough regions are both connected to this complex green system whereas the financial district is relatively isolated and forms a pocket of heavily urbanized grounds. In concordance with these landscape observations, a greater number of bird families and more foliage gleaners collided in urban areas with more greenery (York Mills and Consilium Place). Thus, species from foliage gleaner guilds are more likely attracted by areas and stop-over habitats that include greater plant diversity that offer closed canopy shelter, and/or that comprise of riparian zones. They will occur in greater abundance and collide in windows of

buildings situated near natural sites or at the end of channels connected to natural sites. The financial district of Toronto is associated with a complex landscape dynamic that can be harder to interpret. Although this area of the city forms a dense cluster of tall buildings, it is also adjacent to Lake Ontario with large amounts of adjoining forested parklands. Migratory species caught in the urban matrix of the financial district could be derived from two distinctive categories of birds; bird species requiring specific types of natural resources flying over Lake Ontario straight from the nearby stop over habitats, or "urban-positive" bird species that are more adapted to urban features and that can take advantage of small parks and individual trees or bushes within the financial district to replenish their energy during migration. Furthermore, there is an important light pollution component that is associated predominantly with tall buildings of the financial district in Toronto. Light attracts and disorient birds that can subsequently get caught in heavily urbanized areas and eventually collide in windows during the night-time or the day-time in an attempt to escape from an unfamiliar and threatening environment (Verheijen 1958, 1981; Herbert 1970; Ogden 1996).

Klem et al. (2009) suggested that BWCs could be moderated by reducing the number of bird attractants near buildings and by reducing the amount of glass on building façades. Fontana et al. (2011) clearly demonstrated the importance of grass, bush, and tree cover as well as tree composition in shaping bird community structure in cities. We found that urban greenery accounts for a significant proportion of the variation observed in BWCs in Toronto. However, from a social perspective, the physical and psychological benefits of urban green spaces (Fuller et al. 2007) cannot be overlooked when attempting to mitigate BWCs. If urban natural environments are valuable assets for both birds (Flather and Sauer 1996) and humans (Vries et al. 2003), alternative solutions to removing green spaces must be considered. A number of buildings around Toronto have recently applied bird window markers on some of their facades and FLAP Canada is currently attempting to measure the efficacy of those strategies.

Our study provides a first estimate of patterns of window collisions at the species level. Further study of the impact of such collisions on local bird communities is an important future consideration. Estimating the various landscape features and building attributes that affect BWCs remains important both at the local and landscape scale. However, studies will benefit by focusing on individual species or clusters of species rather than by generalizing their results to all bird species combined. The impact of BWCs on bird populations will remain difficult to assess unless careful and detailed observation is carried at the species level, coupled with distribution data, and analyzed at the community level rather than considering all species to be equivalent.

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