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Bird-Window Collisions And Reflection As A Daytime Risk Factor

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APPROVAL PAGE

This Thesis is submitted in partial fulfillment of
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Master of Science

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COMPLIANCE PAGE

Research approved by

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ABSTRACT

Bird-window collisions account for millions of bird deaths annually in the United States. Despite many correlative studies citing the potential influence of reflective glass on daytime collision risk, few studies have explicitly tested this hypothesis. We aimed to determine whether reflection from a window influences daytime collision risk by manipulating the lighting conditions on exterior and interior window surfaces. We conducted this research within a flight tunnel in which domesticated zebra finches (*Taeniopygia guttata*) flew towards a window structure with two windows situated behind a mist-net. We assessed collision risk and flight velocity through 3D videography. We predicted that risk of collision and flight velocity would be greater when windows were manipulated to reflect more light, regardless of exterior lighting conditions. We found no support for our predictions. In contrast, we found that collision risk decreased in the presence of a reflection during bright, midday exterior lighting conditions. Some trends lacking statistical support suggest that reflection may increase collision risk, but likely only at certain times of day. We documented a greater number of collisions and slightly increased flight velocity towards windows which reflected more light in the morning. Reflection has often been hypothesized and documented as a detrimental risk factor. We suggest that the influence of window reflection on daytime window collisions is more complex than assumed and might involve previously unaccounted properties of light such as polarization. Mitigation technology has often been tested in the absence of ecologically relevant lighting conditions which may solely influence risk of collision. We call for the implementation of more robust, standardized methods of testing which account for realistic lighting conditions which birds might experience. Altering lighting conditions throughout the day could be implemented as an additional mitigation strategy, though the influence of lighting conditions on collision risk needs to be studied on a broader scale.

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Chapter 1

Bird-Window Collisions and Reflection as a Daytime Risk Factor

Introduction

Urbanization has led to increased contact and conflict between humans and wildlife. While some species thrive in urban environments, the majority have experienced drastic declines. Anthropogenic change such as habitat destruction and increasing prevalence of human-made structures in the landscape has resulted in substantial declines in bird populations over the last 50 years (Rosenberg et al, 2019). In particular, the increased presence of artificial structures such as cell phone towers, power lines, wind turbines, commercial buildings, and residences within the infrastructure of the United States has led to a subsequent increase in the number of deadly collisions with these structures (Drewitt & Langston, 2008; Erickson et al, 2001; Loss et al, 2015). Collisions with artificial structures are evolutionarily recent, meaning that many bird species have not yet adapted to avoid this source of mortality. Some species experience fewer collisions than others as a result of various species-specific factors such as habitat preference, but seemingly no species is exempt from the risk of collisions (Klem, 1989, 2006). Thus, collisions with structures have resulted and continue to result in large-scale mortality.

Bird-window collisions result in approximately 1 billion bird deaths annually (Loss et al, 2014). Bird-window collisions happen in nearly every weather condition, season, and time of day (Klem, 1989) but the number of collisions that accumulate is dependent on several factors. Species-specific factors that increase susceptibility to window collisions include taxonomy, migratory status, and innate behavior. Songbirds (avian order Passeriformes) are found most often as collision victims in comparison to any other order (Brown et al, 2020; Cusa et al, 2015; Elmore et al, 2020; Hager et al, 2008;

Hager & Craig, 2014; Riding et al, 2019; Wittig et al, 2017). Within this order, migrants are typically more susceptible to collisions than resident species (Bracey et al, 2016; Hager et al, 2008; Hager & Craig, 2014; Wittig et al, 2017). Nocturnal long-distance migrants are at highest risk of window collision with some species being identified as "super colliders" (Arnold & Zink, 2011), which include the Golden-winged Warbler (*Vermivora chrysoptera*), Canada Warbler (*Cardellina canadensis*), Kentucky Warbler (*Geothlypis formosa*) and Wood Thrush (*Hylocichla mustelina)* (Elmore et al, 2020; Loss et al, 2014). All of the aforementioned species have also been listed as Birds of Conservation Concern (United States Fish & Wildlife Service, 2008). Innate behavior, such as foraging behavior, can also increase susceptibility to collisions. For example, the consumption of pear fruit by Cedar Waxwings during the winter season has been shown to increase susceptibility to window collisions on a university campus (Brown et al, 2020).

While some species are inherently more susceptible to collisions, vulnerability to collision can be highly dependent on additional structural and landscape-level factors. Bird-window collisions occur most often at residential and low-rise buildings and less often at high-rise buildings (Loss et al, 2014; Machtans et al, 2013). Unsurprisingly, buildings and residences that contain a greater abundance of glass typically cause greater numbers of collisions (Borden et al, 2010; Cusa et al, 2015; Elmore et al, 2020; Loss et al, 2019; Ocampo-Peñuela et al, 2016). At the façade level, the number of collisions increases with length, height, and proportion of glass (Riding et al, 2019). Expanding outward to the landscape level, the presence of feeders has been shown to increase collision risk (Klem et al, 2004; Kummer & Bayne, 2015; Kummer et al, 2016). Lastly, collision risk increases in the presence of vegetation or greenspace, especially for species that typically reside in forested habitats (Borden et al, 2010; Brown et al, 2020; Cusa et al, 2015; Kummer et al, 2016; Loss et al, 2019). Taken together, collision risk is not constant throughout a landscape. Rather, collision risk varies as a result of certain building and landscape attributes in addition to underlying species-specific factors.

The presence of Artificial Lighting at Night, or ALAN, has been emphasized as the most important risk factor involved in collisions (Evans-Ogden, 1996). It is proposed that ALAN disorients and entraps birds in urban areas, increasing risk of window collision (Evans-Ogden, 1996; Herbert, 1970; Van Doren et al, 2017). If ALAN does not directly cause a collision, the entrapment effect of artificial light can increase the likelihood of exhaustion, starvation, predation and subsequently, daylight collision (Evans-Ogden, 1996; DeCandido & Allen, 2006). Multiple studies have supported the hypothesis that the presence of ALAN increases collision risk in urban areas and thus, the emphasis on ALAN as the primary determinant of collision risk has persisted (Evans-Odgen, 2002; Parkins et al, 2015; Winger et al, 2019; Lao et al, 2020).

Recent research suggests that window reflection might be just as detrimental or more detrimental to birds in comparison to ALAN, which is in contrast to the claims of Evans-Ogden (1996). Glass area and proportion of surrounding vegetation are stronger predictors of collision risk in comparison to ALAN, suggesting that artificial light at night might be less important than originally proposed (Loss et al, 2019). Additionally, a substantial number of collisions have been documented at urban buildings which emitted little to no artificial light at night but had greater window coverage and nearby vegetation (Gelb & Delacretaz, 2009). These findings do not preclude the importance of ALAN. Rather, they emphasize the importance of studying window reflection as a potential driver of collisions.

The potential influence of reflection on bird-window collisions has been cited since the late 1900s (Banks, 1976; Klem, 1989, 1990). Observations that support the notion that birds cannot distinguish between reflected and realized habitat have dated back even further (Censky & Ficken, 1982; Ritter & Benson, 1934). Unlike humans, birds lack refined binocular vision (Martin, 2009, 2011), thus the two-dimensional vegetation reflected in a window likely appears similar to three-dimensional vegetation as a bird flies towards a window structure. Given the limitations of avian vision and cognition, it has been hypothesized that reflections deceive and attract birds, causing a greater number of collisions than would be expected in the absence of reflection (Borden et al, 2010; Gelb & Delacretaz, 2006, 2009; Klem, 1989, 1990; Kummer & Bayne, 2015; Kummer et al, 2016; Parkins et al, 2015; Wittig et al, 2017).

There is limited indirect and direct evidence to suggest that reflection is an important risk factor during the daytime. Collision risk has been shown to increase when there is a higher proportion of glass, but also a presence of nearby trees (Borden et al, 2010). The presence of or increased coverage of reflective windows has been shown to positively correlate with the number of collisions documented (Brown et al, 2020; Cusa et al, 2015; Kummer et al, 2016). One piece of direct evidence demonstrated that in a pseudo-field environment, the presence of a mirror caused a greater number of fatal collisions in comparison to a clear window (Klem & Saenger, 2013). While there is some evidence that suggests reflection could be detrimental to birds flying towards windows, almost all of the studies have taken a correlative approach rather than an experimental approach. Therefore, there is minimal direct evidence that a bird's perception of a reflection increases collision risk.

Windows can become reflective as a result of the inherent window properties or the lighting conditions surrounding the window. The potential influence of reflections that form on mirrored windows or windows with reflective coatings has been emphasized (Brown et al, 2020; Cusa et al, 2015; Klem & Saenger, 2013), while the influence of reflections that form as a result of lighting conditions have rarely been considered in the collision literature. The intensity of the reflection seen on the exterior of a clear window can change as a function of the interior and exterior light intensity surrounding the window (Knight, 2017). As a result, a clear window may not always produce a strong reflection of the surrounding habitat. Rather, the reflective nature of the window changes throughout the day. When the interior of a clear window is lower in intensity, the window appears most strongly as a reflection of the surrounding habitat. Upon increasing the lighting intensity on the interior of a window, the reflected image becomes less visible as the interior lighting masks the reflected image (Figure 1; A vs B, C vs D). Given that the intensity of reflection changes as a function of lighting conditions, the effect of reflection on collision risk is not likely to be constant in various lighting conditions.

Our main research objective was to determine whether the presence of a reflection in a clear window influences collision risk. Instead of exposing birds to inherently mirrored or reflective windows, we took a different approach and manipulated the lighting conditions on the interior of the windows in order to create a reflective and less-reflective condition. We investigated our objective by quantifying collision risk within a flight tunnel as birds were flown under these conditions at two times of day (morning and midday). Conducting this study in a flight tunnel allowed us to control lighting conditions while also allowing us to obtain a sufficient sample size in a short period of time; though we recognize that performing these tests in field conditions would also be important.

In order to address our main research objective, we aimed to answer two research questions. Our first question was: Does the presence of a reflection on the exterior of a window increase collision probability? Further, does the effect of reflection vary at different exterior light intensities (or times of day)? We predicted that when birds approach more reflective windows, collision probability would increase. We also predicted that this effect would be consistent in different exterior lighting intensities. Our second question that we aimed to answer was: Does the presence of a reflection on the exterior of a window influence flight velocity towards the window? Additionally, does any effect of reflection on velocity remain consistent at different exterior light intensities (or times of day)? We predicted that regardless of exterior lighting intensity, flight velocity would be increased towards more reflective windows.

Identifying risk factors involved in bird-window collisions provides utility in predicting collision vulnerability at various buildings and in various species, but many risk factors have been identified as correlations that lack direct evidence of causality. In order to more clearly assess the impact of various risk factors on collision risk, experimental studies must be conducted. Our study took an experimental approach in determining the influence of reflection on collision risk. By clearly identifying risk factors, we can more properly tailor solutions on a case-by-case basis in order to ensure reductions in the net total number of collisions. As the world continues to develop, collisions with building structures will continue to pose a large risk to bird populations. Therefore, learning more about the factors that cause birds to collide with windows is essential for conservation efforts.

