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Research Paper

## Do lighting conditions influence bird–window collisions?

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**ABSTRACT.** Bird–window collisions account for approximately one billion bird deaths annually in North America. Highly reflective or mirrored glass is associated with increased collision risk, but little is known about whether the reflection caused by differential lighting of otherwise clear glass influences the risk of window collisions. We aimed to determine whether reflection from a clear window influences daytime collision risk by manipulating the lighting conditions on exterior and interior window surfaces. In a flight tunnel, we flew domesticated Zebra Finches (*Taeniopygia guttata*) toward windows manipulated to be of higher or lower reflection and recorded collision risk and flight velocity using three-dimensional videography. We predicted that the risk of collision would be greater when windows were manipulated to be more reflective. We found no support for this prediction. In contrast, we found that collision risk decreased in the presence of a stronger reflection during bright, midday exterior-lighting conditions. We suggest that the influence of window reflection on daytime window collisions is more complex than often assumed and might involve previously unaccounted properties of light, such as the polarity of light. Lastly, we recommend directions for future collision research and non-invasive mitigation strategies which involve the manipulation of interior lighting throughout the day.

## Les conditions d'éclairage influent-elles sur les collisions d'oiseaux avec les fenêtres?

**RÉSUMÉ.** Les collisions d'oiseaux avec les fenêtres représentent environ un milliard de mortalités d'oiseaux par an en Amérique du Nord. Les vitres très réfléchissantes ou à effet miroir sont associées à un risque accru de collision, mais on sait peu de choses sur l'influence de la réflexion causée par l'éclairage différentiel d'une vitre autrement claire sur le risque de collision. Nous avons cherché à déterminer si la réflexion d'une fenêtre claire influe sur le risque de collision de jour en manipulant les conditions d'éclairage sur la surface de fenêtres extérieures et intérieures. Dans un tunnel de vol, nous avons fait voler des Mandarins de Timor (*Taeniopygia guttata*) domestiques vers des fenêtres éclairées pour avoir une réflexion plus ou moins élevée, et nous avons enregistré le risque de collision et la vitesse de vol en utilisant la vidéographie tridimensionnelle. Nous avons prédit que le risque de collision serait plus élevé lorsque les fenêtres étaient éclairées pour être plus réfléchissantes. Nous n'avons trouvé aucune confirmation de cette prédiction. En revanche, nous avons constaté que le risque de collision diminuait en présence d'une réflexion plus forte dans des conditions d'éclairage extérieur intense en milieu de journée. Nous sommes d'avis que l'influence de la réflexion des fenêtres sur les collisions de jour est plus complexe que ce qui est souvent avancé, et pourrait mettre en cause des propriétés de la lumière non prises en compte auparavant, comme sa polarité. Enfin, nous recommandons des orientations pour les futures recherches sur les collisions et des stratégies d'atténuation non invasives qui incluent la manipulation de l'éclairage intérieur tout au long de la journée.

**Key Words:** *avian conservation; bird-window collisions; flight tunnel; sensory ecology; urbanization*

## INTRODUCTION

Bird–window collisions throughout North America result in approximately 1 billion bird deaths annually (Loss et al. 2014, Machtans et al. 2013). Though many avian taxa are affected, passerines (songbirds) are the most common victims of such collisions (Riding et al. 2020, Brown et al. 2020, Elmore et al. 2020). Within passerines, migrant species are typically more susceptible to window collisions than resident species (Hager et al. 2008, Hager and Craig 2014, Bracey et al. 2016, Wittig et al. 2017).

While perhaps a notable number of collisions occur during the night, when artificial lighting likely influences risk of collision (Evans Ogden 1996, Van Doren et al. 2017), daytime collisions

cause significant avian mortality (Klem 1989, Gelb and Delacretaz 2006, Loss et al. 2019). It is thought that the reflection off the glass surface causes birds to misperceive windows as open space or extensions of habitat (Ritter and Benson 1934, Banks 1976, Censky and Ficken 1982, Klem 1989, 1990, Kummer et al. 2016, Wittig et al. 2017). Accordingly, there is some evidence to suggest that reflection increases the risk of bird–window collisions. For example, when there is more glass surface area on window facades, there are more collisions (Borden et al. 2010, Cusa et al. 2015, Kummer et al. 2016, Brown et al. 2020). When reflection is maximized by replacement of a window with a mirror or the application of a highly reflective coating, researchers have observed more collisions (Klem and Saenger 2013, Cusa et al. 2015, Brown et al. 2020, 2021).

While there is some evidence to support the hypothesis that reflection increases the risk of bird–window collision, we are not aware of any studies that have manipulated the degree of reflection to vary between conditions that birds would experience in common urban and suburban window interactions. Specifically, the intensity of the reflection from the exterior surface of a clear window can change as a function of the interior and exterior light intensity surrounding the window (Knight 2017). When the exterior of a clear window experiences relatively higher intensity light compared with its internal surface (e.g., direct sunlight on the exterior surface and dim or no artificial lighting on the interior surface), the window will reflect more strongly. However, if the interior lighting is brightened and the exterior ambient lighting becomes less intense, the same window will reflect far less light and, perhaps, might pose less of a collision hazard to birds. Hence, reflection from a clear window will vary as a function of both the exterior ambient light and the interior artificial lighting of the building. Birds will experience this variation daily and, hence, the threat posed by a window might change according to these exterior and interior-lighting conditions.

Our primary research objective was to determine whether the presence of a reflection on clear windows influences birds' risk of collision, though we do acknowledge that reflections on mirrored and tinted panes could play an important role as well. We varied the reflective properties of windows by manipulating artificial conditions on the interior surface of the windows through differential artificial lighting (lower vs higher) and the exterior surface by performing experiments at different times of day (morning = lower, midday = higher). We combined these lighting treatments in a factorial manner and quantified collisions and avoidance of windows in a flight tunnel to allow for standardized exposure to the windows (Swaddle et al. 2020). Following previous hypotheses, we predicted that birds will be more likely to collide with windows when there is greater reflection. While windows can reflect a variety of scenes, we decided to focus on the reflection of sky.

## METHODS

### Ethics statement

The protocol outlined below was approved by the William & Mary Institutional Animal Care and Use Committee (IACUC-2019-0-9-22-13861-jpswad).

### Experimental subjects

We used a total of 100 adult, domesticated Zebra Finches (*Taeniopygia guttata*) in this study. 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 Avian 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 similar 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-collision studies as species in the Passeriformes taxon 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 flight trials (Klem and Saenger 2013). We also know that Zebra Finches respond similarly to a wild-caught species (Brown-headed Cowbird, *Molothrus ater*) in flight trials (Swaddle et al. 2020).