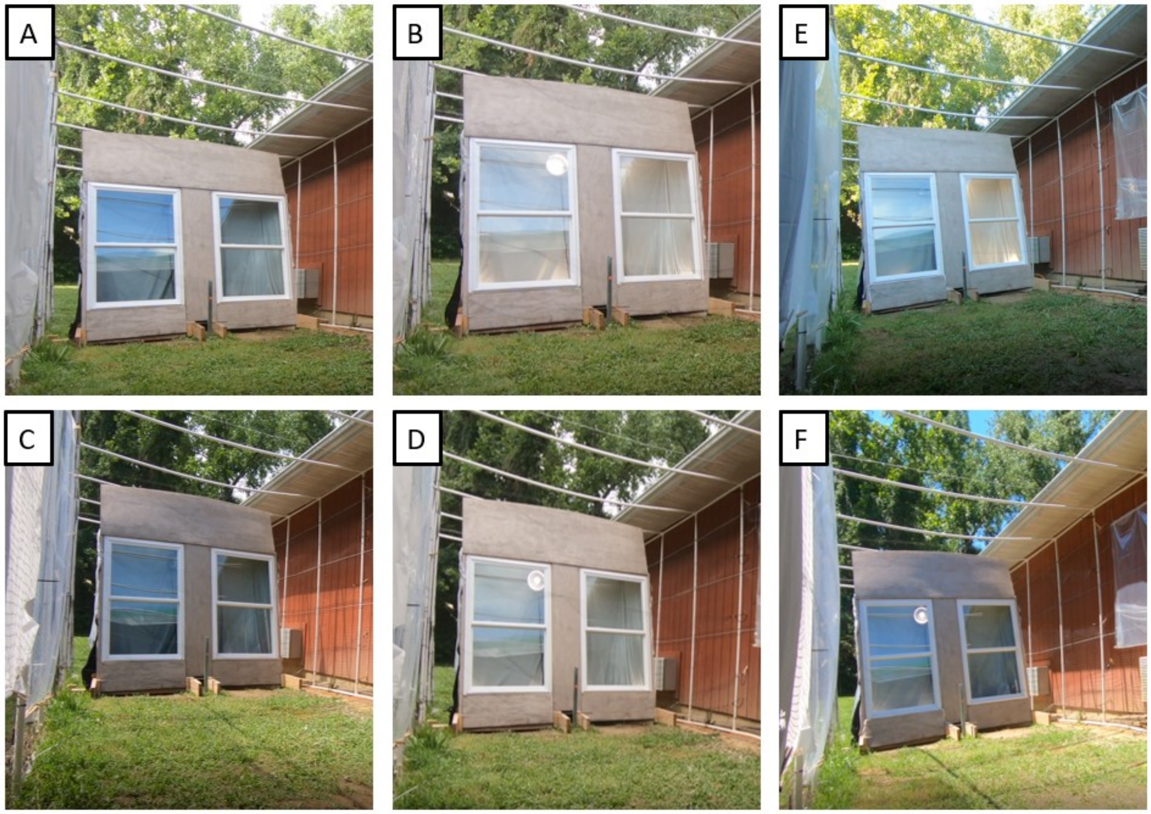


Figure 1. A visual representation of the 6 treatments. Two intensity conditions (lower and higher) in both the interior and exterior were combined pairwise in order to form 6 overall treatments. **(A)** lower interior, lower exterior; **(B)** higher interior, lower exterior; **(C)** lower interior, higher exterior; and **(D)** higher interior and higher exterior. **(E)** and **(F)** represent the two choice treatments in morning, low exterior conditions and midday, high exterior conditions, respectively.

Methods

Ethics statement

The flight tunnel protocol outlined below was approved by the William & Mary Institutional Animal Care and Use Committee (IACUC-2019-09-22-13861-jpswad).

Experimental subjects

We used a total of 100 adult, domesticated zebra finches (*Taeniopygia guttata*; n =16-17 per treatment group) in this study, all of which appeared to be in healthy condition. Prior to flight trials, birds were housed in three outdoor free-flight aviaries (3 x

3 x 2.5 m) in Williamsburg, Virginia, USA, and had access to ad libitum millet blend food (Volkman science diet), drinking water containing vitamin supplements, perches, and bathing water. Birds were tested in groups of approximately 25 individuals. Two to three days prior to flight trials for a particular group of birds, they were moved into one indoor free-flight room that offered the same housing conditions as the outdoor aviaries except they were kept at approximately 21°C and on a long-day 18:6 L:D photoperiod. Birds were moved indoors for ease of capture prior to flight trials.

Zebra finches are a suitable model for window collisions studies as they are Passeriformes and this taxa are the most frequent victims of window collisions (Loss et al, 2014). The finches used in the study were raised in captivity and were somewhat accustomed to human presence and handling. Using a captive reared species might minimize some effects of human-induced stress on bird behavior during trials (Klem & Saenger, 2013).

Thirteen of the birds used in the study were previously exposed to tunnel conditions, of which five having been exposed to similar window flight trials (Swaddle et al, 2020). Seven of the thirteen finches had been used in a study approximately one month prior to the aforementioned trials. The prior study tested the effects of multiple acoustic warning signals on bird behavior relative to a collision hazard in a similar flight tunnel set-up to the one described below. Birds used in the warning signal study were exposed to the flight tunnel multiple times but were never exposed to a window structure. One finch was used in a pilot trial for the warning signal study, during which the bird was released once towards a collision hazard in the presence of a warning signal, but this bird was also not released towards a window structure and was not used in the three months prior to our experimental trials. Though these 13 finches had prior exposure, we did not detect signs of tunnel habituation in their flight responses, as would be shown by hesitancy to fly towards the window structure.

Flight tunnel

In order to assess the behavior of the experimental subjects in relation to the various lighting conditions surrounding two window structures, we used a flight tunnel with a simulated façade at the far end of the tunnel (Figure 2). The flight tunnel was constructed inside an open aviary structure exposed to outdoor conditions. The tunnel consisted of a PVC pipe frame (length x width x height: 14.5 x 3 x 2.5 m) enclosed with fine netting. Within this large tunnel we built a dark, open-ended 'release' tunnel (7 x 1.2 x 1.2 m) of opaque black material. This darkened release tunnel comprised the first 7 m of the flight tunnel, but only the last 2 m of the darkened release tunnel were used for the flight trials. A similar release-to-flight tunnel arrangement has been used in other flight studies (Goller et al, 2018; Klem, 1990, 2009; Rössler et al, 2015; Sheppard, 2019). The flight tunnel arrangement described here was used recently to test the effectiveness of window collision mitigation technology with both domesticated zebra finches and wild-caught brown-headed cowbirds (*Molothrus ater*) (Swaddle et al, 2020).

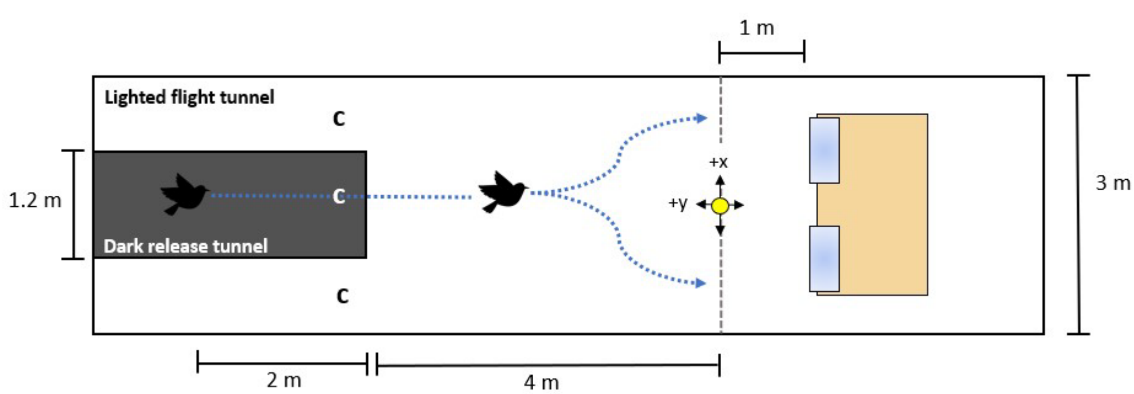


Figure 2. Flight tunnel schematic. Subjects were released 2 m from the opening of the darkened release tunnel towards the lighted flight tunnel which housed a simulated façade. The façade had two windows, which were separated by 0.5 m. A mist-net was placed approximately 1 m in front of the façade to avoid any unnecessary mortality. Subjects were recorded with 3 GoPro cameras (labeled with the letter 'C') for later flight

scoring and 3-D reconstruction of flight path. The origin of the scene was set on the ground at the midpoint between the two windows. The x-axis extended from the left to the right of the window structure, the y-axis extended from the opening of the release tunnel to the window structure and the z-axis (not noted) extended from the ground to the ceiling of the flight tunnel.

The window structure was built primarily from plywood (Figure 1). There were two wooden frames, separated by 0.5 m, that held the two single-hung replacement windows that are commonly used on residential properties in our area (Pella 250 Vinyl glass double-glazed replacement windows) (Figure 3). We painted the window structure with a beige-colored spray paint (Krylon Colormaxx spray paint, Satin Pebble) in order to simulate the side of a residential or commercial building. The window structure extended from the floor to the ceiling of the flight tunnel in order to properly simulate a façade in which the windows would be located in the center with building extending above and below the windows. The window structure was sized so that there were approximately 0.5 m gaps between the edge of the window structure and each side of the tunnel, allowing birds to avoid the window structure to the left and the right. The whole window structure was tilted backwards at 15° from vertical so that the windows primarily reflected the sky and not the flight tunnel.

Figure 3. Most common types of window structures in commercial buildings (A-E) and residences (F-J) in Williamsburg, VA. Single-hung windows **(E-J)** are the most commonly used windows in the area and thus, were selected for use in our study.

We placed three digital video cameras (GoPro HERO7 Black cameras at 1440 resolution, 60 frames per second, linear shooting mode) surrounding the opening of the darkened release tunnel to capture bird movement within the 4 m active section of the lighted flight tunnel (Figure 4). The cameras were each placed at different heights and had different views of the birds' flight (Figure A2.1). This allowed us to obtain 3-D coordinates and extract velocity measures (Jackson et al, 2016), which is explained in more detail below.

Figure 4. Camera set-up. Three GoPro HERO7 Black cameras captured flight behavior in the 4 m active section of the flight tunnel. Cameras were situated in a triangular formation, with the two lower cameras being slightly offset in order to capture the most comprehensive view of each flight. The starting point of each flight is indicated on the image with a yellow arrow.

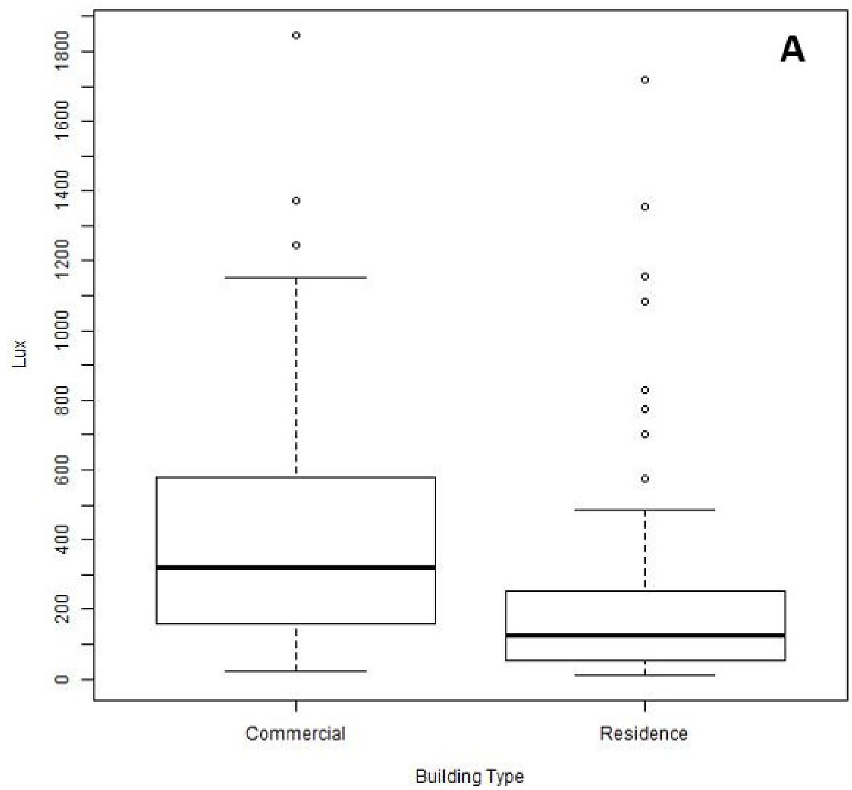
Lighting measurements to calibrate experimental treatments

In order to design a study that used realistic lighting conditions on the interior surface of a window structure, we measured artificial lighting parameters in representative buildings around Williamsburg, VA during December 2019. Within each building (16 residential, 30 low-rise commercial), we used a handheld spectrometer (WaveGo, Ocean Insight) to collect irradiance spectra and lux measurements. Specifically, within each building we obtained four measurements each from a separate room at a point that was furthest from windows while the artificial lighting was illuminated in order to isolate the intensity of artificial lighting, separate from the effects of natural lighting entering the windows. During the same time period (December 2019), we also obtained exterior recordings of irradiance and lux 0.2 m from the surface of each window in the window structure within the flight tunnel. Specifically, we obtained measurements 30 mins after sunrise, at 1200, and 30 mins before sunset. Collectively, these interior and exterior lighting measurements were used to inform the target lux ranges for our lighting treatments, described below.

Lighting treatments

We designed two levels of interior (lower/higher) and exterior (lower/higher) lighting treatments. Our measurements of interior artificial lighting intensity from representative buildings in our area ranged from 12 to 1,847 lux (commercial range = 23-1,847 lux, median = 319 lux; residential range = 12-1,719 lux, median = 126 lux; Figure 5A). Hence, we subjectively defined the lower level of our experimental interior lighting treatment to be approximately 100 lux as to remain below the median of residences, though values ranging from approximately 1 to 319 lux were accepted as low intensity. We defined the higher level of our experimental interior lighting treatment to be approximately 1,150 lux in order to maximize the variation between the low and high intensity targets, but still remain within the realistic range of lighting intensity in commercial buildings or residences. Any value above 319 lux was accepted as high intensity. We manipulated interior lighting intensity in our experiment by illuminating bulbs of different wattage in a light-sealed area behind each of the installed windows. We illuminated one 40 W bulb to create the lower interior light intensity treatment and illuminated three 100 W bulbs to produce the higher light intensity treatment.