Thirteen of the birds used in the study were previously exposed to tunnel conditions, of which five had flown in window-collision trials (Swaddle et al. 2020). All birds with prior exposure rested (i.e., they were not handled or flown down the tunnel) for at least 1 month prior to flight trials. Some birds (namely, the subjects with prior window exposure) had up to 8 months of rest. Though these 13 birds had prior exposure, we did not detect signs of habituation to the tunnel as would be shown by hesitancy to fly toward the window structure. In order to account for the potential influence of prior exposure on collision risk, we included prior exposure as a categorical predictor variable in preliminary models.

### Flight tunnel

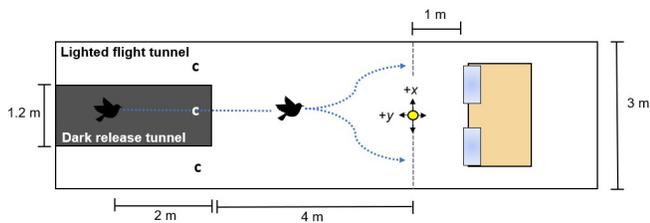
We flew birds in a long, narrow flight tunnel that had a simulated building facade, with two side-by-side windows, placed at the far end of the tunnel (Fig. 1; Swaddle et al. 2020). A mist net was placed approximately 1 m in front of the facade, from floor to ceiling and side to side, to avoid any unnecessary mortality. 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. We released birds within this darkened tunnel, where they flew for 2 m before emerging into the larger, lighted flight tunnel. The dark-to-light contrast encouraged birds to fly toward the window structure so that they would have the opportunity to interact with the window structure. A similar release-to-flight tunnel arrangement has been used in other flight studies (Klem 1990, 2009, Rössler et al. 2015, Goller et al. 2018, Sheppard 2019).

The building facade was built primarily from plywood and consisted of two wooden frames that were separated by 0.5 m (Fig. 2). These two frames each held a single-hung replacement window that is commonly used on residential properties in our area (Pella 250 Vinyl glass double-glazed replacement windows) (Fig. A1.1). We painted the plywood with beige-colored spray paint (Krylon Colormaxx spray paint, Satin Pebble) in order to look similar to the side of a residential or commercial building. The building facade extended from the floor to the ceiling of the flight tunnel and was sized so that there was a 0.5 m gap between the edge of the facade and each side of the tunnel, both left and right, allowing birds to avoid the whole structure to either the left or right side. Birds were unable to avoid the facade by flying above or below it as there were no gaps between the facade and the floor or the ceiling of the tunnel.

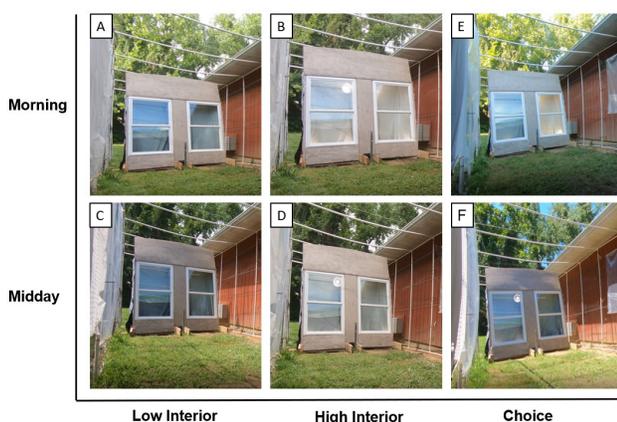
The whole window structure was tilted backward at 15° from vertical so that the windows primarily reflected the sky and not the flight tunnel. Given that the reflections were primarily sky,

reflections in the two windows were nearly identical. Additionally, the building structure was placed in the same marked location to keep the reflected image the same across trials. Nonetheless, there was some variability in weather and thus, the reflected image across trials. We accounted for this variability in preliminary analyses. During all experiments, the sun appeared slightly behind the windows and there was no perceptible glare off any window during trials.

**Fig. 1.** 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, 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 geometric origin of the scene (in yellow) and the dimensions of the tunnel are included below.



**Fig. 2.** 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. Each interior treatment was created with 1–3 light bulbs of various wattage, as shown in B, D, and F below.



We placed three digital video cameras (GoPro HERO7 Black, 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 (Fig. A2.1). The cameras were each placed at different heights and had different views of the birds’ flight (Fig. A2.2). This allowed us to obtain 3-D coordinates and extract velocity measures (Jackson et al. 2016).

## 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 minutes after sunrise, at 1200, and 30 minutes before sunset. Collectively, these interior- and exterior-lighting measurements were used to inform the target lux ranges for our lighting treatments.

## 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 1847 lux (commercial range = 23–1847 lux, median = 319 lux; residential range = 12–1719 lux, median = 126 lux; Fig. A1.2). We defined the lower level of our experimental interior-lighting treatment to be approximately 100 lux so as to remain below the median of residences. We defined the higher level of our experimental interior-lighting treatment to be approximately 1150 lux in order to maximize the variation between the lower and higher treatments but still remain within the range of lighting intensity in commercial buildings or residences. We manipulated interior-lighting intensity in our experiment by illuminating bulbs of different wattages in a light-sealed area behind each of the installed windows. The openings behind the windows were separated with an opaque black cloth such that the lighting behind each of the windows was completely independent. We illuminated one 40-W bulb (GE Refresh 40-Watt A21 Daylight Dimmable LED) to create the lower interior light-intensity treatment and illuminated three 100 W bulbs (GE Refresh 100-Watt A21 Daylight Dimmable LED) to produce the higher interior light-intensity treatment.

Measurements of exterior-lighting conditions in the flight tunnel ranged from about 14 to 38,653 lux (direct light range = 4245–38,653 lux, median = 26,307 lux; indirect light range = 14–13,804 lux, median = 878 lux; Fig. A1.2). 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 defined the lower exterior-lighting treatment to be approximately 10,000 lux (maximum light intensity <20,000 lux) and the higher exterior-lighting treatment to be approximately 40,000 lux (range 20,000 to 100,000 lux). We set our low and high exterior target values as values toward the higher end of the preliminary lux ranges given that exterior light is more intense in the summer seasons. 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 weather, lighting conditions measured during two midday treatment trials more closely matched the lux ranges of a lower exterior-lighting treatment. Those flights were classified in the lower exterior-lighting treatment. All interior- and exterior-lighting conditions were verified by spectrometry data on each day of experimentation.

We combined the two levels of interior- and exterior-lighting conditions to form six treatment groups (Fig. 2). In four of the treatments, both the windows in the building facade 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.

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. Which window (left or right) received which interior light treatment was balanced over trials to avoid side bias. We refer to these two treatments 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 (Rössler et al. 2015, Sheppard 2019).

### Lighting metrics

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

Because each interior- and exterior-lighting condition differed in their irradiance of red and blue wavelengths of light (Fig. A1.3), 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 birds’ visual sensitivity does not extend past 700 nm (Bennett et al. 1996).

Given that Zebra Finches are sensitive to ultraviolet (UV) light (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. There was little to no UV light on the interior windows; therefore, we did not calculate an interior/exterior ratio for this metric.

### 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. 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 (Fig. 1). 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. If a bird did not fly successfully in the first release, birds were released a maximum of 2 more times. If the bird flew successfully in at least one release during control and treatment flights, the bird was retained in the study. A control or treatment flight was considered successful if the bird flew at least 4 m from the release point along the y-axis, by which point the bird had flown more than 50% (3 m) of the way toward the window structure (in treatment flights) relative to its starting position. 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, n = 16 or 17 per treatment group), ensuring that there was an approximately even number of males and females in each treatment group. The order of treatments was randomized.

We recorded all flight trials, controls, and treatments on three GoPro cameras. The total volume of the recorded scene was approximately 30 m<sup>3</sup>. We used both audio (through a walkie-talkie placed next to each camera) and visual (flashlight) signals to synchronize the three cameras at the beginning of each recording period. After synchronizing 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 extrinsically 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 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 (Jackson et al. 2016).

### 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. Flights were scored primarily using the ending position of a bird’s flight. Our assessment of collision was based on the distance the bird flew down the tunnel and their combined horizontal and

vertical placement relative to the window. 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 (i.e., a bird collided with the mist net in a position that aligned with the plywood, or outside of the building facade, or did not reach the mist net), the trial was scored as an avoidance of window collision. We were not concerned with flights that aligned with the facade as this study was designed purely to study the birds’ interactions with windows. Hence, our focus was on whether birds avoided the windows or not. Birds rarely hit the mist net in a position that was not easily discerned as a collision or avoidance. In this case, flight paths were extrapolated 1 m past the mist net using the positioning of their body prior to hitting the net and scored accordingly. Qualitative flight trajectories, obtained through frame-by-frame flight tracking, were further used to verify each scoring.

### 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 (van Rossum and Drake 2009, Jackson et al. 2016) to synchronize 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 small error in reconstruction.

The geometric origin of the scene was set on the ground at the midpoint between the two windows (from left to right). 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 extended from the ground to the ceiling of the flight tunnel (Fig. 1).

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 4 m in control flights) or stopped flying. From these digitizations, we calculated velocity of each bird per frame of video (distance traveled 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, only 3 velocity metrics were calculated (V10, V5, V0). This averaging technique acted to smooth the velocity data, further minimizing the effect of single-frame digitization errors.

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 in its treatment flight compared with its control flight. Considering that we used 100 different Zebra Finches in our study, the within-individual change in velocity, rather than the raw velocity values, were used in our models.

### Statistical analyses

To examine whether there were systematic differences in exterior lighting conditions on either side (left vs right) of the building facade at the same time point, we compiled high exterior and low exterior measurements and employed two 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). All the data, including morning and midday collision risk data, were combined for the initial analyses. 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, time of day, and prior exposure. We included an exploratory model with weather (sunny or cloudy) and treatment as predictors in order to eliminate variable sky reflections as a potential predictor of collision risk. None of the models performed better than the null, so these variables were omitted from any subsequent analyses. In addition, we conducted exploratory analyses in order to determine whether the interaction of interior and exterior light would be a better predictor of collision risk in comparison to our reflection metric. We averaged interior and exterior values for each treatment flight trial and included these averaged values in the interaction model. The interaction model, when run with all data or split by morning and midday, performed worse than the models which included the reflection metric. Therefore, we considered our reflection metric to be the most informative predictor which includes both interior and exterior-lighting conditions. In hindsight, this makes sense as the computed reflection metric likely captures more information about the lighting conditions that each bird experienced.

We first ran a number of univariate models including the 10 predictor variables, assuming that the potential effects of the 10 predictor variables remained consistent in both morning and midday. None of the univariate models outperformed the null model. Modifying our initial assumption that subjects behaved similarly relative to certain predictors in both the morning and midday treatments, we opted to include an interaction term (time of day, a categorical variable) in every univariate model previously run. Including an interaction term for time of day improved model fit of the top-performing models, therefore, we opted to employ additional logistic regression analyses with the data split by morning (treatments a and b) and midday (treatments c and d) for ease of interpretation.

For the split analyses, we included the same set of models with 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, depending on the time of day. A

full list of the models run is provided (Table A3.1–3.3). Results from both the combined logistic analyses and the analyses split by time of day are included below.

We compared models using Akaike’s Information Criterion with small sample correction (AICc, Burnham and Anderson 2002) using the R package “MuMIn” (Barton 2020). We only considered models that returned AICc values > 2 below the AICc of the null model. When splitting the data by morning and midday, multiple models outperformed the null model; therefore, 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 and Moussalli 2011) in either the morning or the midday, we employed a full-model averaging approach using the “MASS” R package (Venables and Ripley 2002).

Due to a low sample size of collision events and a preference for the right window, we did not perform any statistical analyses of data generated by the two “choice” treatments (e: 3, f: 4) and we did not consider data from those treatments any further.

We ensured that 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).

## RESULTS

### Side bias of lighting treatments

We compared lighting conditions of the left and right windows when mounted in the facade in the flight tunnel. There was no indication that exterior light conditions differed between left and right windows at a single time point, regardless of whether trials were conducted in low or high exterior conditions (lower exterior light treatment, Wilcoxon signed-rank Test,  $W = 198$ ,  $p = 0.623$ ; higher exterior light treatment, Wilcoxon signed-rank Test,  $W = 184$ ,  $p = 0.501$ ; Fig. A4.2).

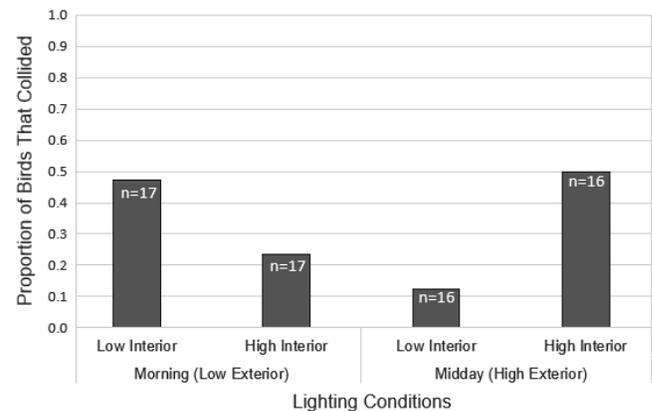
### Assessment of risk of collision

During control flights, the birds often flew the entire length of the flight tunnel. Only 11% (11) of subjects stopped short of 6 m. During treatment flights, birds most 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 29% (20 cases) of avoidances, subjects were adjudged to have been on course to collide with the building facade around the windows. These potential collisions (if the birds had flown further) were evenly distributed throughout the treatments (a: 4, b: 2, c: 4, d: 2, e: 5, f: 3). We did not classify these cases as collisions in our analyses as they do not explicitly address our hypothesis that reflection increases risk of window collision. In total, we recorded 29 window collisions, which represented 29% of treatment flights (Fig. 3).