Measurements of exterior lighting conditions in the flight tunnel ranged from about 14 to 38,653 lux (direct light range = 4,245-38,653 lux, median = 26,307 lux; indirect light range = 14-13,804 lux, median = 878 lux; Figure 5B). Much of this variation was accounted for by time of day and whether sunlight fell directly or indirectly on the sensor of the spectrometer. Informed by this variation, we subjectively defined the lower exterior lighting treatment to be approximately 10,000 lux (maximum light intensity <20,000 lux). We defined the higher exterior lighting treatment to be approximately 40,000 lux (range 20,000 to 100,000 lux). We set our target values as values within or beyond the upper quartiles of our indirect and direct lighting ranges, as to account for the increase in lighting intensity from the winter to the summer months. We created these exterior lighting conditions by conducting trials at different times of day. The lower exterior lighting trials were conducted from 0800 to 1000. During this time, the windows received indirect sunlight. We ran the higher light intensity trials from 1100 to 1300, when the windows received direct sunlight. Due to overcast midday conditions, we ran two flight trials in lighting conditions that matched the lower exterior treatment. Those flights were classified in the lower exterior lighting treatment. All interior and exterior lighting conditions were verified by spectrometry data.


A
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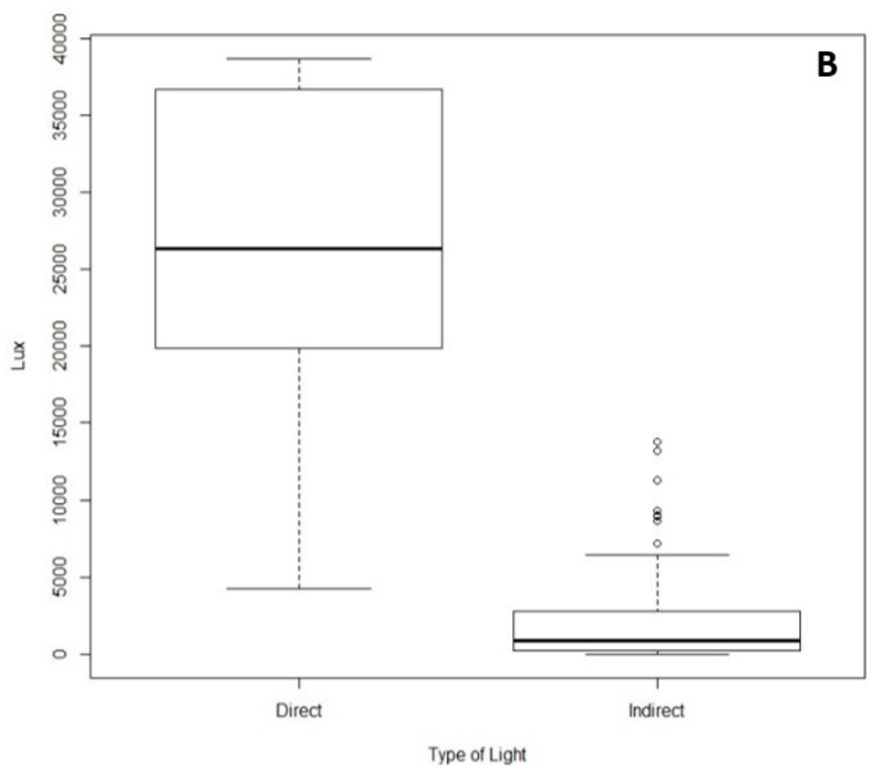
Building Type


B
Lux
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35000
30000
25000
20000
15000
10000
5000
0
Direct
Indirect
Type of Light

Figure 5. Pre-trial interior artificial light and exterior light measurements. (A) Artificial lux measurements were taken at 30 commercial buildings and 16 residences in the Williamsburg, VA area during the month of December (2019). Measurements were taken in 4 separate rooms within each building or home as far from windows as possible, to minimize the influence of natural light on interior measurements. Data is plotted based on commercial vs. residential classification. **(B)** Exterior lux measurements were taken in the constructed flight tunnel during December (2019). Light measurements were taken at 3 time points (30 mins after sunrise, midday and 30 mins before sunset) and were classified by whether sunlight was directly or indirectly hitting the sensor of the WaveGo spectrometer.

Immediately prior to running a set of flights for a particular treatment, we recorded light intensity measurements with the WaveGo spectrometer or with a handheld light meter (LT300 light meter, Extech Instruments), which we calibrated for lux readings relative to the spectrometer. Specifically, we obtained light intensity measurements 0.2 m from the interior surface of the installed windows, with and without the artificial illumination, as well as measurements 0.2 m from the exterior surface of each of the installed windows. For every measurement, we held the recording instrument (spectrometer or light meter) vertically, such that the sensor faced directly upward. In order to determine the lux of the artificial lighting alone, the interior lighting measurement with the lights off was subtracted by the interior lighting measurement with the lights on.

We combined the two levels of interior and exterior lighting conditions to form six treatment groups (Figure 1). In four of the treatments, both the windows in the flight tunnel received the same lighting treatments. This led to factorial combinations of (a) lower interior, lower exterior; (b) higher interior, lower exterior; (c) lower interior, higher exterior; and (d) higher interior, higher exterior lighting conditions. Conditions in which the interior lighting was lower (less intense) relative to the exterior lighting conditions create more reflection off the exterior surface of the window and, potentially, a greater risk of window collision.

In the final two treatments, we altered the interior lighting conditions of one window relative to the other within a trial (i.e. one window received the lower interior lighting while the other window received the higher interior lighting condition). This was repeated in both (e) lower exterior (morning) and (f) higher exterior (midday) lighting conditions, to give two further treatments. We refer to these trials as “choice trials” as birds could have exhibited a choice of which window to avoid or collide with. Such choice trials are common in the experimental design of many flight tunnel tests of window collisions (Klem, 1990, 2009; Rössler et al, 2015; Sheppard, 2019). Which window (left or right) received which interior light treatment was balanced over trials to avoid side bias.

Lighting metrics

In order to summarize the lighting conditions that birds experienced during treatment flights, we calculated a number of light metrics. Light metrics were only calculated for birds exposed to treatments a-d. In order to objectively summarize the degree of reflection seen in the windows, we divided the interior lux values by the exterior lux values for each window at a particular time point. We averaged the lux ratio surrounding both windows in order to obtain one metric that summarizes the reflection seen in the windows during a particular flight. A smaller value for this lux ratio corresponds to a greater overall reflection.

In preparation for the analyses of flight velocity, we classified our reflection metric data into four quartiles for the morning and midday separately (I = minimum to 25th percentile, II = 25th percentile to median, III = median to the 75th percentile, IV = 75th percentile to maximum). Each bird was assigned a particular quartile based on what quartile the experimental lighting conditions fell under. Transforming our reflection metric from a continuous to a categorical variable allowed us to analyze the velocity data by means of an ANOVA, which is explained in further detail below.

Because each interior and exterior lighting condition differed in their irradiance of red and blue wavelengths of light (Figure 6), we also calculated a red and blue irradiance ratio by dividing interior irradiance by exterior irradiance to account for variability that might arise from spectral differences. Irradiances of blue and red light, respectively, were calculated by summing the irradiance of light from 400-500 nm (blue) and 600-700 nm (red), separately. Irradiance values above 700 nm were not included as bird sensitivity does not extend past 700 nm (Bennett et al, 1996). Note that while we characterized these ranges of wavelengths as “blue” and “red” for simplicity, these ranges do include violet and orange wavelengths of light as well. Similarly to our reflection metric which encompasses all wavelengths of light, we averaged the ratios from both windows to obtain one measurement that summarizes the degree of blue or red light reflection during a particular flight.

Given that zebra finches are UV-sensitive (Bennett et al, 1996), we also included a metric that summarized the total irradiance of UV light (300-400 nm) on the exterior of windows. We did not include irradiance measures below 300 nm as bird visual sensitivity does not extend below this value (Bennett et al, 1996). There was little to no UV light on the interior of windows in any case; therefore, we did not calculate a ratio for this metric.

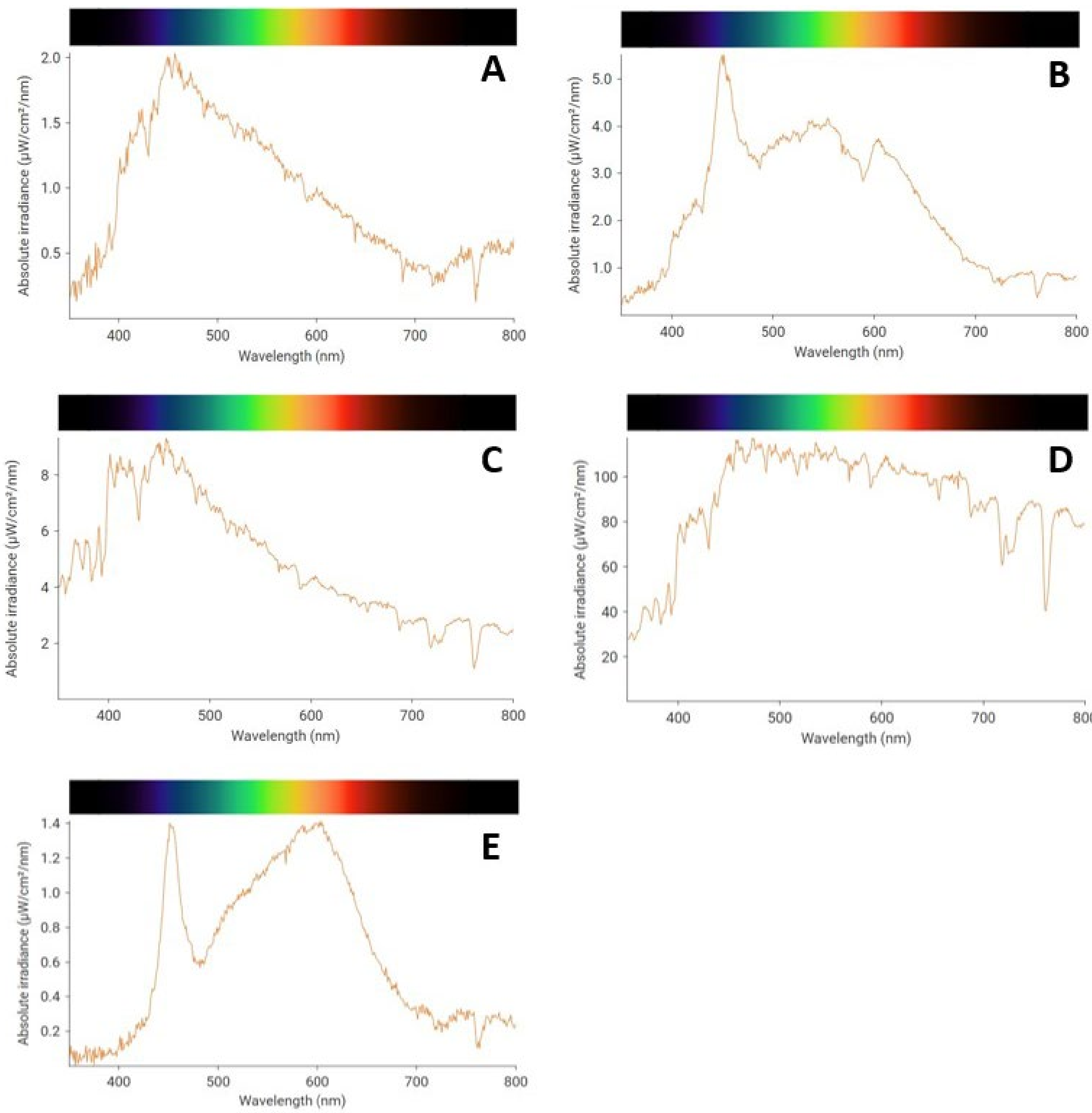


Figure 6. Irradiance spectra for the two interior and two exterior intensity conditions. Each irradiance spectra indicates the absolute irradiance at each wavelength, with the accompanying visual spectrum atop the chart. Irradiance spectra are provided for the two interior intensity conditions: low **(A)** and high **(B)**. Additionally, irradiance spectra are provided for the two exterior intensity conditions: low **(C)** and high **(D)**. Low intensity conditions are rich in the UV and blue wavelengths of light, while high intensity conditions contain a greater irradiance of orange and red wavelengths of light. The target interior spectra for trials were determined by visually inspecting the spectra typical of artificial light in residences and commercial buildings. **(E)** represents the spectra typical of most residences and commercial buildings which we aimed to reproduce (see ‘B’).