Our logistic regression analyses which included the combined morning and midday data revealed one probable model explaining window-collision risk (Table A3.1). Velocity 20 frames from the end was the strongest predictor of collision risk, but the effect of this variable was dependent on the time of day (Table 1). In the morning, collision risk increased with increasing velocity

20 frames from the end of the flight. In contrast, increased velocity 20 frames from the end of the flight led to decreased collision risk at midday.

**Fig. 3.** 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.



**Table 1.** List of the predictors included in the top overall model. One interaction model outperformed the null model when the data was pooled to include both the morning and the midday collision risk data. The estimates for each predictor included in the model and their interaction is listed ( $\pm$  1 SE).

Predictor	$\beta$ est.	-1 SE	+1 SE
Intercept	-0.85		
Time of day (Midday)	0.05	-0.53	0.64
Velocity at 20 frames	1.62	0.92	2.31
Midday * Velocity at 20 frames	-1.74	-2.53	-0.96

When split by time of day, our logistic regression analyses revealed three probable models which explain window-collision risk in the lower (morning) exterior-lighting flights (Table A3.2). The top-performing models included the following predictors: relative 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 positively predicted risk of collision in the morning and was the only predictor to have model-averaged standard errors that did not overlap 0 (Table 2).

A separate set of logistic regression analyses revealed two probable models that explained window collisions during higher (midday) exterior-lighting flights (Table A3.3). The top-performing models included interior-lighting treatment and exterior UV irradiance as predictors. Interior lighting treatment was the only predictor to have model-averaged standard errors that did not overlap 0 (Table 2). The risk of window collision decreased in the presence of a lower interior-lighting treatment. In this situation, we expected to see the strongest reflection off the exterior surface of the windows, which Emerson verified visually prior to each set of trials. Hence, the results from the

**Table 2.** 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 ( $\pm 1$  SE). “Low intensity treatment” corresponds to the low intensity interior treatment, or our reflective condition. Velocity at 20 and at 15 frames were correlated with each other and so appeared in separate models.

	Predictor	w	$\beta$ est.	-1 SE	+1 SE
Morning	Intercept		0.37		
	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		-0.13		
	Low intensity treatment	1.00	-2.17	-3.23	-1.11
	Exterior UV irradiance	0.37	0.24	-0.22	0.70

higher midday exterior-lighting model conflicted with our a priori prediction.

## DISCUSSION

The presence of a stronger reflection from the exterior surface of clear windows influenced collision risk but not in the direction that we or other studies had predicted. The presence of a stronger reflection in bright, midday conditions decreased the risk of collision rather than increasing collisions. These findings suggest that reflection from 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 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 (though this latter pattern was not statistically supported). Given that previous studies have reported an increase in risk of collision with increased reflection from windows (Kummer et al. 2016, Brown et al. 2020, 2021) our findings appear somewhat perplexing. However, there is some precedence for the patterns we found. Gelb and Delacretaz (2006) documented a near 50% decrease in the number of collisions from the 0900–0930 time frame to the 1200–1230 time frame at a building with reflective glass panels mounted into a brick exterior. This aligns with our results which indicate a decrease in collision risk from morning to midday as birds were exposed to windows with stronger reflections. It is possible that the decrease in the number of collisions from morning to midday could be a function of a bird’s perception of light reflected off the windows at the two time points rather than a decrease in bird activity or density at midday. Previous studies bolster this idea by asserting that density is not the most important predictor of collision risk (Hager et al. 2008), however, we acknowledge that we cannot rule out the influence of bird density and/or activity levels on temporal patterns of collisions.

One potential explanation for why increased reflection leads to decreased risk of collision at midday, compared with the morning, is that there is relatively more UV light present at midday. With more ambient UV light there could be more UV reflection, making reflective windows more visually obvious compared with the same window in the morning. We explored the validity of this UV contrast hypothesis by building models for the morning and midday data with both exterior UV irradiance and interior treatment as predictors. Model-averaged  $\beta$  coefficients and standard errors revealed no substantial effect of exterior UV irradiance on collision risk. Thus, increased UV does not appear to predict a decrease in collisions.

A more probable alternative hypothesis to explain why increased reflection is associated with lower risk of collision at midday is that the lighting treatments could produce a contrast in the polarization of light, making reflective windows more visually conspicuous at midday compared with the early morning. Birds utilize linearly polarized light cues in navigation (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 window-collision risk (Lao et al. 2020). Though we did not measure the polarization of light, glass windows are known to polarize reflected sunlight in ways that mislead animals (Kriska et al. 2008). 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 increasingly unpolarized (Muheim 2011). Dark and shiny surfaces like windows polarize light to a greater degree and backlighting should act to reduce exterior polarization (Kriska et al. 2008, Horváth et al. 2009). Thus, our darker interior treatments (i.e., those with less interior illumination (treatments a and c) should have produced a greater percentage of polarized reflected light in comparison to our more brightly-lit interior treatments (treatments b and 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 observation, we tentatively 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 conspicuous compared with the background sky. This contrast hypothesis could explain previous research which has shown no influence of window polarization patterns per se on collisions (Lao et al. 2020). According to this polarization contrast hypothesis, the influence of polarized light cues reflected from windows would be dependent on sky polarization patterns which change throughout the day. This could also explain why we saw very few collisions in choice treatments. In choice treatments, polarization patterns of the two windows were likely different. The contrasting polarization patterns could have alerted birds to the barrier. We suggest that the polarization of light be delved into as a risk factor in bird–window collisions in the future. Considering that we did not see an effect of our reflection metric on collision risk, it is not likely that light intensity itself is an important determinant of collision risk.

In a more intuitive manner, our data indicate that birds are more likely to collide with windows when they fly faster, presumably because birds have less time and space to adjust their flight to avoid collision (cf. Swaddle and Ingrassia 2017, Swaddle et al. 2020, Boycott et al. 2021). It is important to note, though, that velocity is not always a good indicator of collision risk. In the afternoon, collision risk decreased with increasing velocity. In this case, individuals that recognized the barrier earlier in flight could have adjusted trajectory while maintaining a constant speed. These observations further emphasize 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.