Flight trials

We conducted flight trials from June to August 2020. We did not run trials if it was raining or if wind exceeded 3 m/s. Most trials were conducted in sunny conditions with little cloud cover and light winds. A flight trial commenced when an experimenter released a bird from the hand at a defined release point 2 m from the open exit of the darkened release tunnel, with the simultaneous vocalization of a startle sound to encourage the bird to fly away from the experimenter. Most birds flew directly from the experimenter toward the windows in the day-lit portion of the flight tunnel and collided with the mist-net placed 1 m in front of the windows (Figure 2). In order for a bird to hit the net, it flew approximately 6 m from the release point.

In order to be included in the study, a bird had to successfully complete one control flight and one treatment flight separated by 2-4 days. A control or treatment flight was considered successful if the bird flew at least 4 m from the release point. A control flight consisted of a flight down the tunnel in the absence of the mist-net or the window structure. Control flights were conducted within the same time periods as their respective treatment flights and were used as a reference point of comparison in analyses. We randomly assigned each bird to one of the six treatments (a to f, described above), ensuring that there was an approximately even number of males and females in each treatment group (n =16 or 17 per treatment group). The order of treatments was pseudo-randomized.

We recorded all flight trials, control and treatment, on three GoPro cameras. The total volume of the recorded scene was approximately 30 m^3. We used both audio and visual signals to sync the three cameras at the beginning of each recording period (i.e. a maximum 2-hour period in the morning or midday). To do this, one walkie-talkie was placed immediately next to each camera and upon trial commencement, a loud alarm tone was played through all the walkie-talkies simultaneously. Immediately after playing the alarm tone, a bright light was flashed at all three cameras. These two signals allowed for the precise syncing of the three videos.

After syncing the three video cameras, we extrinsically calibrated the three cameras in order to obtain information on the scale of the recorded scene. In order to calibrate the cameras, we recorded the movement of a wand structure (a wooden dowel, length = 0.46 m, with two spray-painted Styrofoam spheres on either end). The wand structure was simultaneously moved and rotated throughout the entire active flying space of the day-lit tunnel by an experimenter. The two spheres were painted bright yellow and pink in order to remain distinguishable from the background. Wand calibrations occurred at the beginning and end of each recording period (i.e. a maximum 2-hour period in the morning or midday).

Scoring of collision and avoidance

Using the video recordings from the three cameras, we assessed whether the bird was likely to have collided with the windows or not. This assessment was based on the distance the bird flew down the tunnel and their horizontal and vertical trajectory. If the bird collided with the mist-net in a position that aligned with a window, the flight was scored as a collision. In “choice” treatments (treatments e and f), we noted which window the bird would have collided with. If a bird flew on a trajectory that did not align with a window or if the bird did not reach the mist-net, the trial was scored as an avoidance of collision.

Generating flight velocity

In order to obtain the three-dimensional coordinates for each flight, we used the open-source software package *Argus* implemented in Python 3.6.2 (Jackson et al, 2016;

van Rossum & Drake, 2009) to sync the videos, calibrate the cameras with intrinsic and extrinsic parameters, digitize global frames of reference, and digitize each flight. Calibrations were achieved using a wand-based, direct linear transformation (DLT) method with sparse bundle adjustment (SBA). Calibrations produced root mean square re-projection errors of less than 2 pixels in most cases, but often below 1 pixel. The error in the reconstructed wand length was 1.06% (0.0049 m) on average, indicating a relatively small error in reconstruction.

The *x*-axis of the resulting scene ran horizontally from the left to the right of the window structure when facing the structure head-on. The *y*-axis ran horizontally along the length of the flight tunnel, from the release point to the window structure. This was largely the direction the birds were flying. The *z*-axis was orthogonal to the *x*- and *y*-axes, extending from the ground to the ceiling of the flight tunnel. The origin of the scene was set on the ground at the midpoint (left to right) below the mist-net (Figure 2). This orientation allowed flight paths to be measured on a global reference system related to the window structure. As a bird flew in a trial and approached the mist-net, their *y*-coordinates approached 0. As the bird deviated to the left or right, their *x*-coordinates became increasingly positive or negative, respectively. As the bird increased its elevation from the ground, their *z*-axis coordinates became increasingly positive.

We digitized the centroid of each bird in each trial in the video sequences between their emergence from the darkened release tunnel to the point where each bird reached the mist-net (or flew for 4 m in control flights) or stopped flying. From these digitizations, we calculated velocity of each bird per frame of video (distance travelled divided by time, m/s). We averaged flight velocity across five frames in the last 25 frames of each bird's flight resulting in five average velocity metrics (classified as V20, V15, V10, V5, V0) for each bird as it approached the end of its flight. One bird had a flight that spanned 15 frames. In that case, 3 velocity metrics only were calculated (V10, V5, V0). This averaging technique acted to smooth the velocity data, minimizing the effect of digitization errors, while also allowing for simpler visualization and analysis of flight velocity.

We computed within-individual change in velocity by subtracting velocity measurements in control flights from those in treatment flights (treatment minus control), for each of the 5-frame sequences indicated above. A negative value indicated a bird flew slower at a particular time point in its treatment flight compared with its control flight.

Statistical analyses

To examine whether there were systematic differences in exterior lighting conditions on either side (left vs right) of the window structure at the same time point, we employed Wilcoxon signed-rank tests.

We employed logistic regression analyses (logit link function) to determine whether lighting conditions influenced collision risk in treatments where both windows received the same interior lighting condition (i.e. treatments a, b, c, and d). We analyzed the data from morning (treatments a and b) and midday (treatments c and d) trials separately as our data visualization revealed reversed responses to lighting conditions in the morning and midday. Collision risk was a binary response variable (0 = avoidance, 1 = collision) in these models. The 10 predictor variables were: treatment, average lux ratio, blue and red wavelength irradiance ratios, exterior UV irradiance and the 5 velocity measures (V20, V15, V10, V5, V0). Continuous variables were scaled and centered prior to analyses. Exploratory logistic regression analyses were run in order to determine whether any extraneous variable had an effect on collision risk. All extraneous variables were categorical and included: phenotype, sex, age, weather, and prior exposure. None of the exploratory models performed better than the null, so these variables were omitted from any subsequent analyses.

In order to determine the most probable models, we first ran univariate models including each of the 10 predictor variables listed above. We included two bivariate models (one interaction model and one additive model) in order to test a post-hoc alternative hypothesis that the combination of exterior UV irradiance and treatment together have an effect on collision risk. A full list of the models split by morning and midday is provided (Tables A1.1 and A1.2).

We compared models using Akaike's Information Criterion with small sample correction (AICc, Burnam & Anderson, 2002) using the R package "MuMIn" (R Core Team, 2019). We only considered models that returned AICc values > 2 below the AICc of the null model. We calculated model weights for each model that performed better than the null and computed model-averaged beta estimates and standard errors for each predictor in all probable models (cumulative weight= 100%). Given that there was no model for which we had strong support (weight > 90%, Symonds & Moussalli, 2011) in either the morning or midday we employed a full-model averaging approach using the "MASS" R package (R Core Team, 2019).

In order to determine the effect of lighting treatments (treatments a, b, c, and d) on the five measures of within-individual change in velocity (V20, V15, V10, V5, V0), we employed two two-way mixed ANOVAs: one for morning flights and one for midday flights. Within-individual change in velocity was the response variable, interior treatment was the among-subjects factor, and frame (20, 15, 10, 5, 0; indicating the last frame in a sequence of five) was the within-subjects factor. We also performed pairwise paired t-tests to determine differences between groups when the *F*-tests in the ANOVA returned statistical support.

In addition, we performed similar two-way mixed ANOVAs but with lux ratio quartiles (I, II, III, IV) as the among-subjects factor. This analysis helped to examine whether our reflection metric influenced flight velocities.

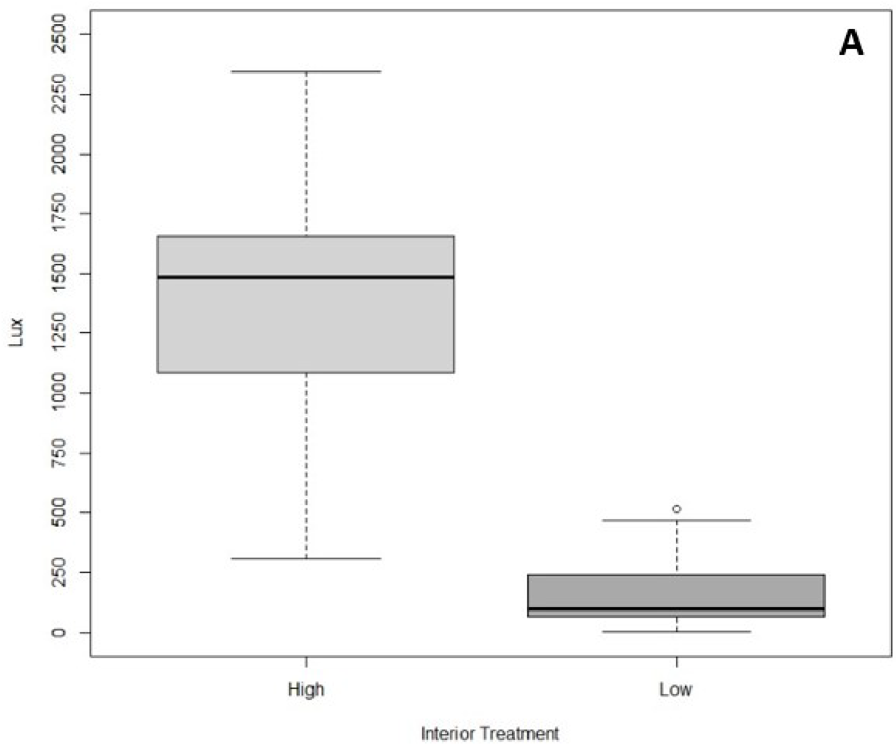
We ensured that the data and residuals met all assumptions of the statistical tests we employed. All analyses were conducted in R version 3.6.2 (R Core team, 2019). We report means ± SE, unless otherwise stated. Due to a low sample size of collision events, we did not perform any statistical analyses of data generated by the two "choice" treatments (treatments e and f).

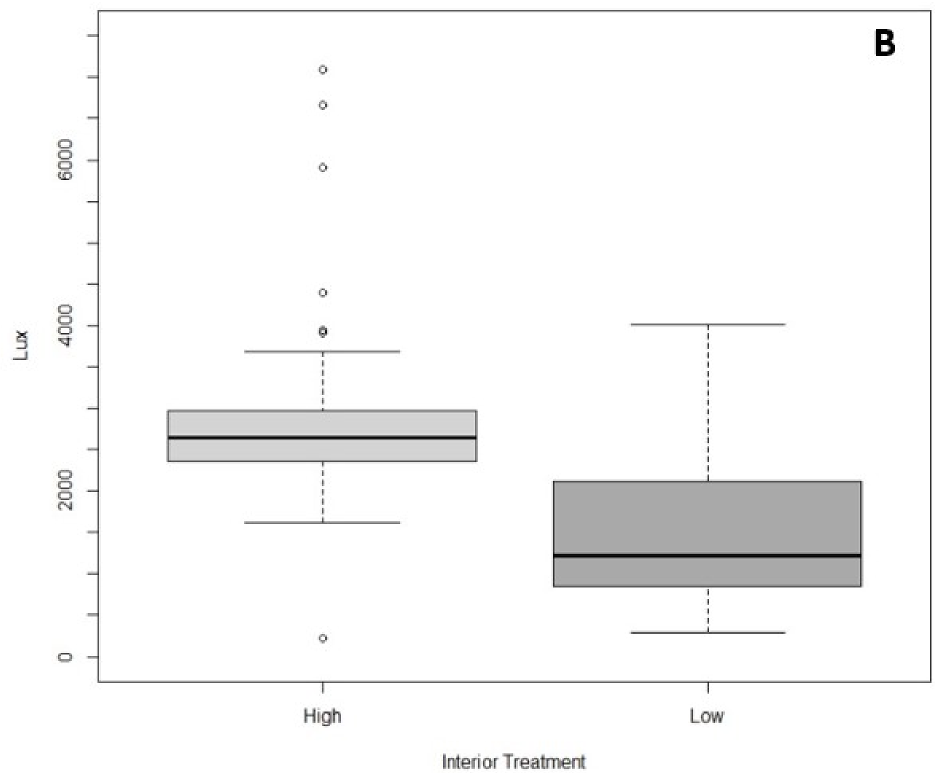
Results

Survey of lighting and definition of lighting treatments

The intensity of artificial interior lighting in treatment flights ranged from 3 to 2,343 lux (mean of lower interior treatment = 162 ± 26 lux, mean of higher interior treatment = 1,402 ± 77 lux; Figure 7A). This matched our target ranges based on the survey of internal lighting at nearby residences and commercial buildings (low intensity target= 100 lux, high intensity target= 1,150 lux; Figure 5A). Hence, our manipulations of interior lighting reproduced lighting conditions commonly experienced in our local area. Our low intensity mean fell within the predetermined range of low light intensity (1-320 lux), while our high intensity mean fell just above the target range (320-1,150 lux). Our high intensity interior conditions reached values that exceeded the target range by just over 1,000 lux.