The surprising influence of lighting that we observed is not accounted for in most published tests of collision mitigation technologies. For example, industry-standard flight tunnel studies have generally 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-collision 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 and Saenger 2013). Taken together with our results indicating that lighting conditions have an unpredicted 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 such 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).

While we attempted to remove all possible confounds, we acknowledge that the mist net could have played a minor role in determining behavior in our tunnel-based study. There were small differences in the number of individuals that avoided the mist net in each treatment (a: 2; b: 6; c: 4; d: 5), which could be due to the interaction of the mist net and lighting conditions. In an attempt to eliminate the mist net as a confound, we opted to remove all the individuals that did not reach the mist net from a post-hoc logistic regression analysis. We assumed that if individuals did not reach the mist net, they likely saw and avoided the mist net rather than the building structure. In this case, the only factor that should have influenced behavior would be the manipulation of lighting in the facade. We ran the analyses similarly to our main analyses. No model outperformed the null when the data was grouped together and an interaction term for morning and midday was included. Upon splitting the data into morning and afternoon and re-running the analyses, the same variables were important in determining collision risk (V20 in the morning and interior treatment in the midday). Notably, our effect sizes increased in comparison to the original analysis (Table 3). We do not believe the mist net played a role in our tunnel experiment but the potential influence of mist nets in future tunnel experiments should surely be considered.

There are a variety of external factors that could have influenced collision risk in our tunnel system that we have not explicitly accounted for. Fine-scale shading patterns throughout the tunnel could have also played a role in collision risk depending on where

birds emerged from the release tunnel. Additionally, a bird’s movement throughout the tunnel could have influenced a bird’s perception of the reflected image and thus, a bird’s decision. Incorporating this level of detail into our study was not feasible, but the influence of these factors could be better understood with additional research that examines the birds’ direction of gaze.

**Table 3.** Additional models were run excluding individuals that stopped prior to the mist-net. We assume that these individuals saw and avoided the mist net rather than the façade. Predictors included in the top models when the data was split by morning and midday are found below. The estimates for each predictor ( $\pm 1$  SE) are included.

	Predictor	$\beta$ est.	-1 SE	+1 SE
Morning	Intercept	-0.39		
	Velocity at 20 frames	1.40	0.67	2.13
Midday	Intercept	0.98		
	Low intensity treatment	-2.59	-3.62	-1.56

One of the limitations of our tunnel-based study is that it might be difficult to translate our results to free-living birds, as captive birds are commonly stressed and might adjust their flight behaviors (Klem and Saenger 2013). We have taken steps to minimize those limitations by using a domesticated strain of Passerine (the domesticated Zebra Finch) and using birds that are accustomed to handling and the presence of humans. In addition, we note that flight responses of domesticated Zebra Finches, from the same colony, to an ultraviolet-scattering window treatment were qualitatively similar to responses of a recently caught wild songbird, the Brown-headed Cowbird (Swaddle et al. 2020). Hence, we believe our choice of study system helps minimize the stress-related effects of captivity while still maintaining relevance to free-living systems.

The overarching goal of this study 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 likely leads to increased reflection is associated with reduced risk of window collision during bright midday conditions. Conversely, there is some weak evidence that increased window reflection is associated with slightly increased risk of collision in less-bright morning conditions. In terms of practical recommendations to reduce actual bird–window collisions, these observations suggest that people should try to keep interior surfaces of windows rather unilluminated during the middle of the day. This mitigation strategy need not be applied when interior lighting is already absent or mirrored panes have been installed. This mitigation strategy would likely be straightforward to deploy and could be achieved by inexpensive light timers. As low-rise residence windows account for the majority of bird–window collisions, our suggestion could lead to increased protection for a large number of birds. The influence of lighting conditions on collision risk warrants further research, especially in in-situ field studies with real buildings and free-living birds, before we are able to make definitive lighting recommendations. However, our preliminary recommendations should help to reduce the number of annual bird–window collisions.

Responses to this article can be read online at:  
<https://www.ace-eco.org/issues/responses.php/2167>

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#### Author Contributions:

Lauren C. Emerson, roles: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, visualization, writing - original draft, writing - review and editing Robin G. Thady, roles: data curation, investigation, methodology, writing - review and editing Bruce A. Robertson, roles: validation, writing - review and editing John P. Swaddle, roles: conceptualization, funding acquisition, methodology, project administration, resources, supervision, validation, writing - original draft, writing - review and editing

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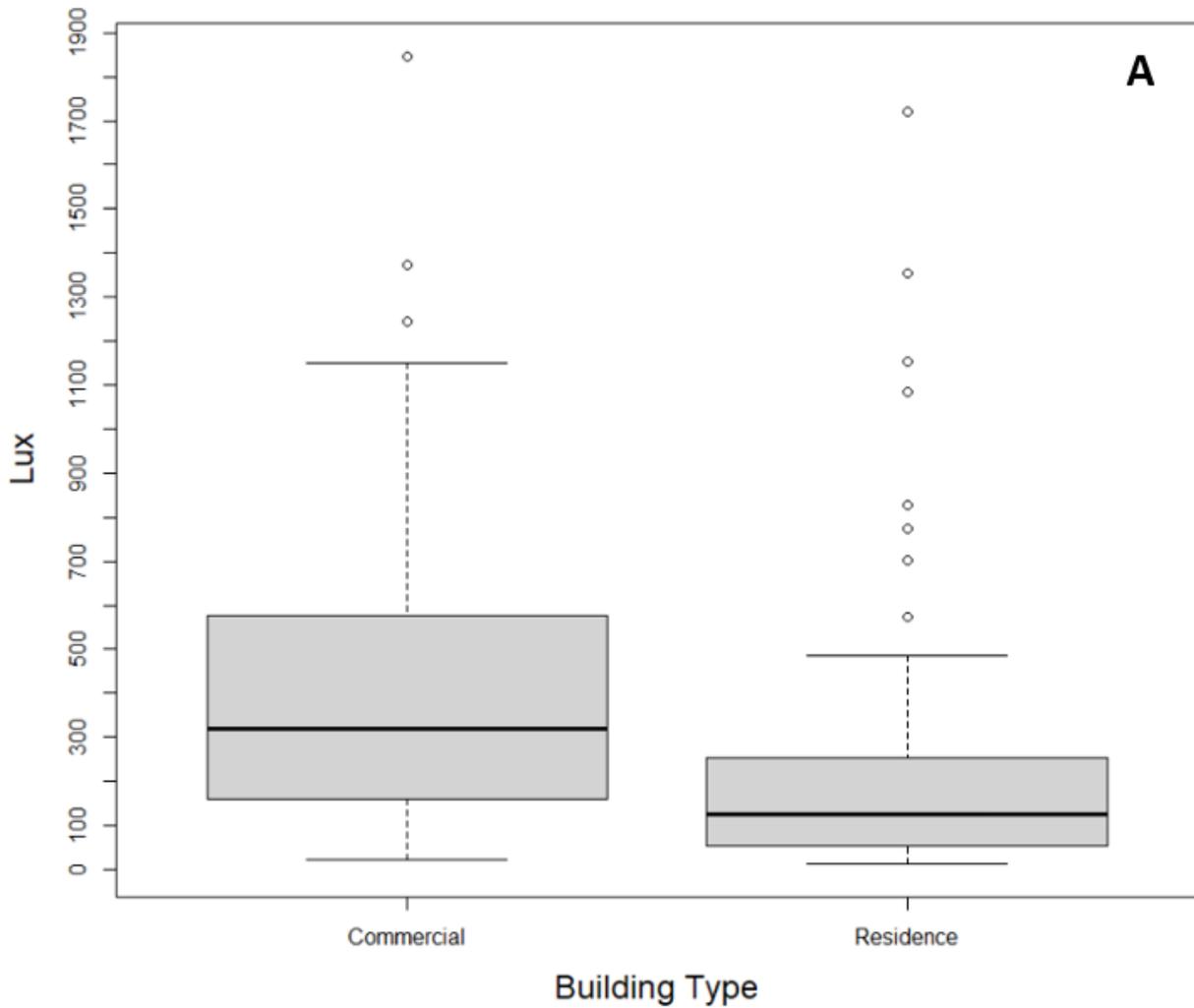