Natural exterior lighting in the treatment flights ranged from 2,643 to 323,808 lux (mean of lower exterior treatment = 6,783 ± 537 lux, mean of higher exterior treatment = 82,868 ± 8,036 lux; Figure 7C). These data matched our target ranges based on the survey of natural exterior lighting conditions in the flight tunnel (low intensity target= 10,000 lux, high intensity target= 40,000 lux; Figure 5B). Our low and high intensity means fell within the predetermined ranges of low and high light intensity (1-20,000 lux; 20,000- 100,000 lux), though our high intensity interior reached values which exceeded the target range by over 200,000 lux.

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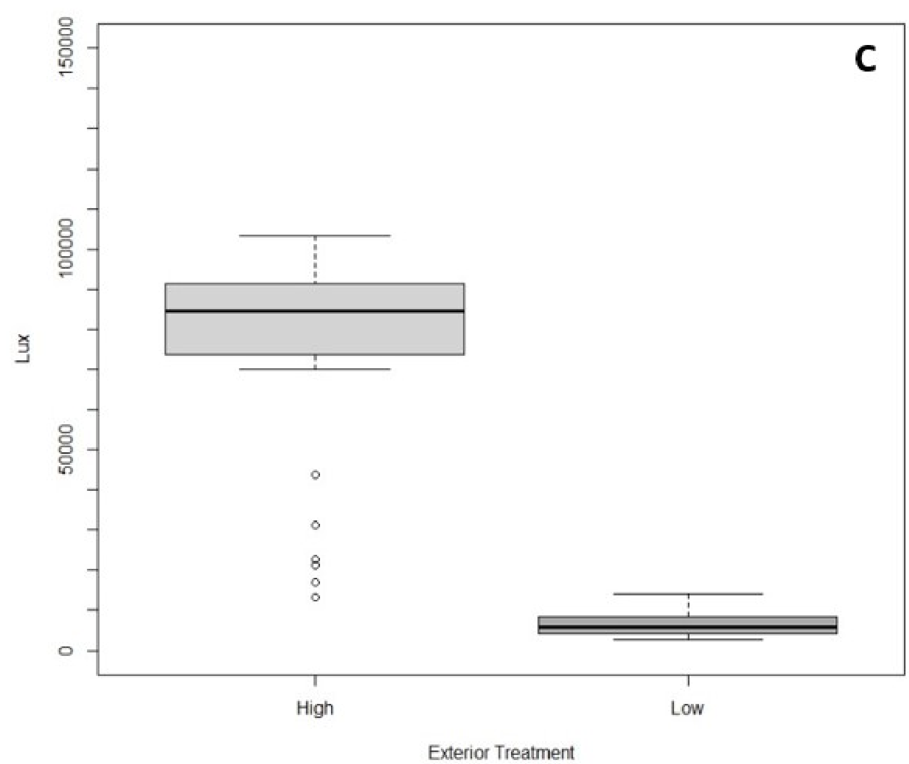
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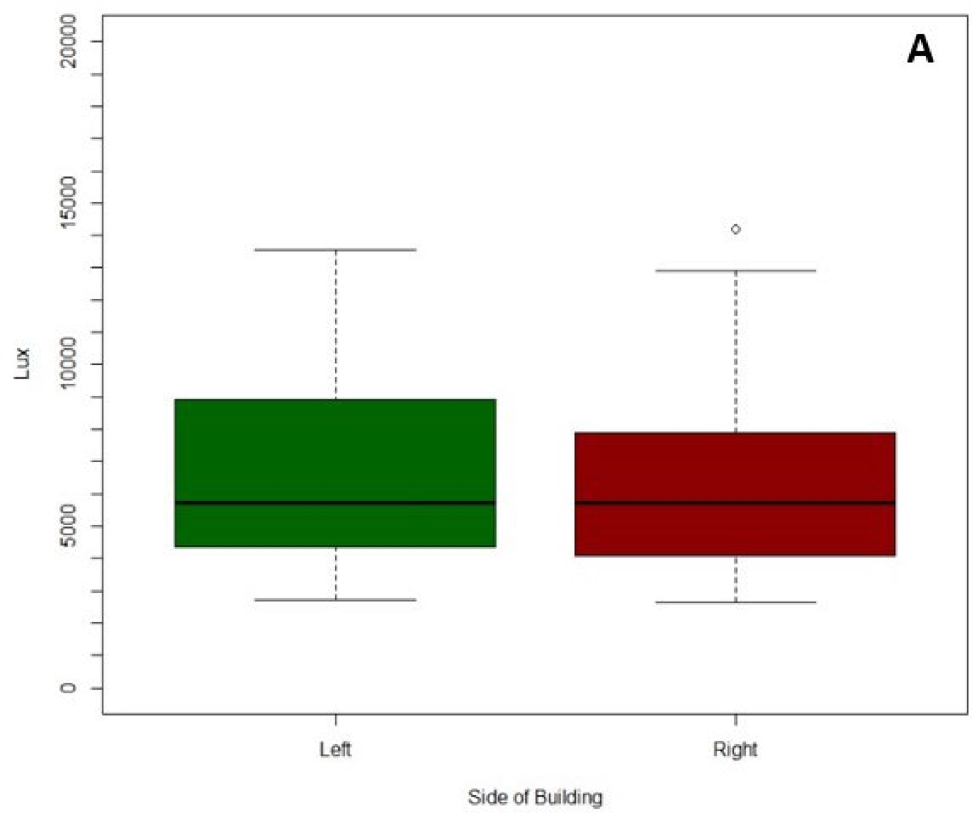
Figure 7. Flight trial interior (A & B) and exterior (C) lighting conditions. All lux measurements were taken 0.2 m from the window with the WaveGo or light meter facing directly upwards. **(A)** represents the intensity of artificial light, calculated by subtracting the interior lux with the artificial light turned on from the interior lux with the artificial light turned off. The interior low light condition was achieved by using one 40 W light bulb on the interior side of the windows while the high light condition was achieved by using three 100 W light bulbs on the interior side of the windows. **(B)** represents the interior light intensity with natural light included, or the realized lighting conditions. **(C)** represents the intensity of exterior lighting treatments. Exterior low light conditions were achieved by conducting trials in the early morning (0800-1000) while high light conditions were achieved by conducting trials midday (1100-1300). A few outliers were excluded in this case for ease of visualization.

We also compared the lighting conditions of the left and right windows when mounted in the façade in the flight tunnel. There was no indication that exterior light conditions differed between left and right windows (lower exterior light treatment, Wilcoxon signed-rank Test, $W = 198$, $p = 0.623$; higher exterior light treatment, Wilcoxon signed-rank Test, $W = 184$, $p = 0.501$; Figures 8A and 8B).



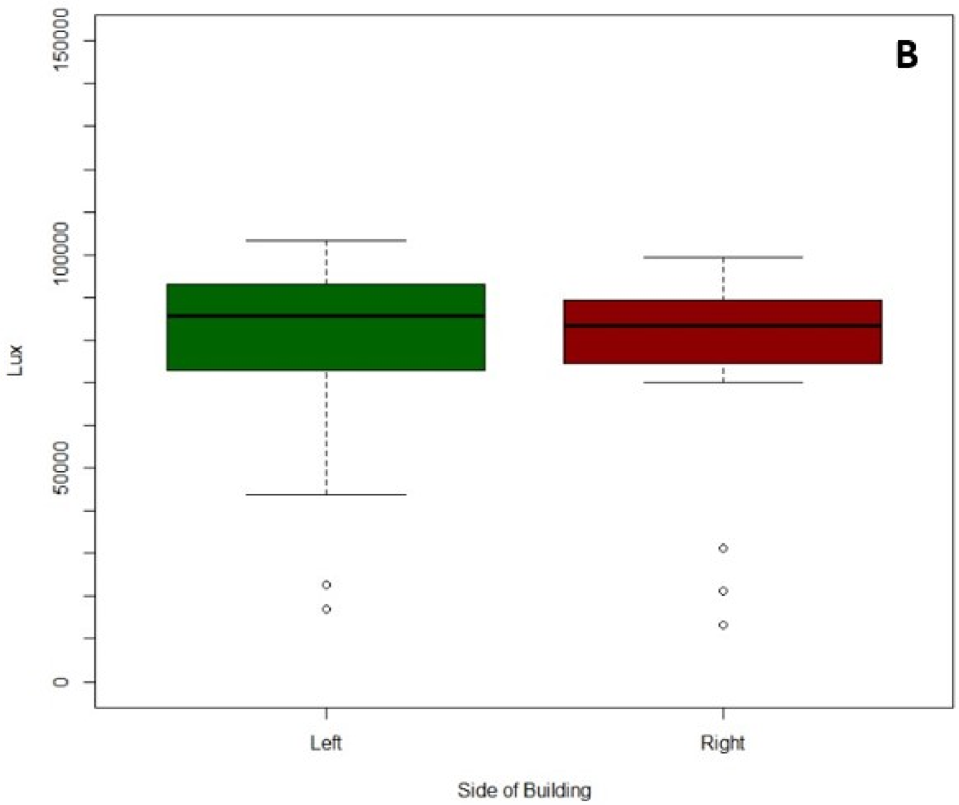


Figure 8. Exterior light measurements split by left and right window in the morning (A) and midday (B). Exterior lux measurements were taken 0.2 m in front of the left and the right window at a singular time point. The left side corresponds to the left window when facing the window structure, which is closer in proximity to the green-painted McCormack-Nagelsen Tennis Center. The right side corresponds to the right window when facing the window structure, which is closer in proximity to the red-painted aviary.

Assessment of risk of collision

During control flights, the birds often flew the entire length of the flight tunnel. Only 11% of subjects stopped short of 6 m. During treatment flights, birds often collided with the mist-net (72%) while the remaining birds stopped short of or reversed flight direction prior to colliding with the mist-net (28%). In 20 (out of 71) cases of avoidance, subjects were adjudged to have been on course to collide with the wooden frame around the windows. These potential collisions were evenly distributed throughout the treatments (a: 4, b: 2, c: 4, d: 2, e: 5, f: 3). Despite there being a notable number of potential collisions with the wooden frame, we did not classify these cases as collisions in further analyses as they do not explicitly address our hypothesis that reflection increases risk of window collision.

We recorded 29 potential window collisions in our study, which was 29% of the treatment flights (Figures 9 and 10). Potential collisions occurred more often at the right window (72.4% of collisions) as opposed to the left window (27.6% of collisions), demonstrating a side bias which likely resulted from the presence of a red-painted building to the right of the tunnel. There was more open space to the left of the tunnel. While this side bias does not affect our interpretation of non-choice treatments, it could influence our interpretation of choice treatments where left and right windows received different lighting treatments. Given the side bias and the low number of potential collisions observed in these choice flights (e: 3, f: 4; Figure 10), we elected not to analyze those data and dropped choice flights from the study.

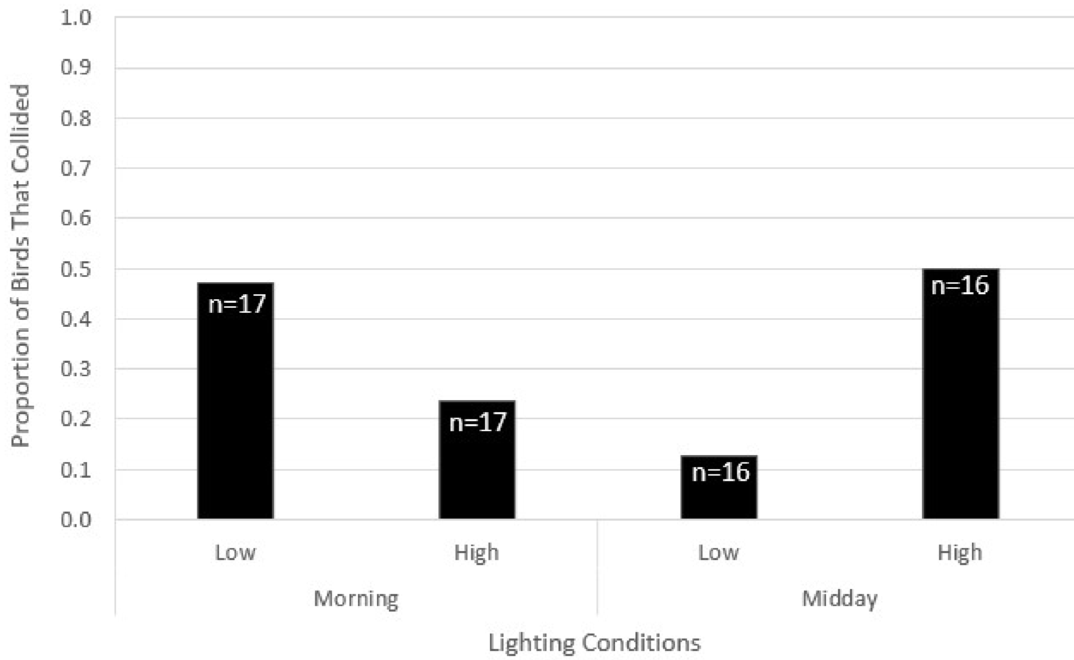


Figure 9. Proportion of birds that were adjudged to collide with either window in the four non-choice treatments (from left to right: a, b, c, d). Flights were scored as collisions if birds hit the mist-net in a position which aligned with a window structure. Sample size is indicated directly on the bars.

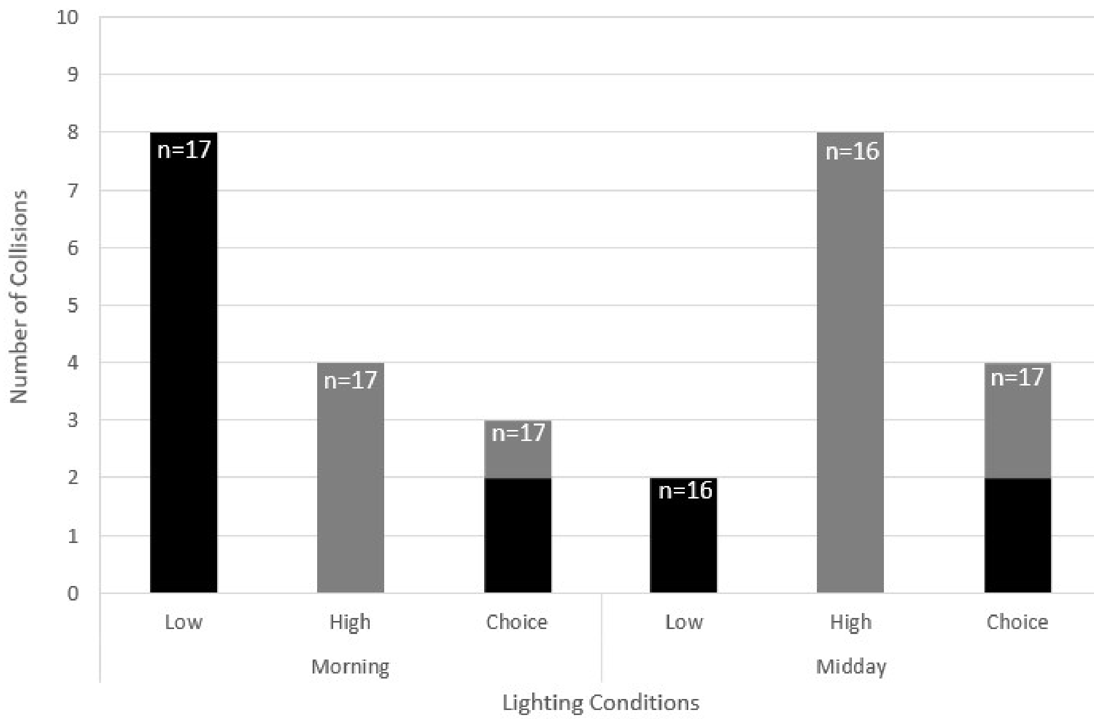


Figure 10. Number of potential collisions observed in each treatment (from left to right: a, b, e, c, d, f), including choice treatments, with sample size indicated directly on the bars. The black portion of the stacked bars for choice treatments indicate the number of potential collisions at windows with a low intensity interior while the grey portion of the stacked bars indicate the number of potential collisions at windows with a high intensity interior. There was a notable side bias (right side) which lowers our confidence in the results shown for the choice treatments.

Our logistic regression analyses revealed three probable models which explain window-collision risk in the lower (morning) exterior lighting flights (Table A1.1). The top performing models included the following predictors: flight velocity calculated 20 and 15 frames from the end of the flight, exterior UV irradiance, and interior lighting treatment. Velocity 20 frames from the end was the strongest predictor of collision risk in the morning and was the only predictor to have model-averaged standard errors that did not overlap 0 (Table 1, Figure 11). Model-averaged beta coefficients (see "Statistical analyses" above) indicated that velocity 20 frames from the end of a flight was a positive indicator of window-collision.

A separate set of logistic regression analyses revealed two probable models that explained window-collisions during higher (midday) exterior lighting flights (Table A1.2). The top performing models included interior lighting treatment and exterior UV irradiance as predictors. Treatment was the strongest predictor and the only predictor to have model-averaged standard errors that did not overlap 0 (Table 1, Figure 12). In this case, window-collision risk decreased in the presence of a lower interior lighting treatment—which was the opposite of our prediction.

	Predictor	w_x	β est.	-1 SE	+1 SE
Morning	Intercept	-	0.07	-	-
	Velocity at 20 frames	0.78	1.27	0.37	2.17
	Velocity at 15 frames	0.14	0.15	-0.28	0.58
	Exterior UV irradiance	0.08	1.70	-4.92	8.32
	Low intensity treatment	0.08	0.16	-0.45	0.77
Midday	Intercept	-	-0.36	-	-
	Low intensity treatment	1.00	-2.17	-3.23	-1.11
	Exterior UV irradiance	0.37	0.24	-0.22	0.70

Table 1. Comprehensive list of all predictors included in the top models split by morning and midday. Predictor weights are included along with model-averaged beta estimates (± 1 SE). "Low intensity treatment" corresponds to the low intensity interior treatment, or our reflective condition.

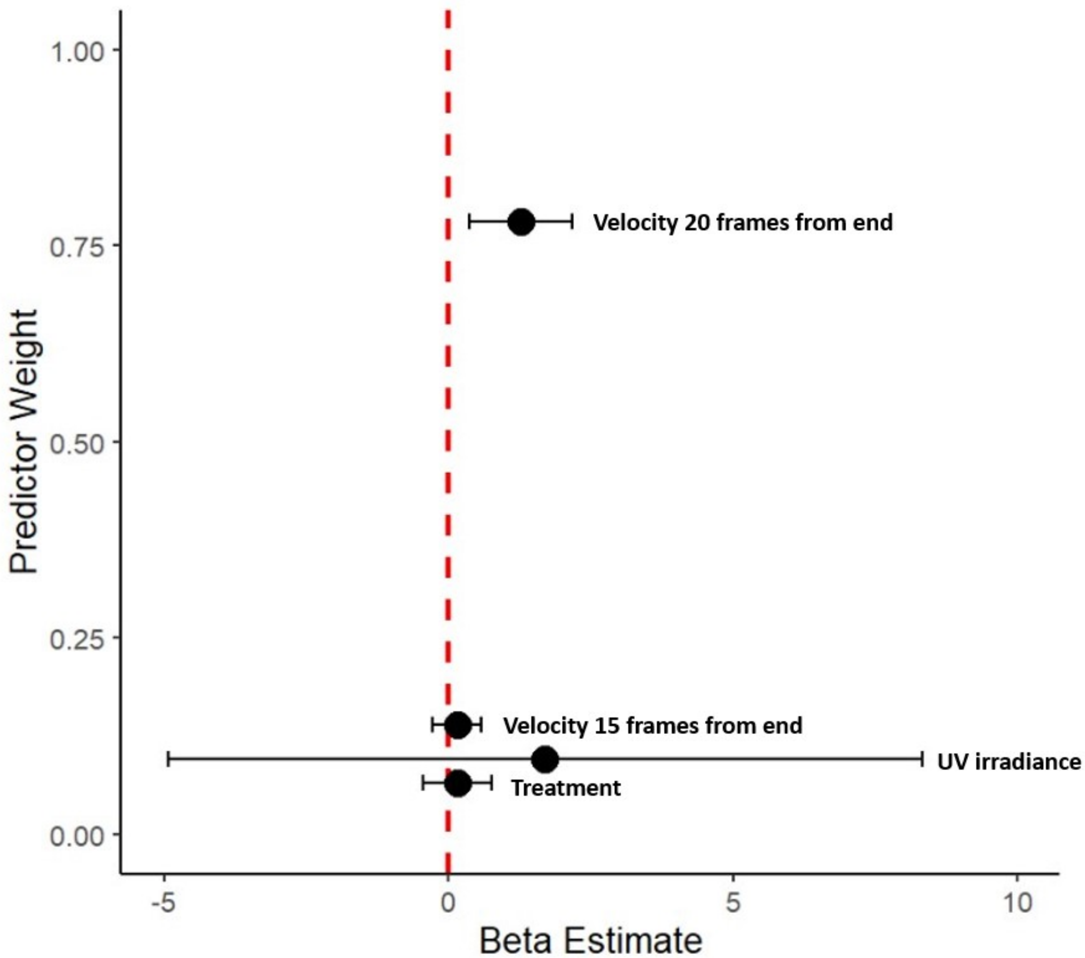


Figure 11. A graphical representation of model-averaged beta coefficients for each morning predictor (± 1 SE) with corresponding predictor weights. Weights for UV irradiance and treatment were identical (0.08), but the two predictors were staggered in the chart for ease of interpretation. "Treatment" refers to the low intensity interior treatment, or our reflective condition, in this case.

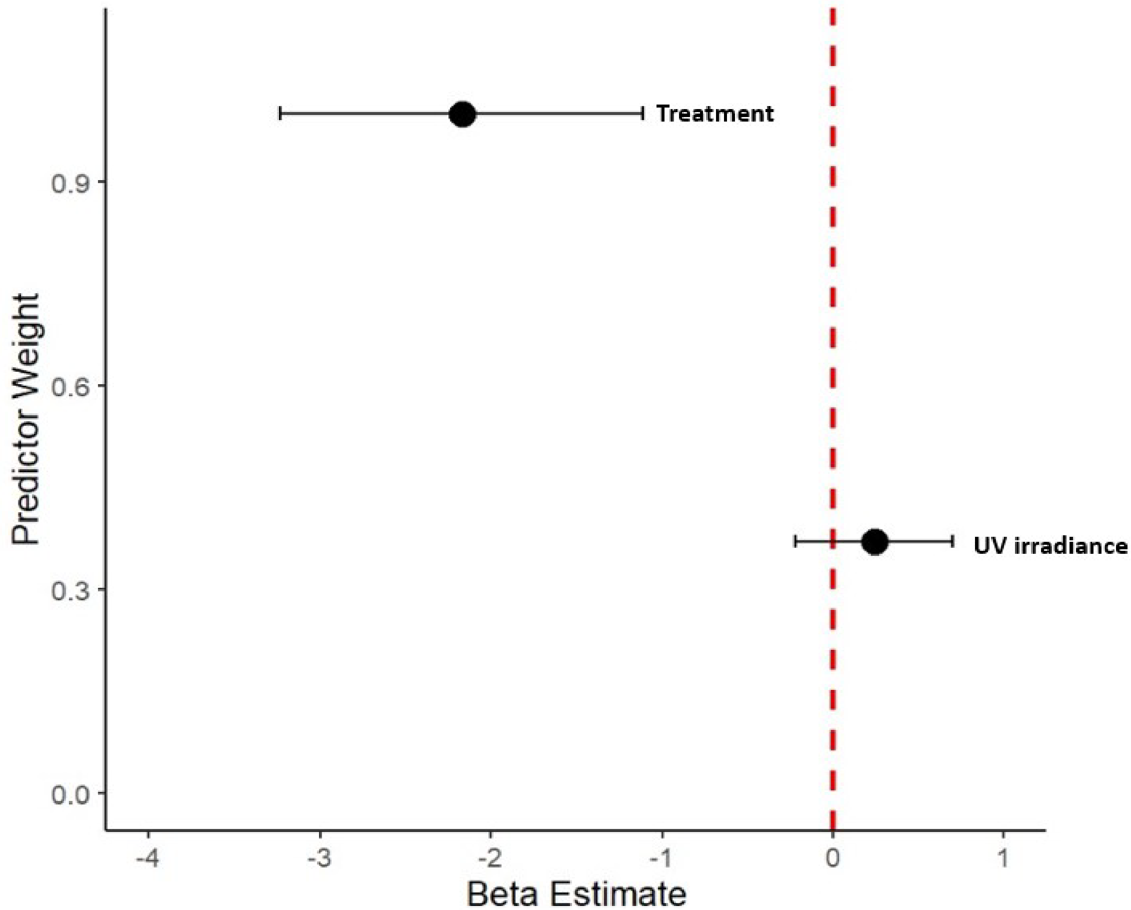


Figure 12. A graphical representation of model-averaged beta coefficients for each midday predictor (± 1 SE) with corresponding predictor weights. A weight of 1 indicates that the predictor was included in all top models. “Treatment” refers to the low intensity interior treatment, or our reflective condition, in this case.