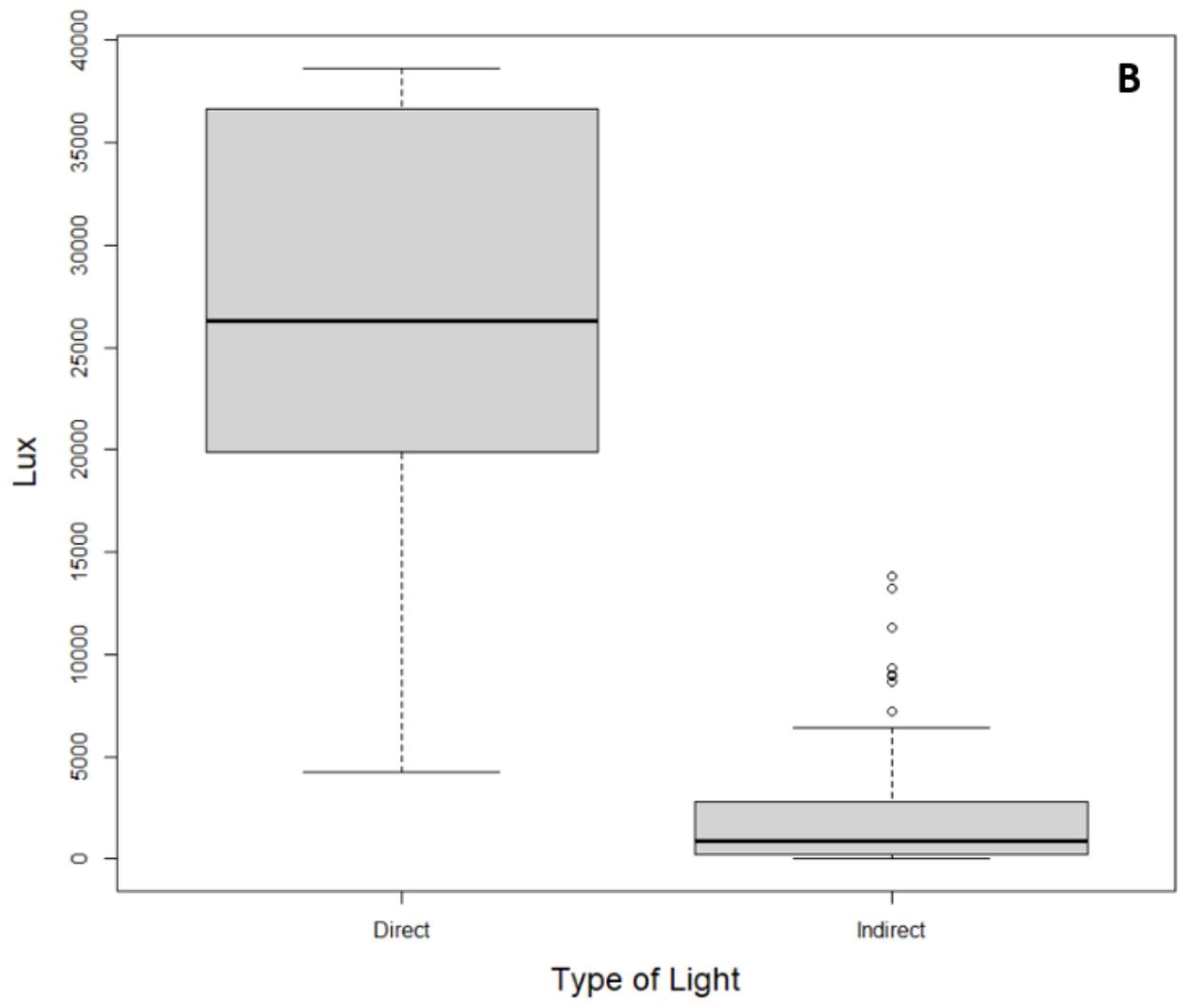
**Appendix 1.** Data collected to determine window type as well as interior and exterior light intensity treatments. Spectra typical of the interior and exterior lighting conditions are also included.