Flight velocity

There was no detectable difference in velocity in control flights of birds released towards each treatment, with control velocity averaging from approximately 4.43-5.13 m/s for each treatment over time. Thus, any differences in average relative velocity over time amongst treatments can be attributed to responses to the treatments themselves.

We calculated relative velocity as the within-individual difference in flight velocity between treatment and control flights (treatment minus control). Regardless of interior treatment or exterior condition, relative velocity decreased over time as birds approached the mist-net ($F_{1.55,49.55}$ = 27.18, p < 0.0001 for morning; $F_{1.83,54.96}$ = 24.74, p < 0.0001 for midday; Figure 13). Post-hoc pairwise paired t-tests revealed a significant decrease in velocity at frame 0 relative to all other frames (p < 0.05). There were no statistically-supported effects of interior treatment on flight velocity ($F_{1,32}$= 0.554, p = 0.462 for morning; $F_{1,30}$ = 0.818, p = 0.373 for midday; Figure 13).

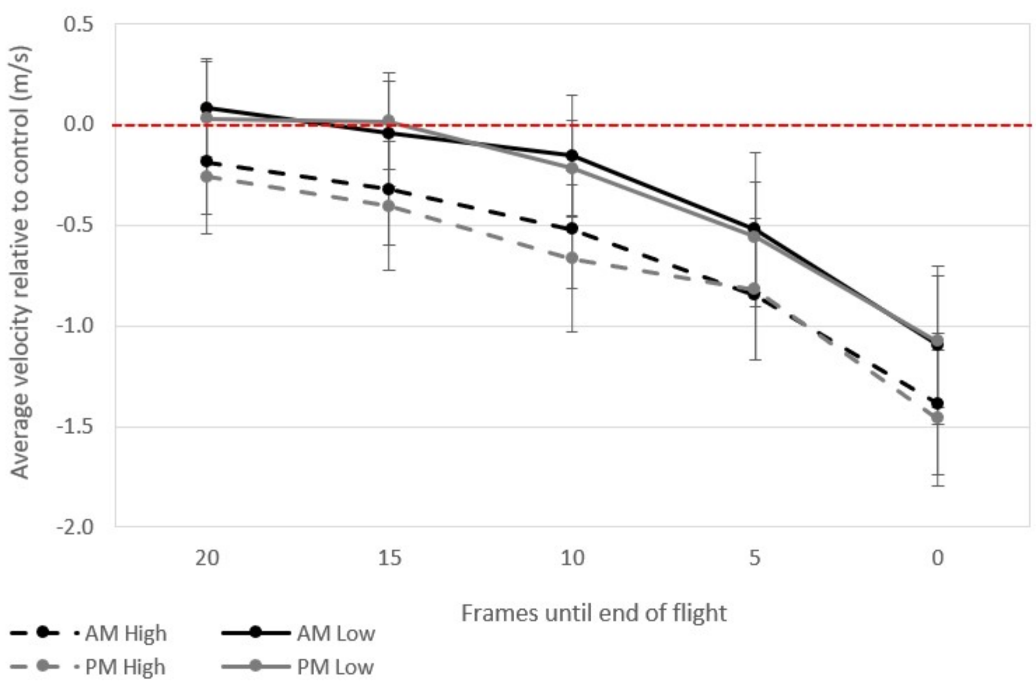
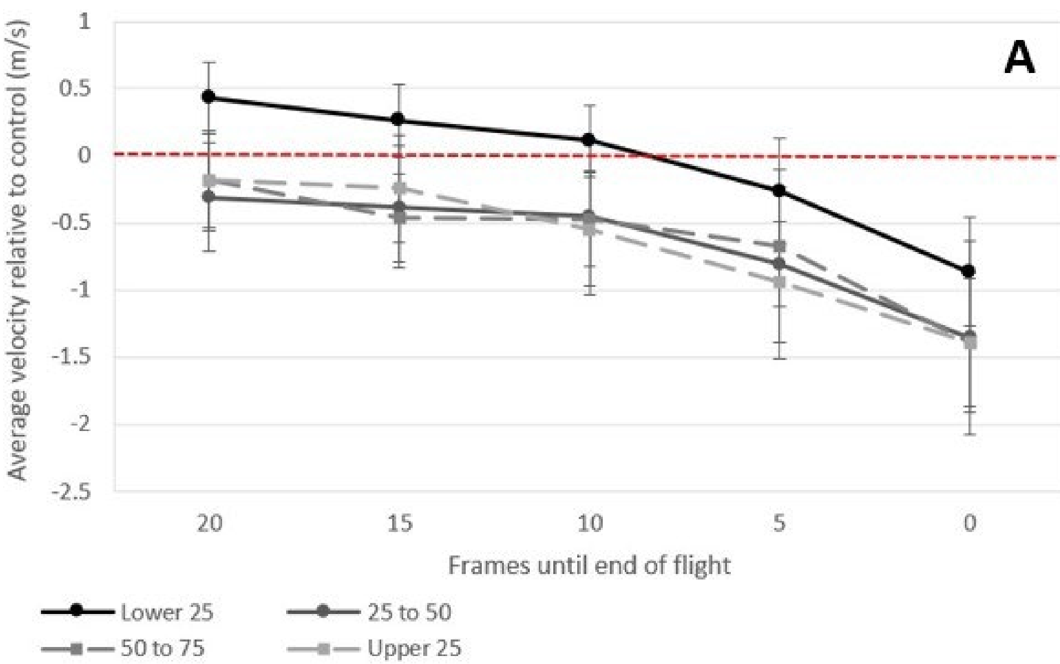


Figure 13. Average relative velocity (± SEM) depicted at 5 time points (20, 15, 10, 5 and 0 frames from the end of flight) for each non-choice treatment. For each

subject, velocity was averaged every 5 frames from the 25th frame to the end of the flight, resulting in 5 velocity measures which summarize the velocity of subjects over the last 25 frames of flight. Relative velocity was then calculated by subtracting the treatment velocity from the control velocity at the 5 time points. A negative value for relative velocity depicts a lower velocity in the treatment condition. “AM High” and “PM High” represent the morning and midday less-reflective conditions, respectively. “AM Low” and “PM Low” represent the morning and midday reflective conditions, respectively (n=16-17).

Our second pair of ANOVA analyses including lux ratio, or reflection, quartiles as the among-subjects factor similarly revealed a decrease in relative velocity over time ($F_{1.52,45.73}$ = 24.17, p = 6.35e-07 for morning, Figure 14A; $F_{1.83,51.22}$ = 24.14, p = 9.27e-08 for midday, Figure 14B). Post-hoc pairwise paired t-tests revealed a significant decrease in velocity at frames 5 and 0 relative to all others ($p < 0.05$). There were no statistically-supported effects of reflection quartile on flight velocity ($F_{3,30}$ = 0.517, p = 0.674 for morning, Figure 14A; $F_{3,28}$ = 0.363, p = 0.780 for midday, Figure 14B).



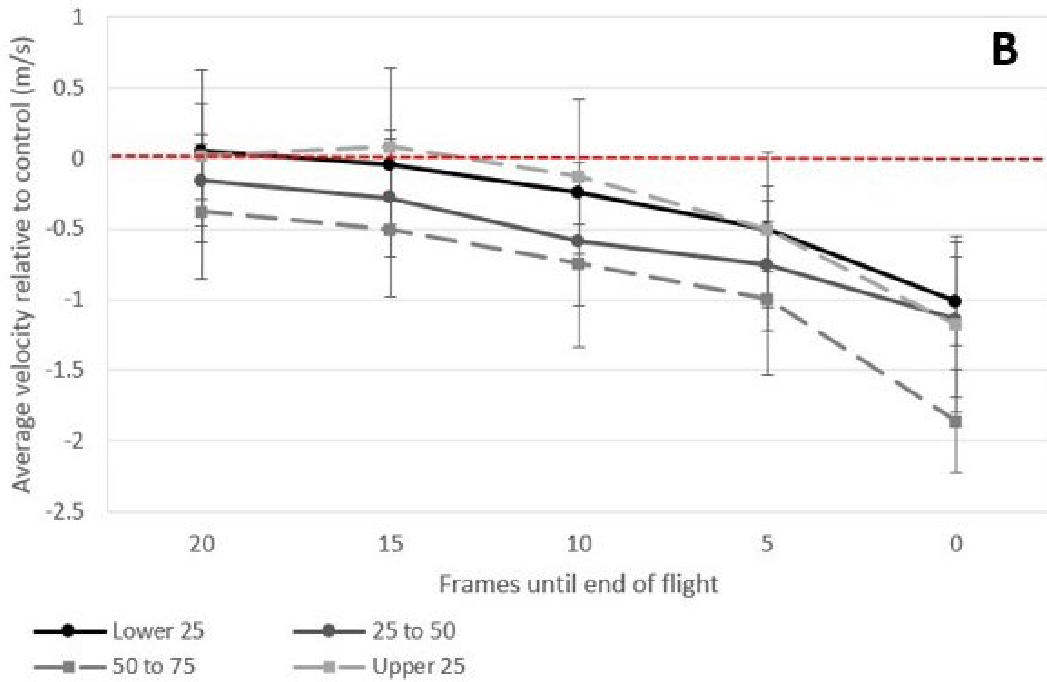


Figure 14. Average relative velocity (± SEM) depicted at 5 time points (20, 15, 10, 5 and 0 frames from the end of flight) for each reflection quartile in the morning (A) and midday (B). For each subject, velocity was averaged every 5 frames from the 25th frame to the end of the flight, resulting in 5 velocity measures which summarize the velocity of subjects over the last 25 frames of flight. Relative velocity was then calculated by subtracting the treatment velocity from the control velocity at the 5 time points. A negative value for relative velocity depicts a lower velocity in the treatment condition. For each treatment flight, a corresponding reflection metric was calculated which summarized the degree of reflection seen as the bird flew towards the treatment condition. Reflection measures were compiled and split into quartiles and flights were then reclassified with one of the four reflection quartiles (n=6-11, **A**; n=6-10, **B**). A lower reflection quartile indicates a greater reflection in the treatment condition.

Discussion

In our controlled flight tunnel experiment, we found that presence of an exterior reflection influenced collision risk, but not in the direction that we or other studies had predicted. The presence of a reflection in bright, midday conditions decreased the risk of collision rather than increasing collision risk. We also found no notable influence of window reflection on the birds’ flight velocity. Interpreted together, these findings suggest that the presence of a reflection on a window might not always increase the likelihood of collision. Additionally, we hypothesize that the visual mechanisms mediating window-collision risk are more complex than often described and may involve other properties of light such as the polarity of light reflected from the window surface.

In midday conditions, we observed a four-fold decrease in potential window collisions when birds were presented with the more reflective window treatment (i.e. lower interior lighting). However, in morning conditions, the number of collisions doubled when birds were presented with the more reflective treatment. Given that previous studies have reported an increase in risk of collision with increased reflection from windows (Brown et al, 2020; Kummer et al, 2016), our contrasting findings between midday and morning light conditions appear somewhat perplexing. However, our observation that increased window reflection around midday is associated with less risk of collision is not without precedence. Gelb and Delacretaz (2006) documented a greater number of collisions from 0900-0930 at a building with reflective glass panels mounted into a brick exterior, which aligns with the somewhat greater number of collisions we observed in morning trials with lower interior lighting. During midday observations (1200-1230) they observed approximately 50% fewer collisions with reflective windows, which is qualitatively similar to our findings for collisions in the lower interior lighting condition at midday.

One potential explanation for the decrease in collision risk in midday light could be the relative increased irradiance of ultraviolet (UV) wavelengths of light. The increased irradiance could cause increased reflection of UV light off the windows at that time of day. We know that zebra finches are UV-sensitive and thus, reflected UV light would likely be distinguishable in an outdoor environment (Bennett et al, 1996; Hunt et al, 1997). The detectability of UV light is dependent on the contrast of the surrounding environment (Cuthill et al, 2000). When there is increased contrast between the UV-reflective object and the background, the reflected UV light is more visible. Relevantly, UV-reflective surfaces or window films can deter birds, including zebra finches, from colliding with windows (Klem, 2009; Sheppard, 2019; Swaddle et al, 2020). UV-reflective windows employed in a pseudo-field environment have shown greater efficacy in deterring birds when installed over a dark interior (Klem & Saenger, 2013). In the context of our experimental treatments, the window with a darker interior (c) would offer the greatest UV contrast and, thus, might alert birds of the window structure. We hypothesize that the decreased irradiance of UV light in the morning (median = 728) relative to midday (median = 5,813) leads to lower UV contrast effects in the morning compared with midday.

We explored the validity of this UV contrast hypothesis by building models with both exterior UV irradiance and interior treatment as predictors. We evaluated an additive model to determine if the irradiance of UV light and treatment separately influence collision risk. We also included an interaction model with interior treatment and UV irradiance as predictors in order to explicitly test our UV contrast hypothesis. Our additive model narrowly outperformed the null, while our interaction model did not outperform the null for the morning nor the midday data. Further, model-averaged beta coefficients and standard errors revealed no substantial effect of exterior UV irradiance on collision risk. Thus, our hypothesis that increased UV irradiance and increased UV contrast reduces collision risk in the midday is not supported by our analyses.

A more probable alternative hypothesis to explain why we observed fewer potential window collisions at midday when there was more reflection is that the polarization of light on the exterior of the windows and in the sky could influence collision risk (pers. comm., Bruce Robertson). We know that birds utilize linearly polarized light cues (Muheim et al, 2006; Muheim et al, 2009), therefore, it is not unreasonable to assume that polarization of light within our flight tunnel and beyond could play a role in determining collision risk. Though we did not measure the polarization of light, our treatments likely differed in their polarization of light. During the morning hours, specifically at sunrise, sunlight becomes vertically polarized in the sky primarily due to the positioning of the sun at the horizon (Muheim, 2011). As the sun reaches its zenith at midday, the polarized light descends to the horizon and the sky becomes unpolarized (Muheim, 2011). Considering the polarization patterns of our window treatments, we know that darker surfaces polarize light to a greater degree as compared to brighter surfaces (Horváth et al, 2009). Thus, our darker interior treatments (i.e. those with less interior illumination, namely treatments: a, c) should have produced a greater percentage of polarized light in comparison to our brighter interior treatments (i.e. treatments b, d). We found that when the sky was likely unpolarized in midday conditions and the window was likely polarizing light to a greater degree, the number of potential collisions decreased. Based upon this finding, we hypothesize that the contrast in polarization between the reflective window and the surrounding sky influences the risk of collision. When the polarization contrast is greatest, the windows should be more clearly visible, and the birds should not perceive them as sky (i.e. extensions of the environment). This finding could explain previous research which has shown no influence of window polarization patterns on the total number of collisions (Lao et al, 2020). Based upon our results, the influence of polarized light cues reflected from windows could be dependent on sky polarization patterns which change throughout the day. As a result, a certain window polarization pattern is likely not always detrimental to birds.

During morning flight trials, we found a positive effect of flight velocity on risk of collision. This finding is rather intuitive as when a bird's velocity increases while flying towards a stationary structure, the bird has less time and space to adjust their flight to avoid collision. It has been previously suggested that collision risk increases with increased velocity (Boycott et al, 2021; Swaddle & Ingrassia, 2017; Swaddle et al, 2020). The results of the current study bolster the claims that greater flight velocity corresponds to greater collision risk and further emphasizes the importance of assessing and implementing mitigation strategies that alert birds at a greater distance from collision hazards so they can adjust velocities and trajectories of flight.

We found a few trends lacking statistical support which suggest that reflection influences collision risk and velocity of flight but perhaps at certain times of day only. In the morning flight trials, we noted an increase in the number of potential collisions when birds were released towards more reflective windows (i.e. lower interior light treatment) (Figure 9). Additionally, we saw a small increase in flight velocity towards more reflective windows and birds appeared to fly faster in comparison to control flights (Figure 14A). These observations suggest that there could be an active attraction to more reflective windows during morning flights. The patterns in our morning dataset could also be explained by a change in conspicuousness of the mist-net. When the interior light is greater in intensity (treatment b), the mist-net is backlit more and might be more visible to birds and, thus, decrease the likelihood of collision and flight velocity. Nonetheless, neither our reflection metric nor our treatment variable was an important predictor of collision risk, and these variables did not significantly influence flight velocity. Thus, there is no quantitative support for the hypothesis that the presence of a reflected image is important in determining collision risk.

One of the benefits of our study is that we experimentally examined the role of lighting conditions on daytime window collisions. Many previous studies have examined the role of lighting on nighttime collisions, as birds are likely affected by Artificial Light at

Night (ALAN) (Evans-Ogden, 1996; Evans-Ogden, 2002; Parkins et al, 2015; Winger et al, 2019; Lao et al, 2020). However, a significant proportion of window collisions occur in the daytime (Klem, 1989; Gelb & Delacretaz, 2006; Cusa et al, 2015; Loss et al, 2019), emphasizing the need to understand the factors that affect the risk of daytime collisions. We have found that the majority of studies considering reflection as a driver of daytime window collisions are correlative or subjective. Human-derived measures, such as the number of trees observed in reflective windows (Gelb & Delacretaz, 2006) or the presence or absence of a reflection at a single time point (Kummer et al, 2016), have often been used to describe the degree of reflection in windows while objective measures of reflection have been excluded. Though the importance of reflection has been explored to some extent, conflicting evidence precludes our ability to make definitive conclusions in regards to this potential risk factor. Some evidence suggests that reflective and non-reflective windows are equally hazardous to birds (Klem, 1989; Klem et al, 2009). In contrast, reflective glass has been shown to result in more collisions when explicitly compared to clear glass (Klem & Saenger, 2013). Our manipulation of lighting indicates that reflection off the exterior surface of a window may have opposing effects according to time of day and exterior lighting conditions. In the early morning, when light is less intense, the reflection of UV light is minimal and the polarization pattern of the window and the sky likely match, reflection is associated with slightly increased risk of collision. However, in bright midday conditions when exterior UV irradiance is increased relative to the morning and the polarization pattern of the window and sky are in opposition, increased reflection is associated with decreased risk of collision. We cannot fully explain these differences, but it is clear that we need to more thoroughly understand the role of window reflection in determining the risks of window collisions during the day.

The surprising influence of lighting that we observed is not accounted for in most tests of window mitigation technologies. For example, industry-standard flight tunnel studies have lacked natural daylight (Sheppard, 2019), excluded direct sunlight (Rössler et al, 2015), and/or reduced reflective surfaces (Rössler et al, 2015, Sheppard, 2019). In-field tests of window mitigation strategies have included natural daylight but have not incorporated the interior, backlighting that is common in buildings (Klem, 1990; Klem et al, 2004; Klem, 2009; Klem & Saenger, 2013). The lack of representation of real-world lighting conditions in experimental research on window collisions indicates a gap in our understanding. Taken together with our results indicating that lighting conditions have influence on risk of collisions, we call for adaptation of standard protocols to incorporate more realistic lighting conditions when assessing products that might reduce the risk of bird-window collisions. To date, we know of only one experimental study that has incorporated realistic lighting conditions where artificial light is present on the interior of windows and natural daylight is present on the exterior of windows (Swaddle et al, 2020).

In addition to altering flight tunnel and other experimental methods, we urge researchers and industry to collaborate on refining real-world field studies of window mitigation strategies. Field surveys have identified multiple factors that influence risk of collisions (Elmore et al, 2021; Loss et al, 2019; Riding et al, 2020) but these surveys have a number of limitations. First, depending on how often an area is surveyed for carcasses resulting from collisions, it can be difficult to distinguish between daytime and nighttime collisions. Second, it can be hard to determine which window or part of a window was struck unless there are distinctive marks left by the collision. This can be especially problematic at high-rise buildings. Third, counting carcasses can severely underestimate the number of actual collisions as the bodies of dead birds can be scavenged or removed (Hager et al, 2012) and/or collisions that are not immediately fatal can be missed. To address these limitations, we advocate for the use of sensors that can record movements of birds (e.g. cameras, radar, thermal imaging) and sensors to record the actual collision (e.g. vibration or acoustic sensors) (Elmore et al, 2021; Gauthreaux & Livingston, 2006; Hu et al, 2017; Ocampo-Peñuela et al, 2016). We are currently developing low-cost vibration sensors that can be applied to windows so that we can experimentally test the effectiveness of mitigation technologies and strategies in real-world situations. We encourage others to also deploy such technology so that more products can be thoroughly assessed in ecological and sensory settings that birds actually experience.

We also suggest that researchers and industry adopt a more objective and quantifiable assessment of window reflection. Classifying the degree of reflection seen by a human could potentially misrepresent the degree of reflection seen by a bird as humans and birds have different visual and cognitive capabilities (Cuthill et al, 2000; Martin, 2011). It is important that we continue to account for the sensory ecology of birds and, thus, more objective measures of lighting variables are preferable. Such measurements should be conducted at different times of day and days of the year, as lighting varies substantially over this time course. Ideally, we could build to a sensory understanding of window collision risk that might allow for rapid assessment of risk of collision as well as designing appropriate mitigation interventions. Our study offers one small step in that direction.

The overarching goal of this research was to identify whether lighting conditions alter risk of birds' collisions with windows by altering the degree of window reflection. Unexpectedly, the combination of exterior and interior lighting that leads to increased reflection is associated with reduced risk of window collision during bright midday conditions. Conversely, there is some indication that increased window reflection is associated with slightly increased risk of window collision in less bright morning conditions. In terms of practical recommendations to reduce actual bird-window collisions, these observations suggest that people should turn on their maximal indoor lighting in the morning but try to keep interior spaces rather unilluminated during the middle of the day. This mitigation strategy would likely have little influence on humans but could potentially benefit multiple species of birds, including those that are high-risk, throughout the United States and beyond. Many bird populations are in decline and we know that window collisions are a major source of avian mortality. As the world continues to urbanize, the risks to birds will increase. Identifying risk factors and adopting mitigation strategies that reduce the number of collisions could alleviate the imminent regional and national extinction of bird populations.

Appendix

A1. Logistic regression models for collision risk data

Predictors Included in Model	AICc	Δ_i	w_i	acc w_i
Velocity at 20 frames	38.93	0.00	0.78	0.78
Velocity at 15 frames	42.41	3.48	0.14	0.92
Exterior UV irradiance + Interior treatment	43.56	4.64	0.08	1.00
Blue light irradiance ratio	45.31	6.38	-	-
Velocity at 10 frames	45.59	6.67	-	-
Average lux ratio	45.82	6.89	-	-
Red light irradiance ratio	46.02	7.09	-	-
Exterior UV irradiance * Interior treatment	46.05	7.12	-	-
Exterior UV irradiance	46.09	7.16	-	-
Null	46.27	7.35	-	-
Interior treatment	46.44	7.52	-	-
Velocity at 5 frames	46.75	7.82	-	-
Velocity at 0 frames	48.53	9.61	-	-

Table A1.1. A comprehensive list of the univariate and bivariate models run for morning flights. AICc values are listed along with ΔAICc scores relative to the top-performing model. ΔAICc scores were used to calculate akaike weights of the most probable models which are listed along with the cumulative weight of all models included in full model-averaging.

Predictors Included in Model	AICc	Δ_i	w_i	acc w_i
Interior treatment	38.65	0.00	0.63	0.63
Exterior UV irradiance + Interior treatment	39.69	1.04	0.37	1.00
Null	41.88	3.23	-	-
Exterior UV irradiance * Interior treatment	42.26	3.61	-	-
Velocity at 15 frames	44.00	5.35	-	-
Velocity at 20 frames	44.05	5.40	-	-
Velocity at 5 frames	44.05	5.40	-	-
Blue light irradiance ratio	44.11	5.46	-	-
Velocity at 0 frames	44.12	5.47	-	-
Exterior UV irradiance	44.13	5.48	-	-
Velocity at 10 frames	44.14	5.49	-	-
Average lux ratio	44.15	5.50	-	-
Red light irradiance ratio	44.16	5.51	-	-

Table A1.2. A comprehensive list of the univariate and bivariate models run for midday flights. AICc values are listed along with ΔAICc scores relative to the top-performing model. ΔAICc scores were used to calculate akaike weights of the most probable models which are listed along with the cumulative weight of all models included in full model-averaging.

A2. Example flight

Figure A2.1. Three camera views capturing a digitized treatment flight. Views from the three GoPro cameras are depicted below with **(A)** depicting the view from the left camera, **(B)** depicting the view from the middle camera and **(C)** depicting the view from the right camera. One flight, which was classified as a collision, is shown in each camera view with the bird's position in the current frame indicated with a yellow arrow. The centroid of each bird was digitized until the bird reached the mist-net or reached the furthest distance in the flight. Flights were only counted as successful if they reached a distance past the overhanging black tarp.

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