**Figure A1.1.** 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.

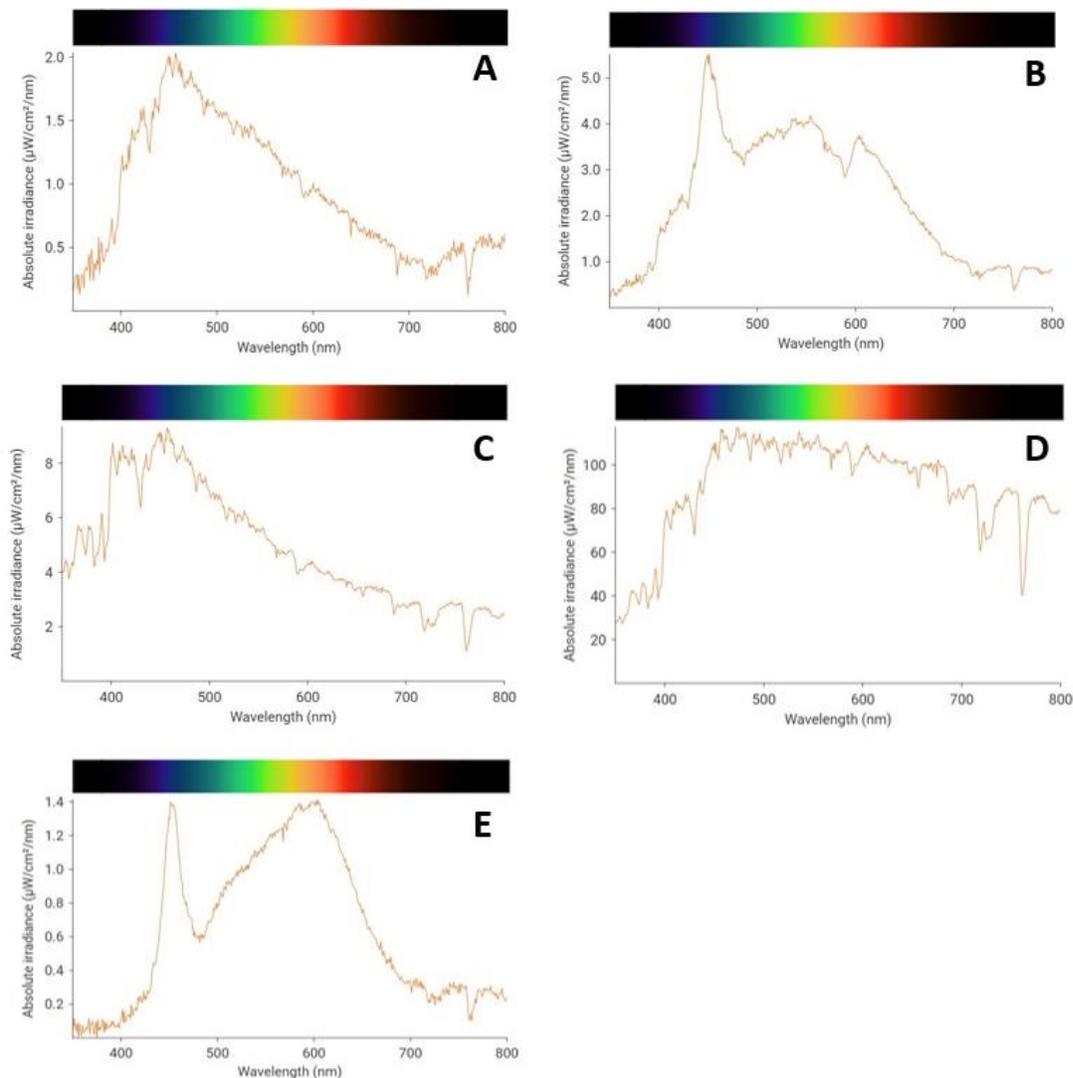


**Figure A1.2.** (A) Artificial lux measurements were taken at 30 commercial buildings and 16 residences in the Williamsburg, VA area during the month of December (2019). Measurements were taken in 4 separate rooms within each building or home as far from windows as possible, to minimize the influence 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.





**Figure A1.3.** Irradiance spectra were obtained while holding the spectrometer with the sensor facing directly upwards on the interior (A and B) or exterior (C and D) of the window. Each irradiance spectrum indicates the absolute irradiance at each wavelength, with the accompanying visual spectrum atop the chart. Example irradiance spectra from trials are provided for the two interior intensity conditions: low (A) and high (B). Additionally, example irradiance spectra are provided for the two exterior intensity conditions: low (C) and high (D). These two interior and exterior lighting conditions were combined pairwise to form the 6 overall treatments. Low intensity interior (A) and exterior (C) conditions are richer in the UV and blue wavelengths of light relative to other wavelengths of light. High intensity interior (B) and exterior (D) spectra show a greater irradiance of all wavelengths of light, but notably contain a greater irradiance of orange and red wavelengths of light relative to low intensity conditions. The target interior spectrum for trials (E) was determined by visually inspecting the spectra typical of artificial light in residences and commercial buildings to find the most common pattern. We chose the light bulbs that best mimic this spectrum (see 'B').

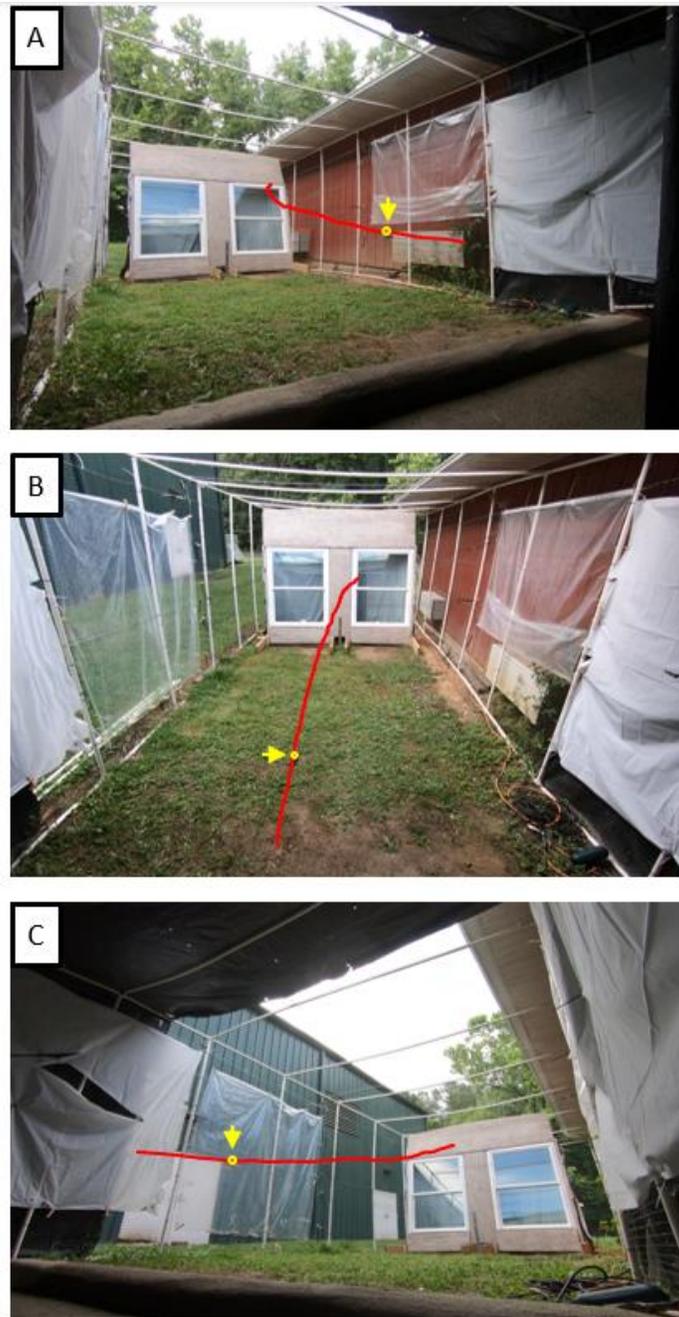


**Appendix 2.** GoPro camera set-up and an example flight.

**Figure A2.1.** Three GoPro HERO7 Black cameras (shown in the red circles) 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.



**Figure A2.2.** 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 complete flight, which was classified as a collision, is shown in red in each camera view with the bird's position in the current frame indicated with a yellow arrow and a yellow circle. 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.



**Appendix 3.** Logistic regression models for the combined data and data split by morning and midday.

**Table A3.1.** A comprehensive list of the univariate and bivariate models run for the combined collision risk data. AICc values are listed along with  $\Delta$ AICc scores relative to the top-performing model. Models that improved with the incorporation of an interaction term are also listed with their accompanying AICc values.

Predictors Included in Model	AICc	$\Delta_i$
Velocity at 20 frames * Time of day	82.83	0.00
Interior treatment * Time of day	84.95	2.12
Velocity at 20 frames	85.08	2.25
Null model	86.08	3.25
Velocity at 15 frames	86.18	3.35
Velocity at 5 frames	86.66	3.83
Velocity at 10 frames	86.94	4.11
Red light irradiance ratio	87.66	4.83
Average lux ratio	87.75	4.92
Interior treatment	87.94	5.11
Blue light irradiance ratio	87.94	5.11
Exterior UV irradiance	88.20	5.37
Velocity at 0 frames	88.20	5.37

**Table A3.2.** A comprehensive list of the univariate and bivariate models run for morning flights. AICc values are listed along with  $\Delta$ AICc scores relative to the top-performing model.  $\Delta$ AICc 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.

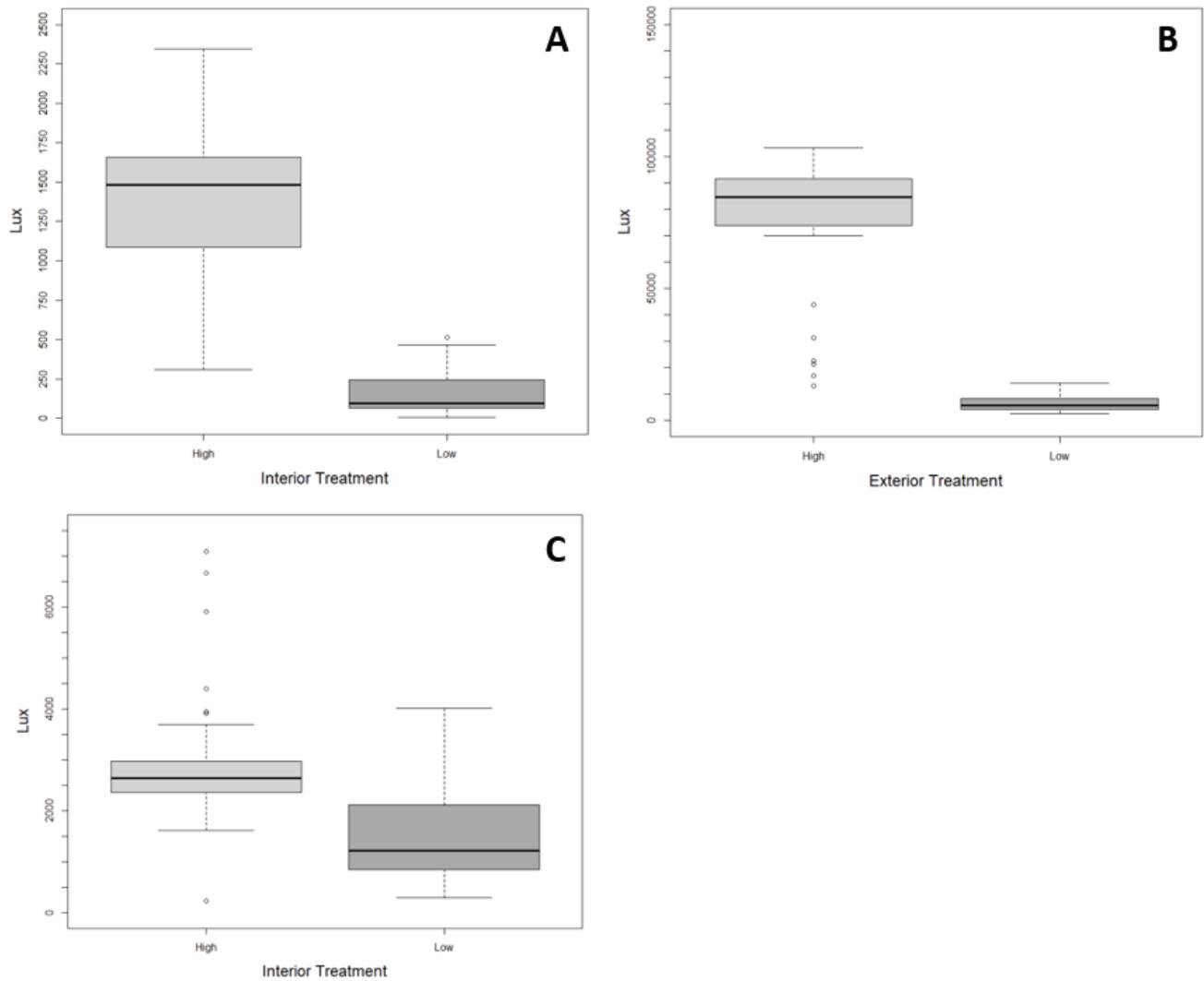
Predictors Included in Model	AICc	$\Delta_i$	$w_i$	acc $w_i$
Velocity at 20 frames	38.93	0.00	0.78	0.78
Velocity at 15 frames	42.41	3.48	0.14	0.92
Exterior UV irradiance + Interior treatment	43.56	4.64	0.08	1.00
Blue light irradiance ratio	45.31	6.38	-	-
Velocity at 10 frames	45.59	6.67	-	-
Average lux 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 A3.3.** A comprehensive list of the univariate and bivariate models run for midday flights. AICc values are listed along with  $\Delta$ AICc scores relative to the top-performing model.  $\Delta$ AICc 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	$\Delta_i$	$w_i$	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	-	-

#### Appendix 4. Flight trial interior and exterior light measurements.

**Figure A4.1.** 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 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. (C) represents the interior light intensity with natural light included, or the realized lighting conditions.



**Figure A4.2.** 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.

