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Using Multimodal Cues To Mitigate Avian Window Collisions

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COMPLIANCE PAGE

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ABSTRACT

Collisions with windows are a leading anthropogenic cause of avian mortality. An estimated 500 million birds fatally collide with windows in North America every year. Visual mitigation strategies are thought to be an effective tool but there are very few robust field studies, and many controlled studies lack ecological relevance. This study seeks to test a window film in a more ecologically relevant manner, as well as introduce a novel element, sound. Previous work indicates that sound is an effective way to prevent collisions with freestanding structures. The sound is hypothesized to prompt a bird's visual attention toward the collision hazard. Therefore, we further hypothesized that a sound cue (4-6 kHz oscillating frequency) used in concert with a visual cue (Solyx brand window film) would increase a bird's ability to avoid a window. We exposed 24 zebra finches (*Taeniopygia guttata*) to four treatments (control, sound, visual, and sound-visual combined as a multimodal cue) in a balanced order in a flight chamber. A mist net ran the width of the flight corridor to prevent collisions from actually occurring. Each flight was filmed using multiple cameras. From these recordings, we reconstructed the flights in three dimensions and derived several key flight metrics (average velocity, end velocity, minimum distance to the structure, turn distance). We combined these metrics in a principal components analysis (PCA) that led to a quantitative categorization (using permutational multivariate analysis of variance, PERMANOVA) of "lower risk" (birds that made avoidance adjustments early in their flight) or "higher risk" (birds that made avoidance adjustments late in flight and those adjudged to collide with windows) flights. This categorization (lower vs higher risk) served as the response variable for a binomial generalized linear mixed model (GLMM). Based on the model, all three treatments (sound, visual, and multimodal) lowered the probability of riskier flight behavior, although the effect of the sound treatment alone was not as statistically supported as the other two treatments (95% confidence intervals overlapped with 0). Though the multimodal treatment appeared to have a slightly stronger effect than the visual alone, there is little statistical support that a multimodal approach is more effective than a unimodal (visual) one. We argue that multimodal strategies for preventing window collisions warrant further investigation and could have utility in situations where the efficacy of a visual treatment is compromised. While the effect of the sound cue alone was not strong, it was more effective than we predicted. Hence, sound may be an alternative deterrent in situations where applying a window film is not practical.

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This Master’s Thesis is dedicated to my family, biological or otherwise.

If you offered me guidance, reassurance, commiseration, or even a good laugh, then know that you helped to make this possible.

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Introduction

We are living in the Anthropocene; our land-use and resource consumption leaves less than a 1/3 of our planet's ecosystems intact (Luyssaert et al. 2014). Even areas that are not yet directly impacted by human-caused development and/or extraction are being harmed by climate change (Steffen et al. 2011). These unprecedented changes to the environment are straining ecosystems and initiating the sixth mass extinction (Barnosky et al. 2011). In addition to higher-than-expected extinction rates, there are widespread decreases in abundance across all taxa. In birds specifically, North America has seen an estimated 29% net loss of abundance over the past half-century (Rosenberg et al. 2019).

It is likely that an important cause of declines in avian populations relates to increasing mortality in collisions with windows (Loss, Will, and Marra 2015). In North America alone, an estimated 500 million individual birds die from window collisions each year (Loss et al. 2014). Despite the pervasive nature of this issue, the mechanisms driving window-collisions are not well understood. There are, however, certain environmental factors that correlate strongly with collisions. For example, researchers have reported more collisions close to urban green space (Gómez-Martínez et al. 2019). Many have assumed the collisions occur because birds perceive windows' reflection of green space as more habitat, and they accidentally fly into a solid glass surface. However, it is also possible that windows near the green space are just more likely to be hit as the green space attracts more birds. It is likely that both mechanisms play a role (Borden et al. 2010), but without experimentation in real world settings we are left to interpret correlative relationships that lack causality.

One potential way to understand how a flying bird perceives the threat presented by a glass window is to interpret how their sensory systems interact with their environment. Humans and birds are both highly visual creatures, but there is one key difference; birds' eyes are located on the sides of their heads. Their highest resolution vision is oriented laterally and as a result, they do not have a large amount of binocular vision (the main type of vision that we use). Flying birds are often looking down at the ground for navigation/foraging cues, or out to the side in order to locate potential predators or foraging opportunities (Martin 2011). When approaching a collision hazard directly, it is in the birds' peripheral vision. This could help explain why birds seem to have trouble distinguishing reflection from reality.

One of the most common strategies for mitigating window collisions is to alter the visual appearance of the window with products like films, decals, and glass treatments. They are hypothesized to work by disrupting the appearance of reflections and/or making transparent glass look more solid to a bird (Klem Jr 2009). Most of the testing on these products is done in dark flight tunnels that force birds to choose to collide with a treated or untreated window (Sheppard 2019). This protocol offers a standardized testing environment but lacks sensory and ecological relevance to help us assess real-world avoidance of window collisions. More researchers are beginning to test window treatments in the field with some encouraging results (Brown, Santos, and Ocampo-Peñuela 2021). However, most of those studies are rather limited in scale and often record data through recovered dead birds and likely miss many sub-lethal collisions events. Rather than counting dead birds in the field or forcing birds to collide, we should endeavor to design more biologically relevant studies (both in the field and the lab) whose data can suggest causality. Understanding how and why birds are able to avoid collisions is critical for engineering the most effective mitigation strategies.

This study investigates a potential way to increase the efficacy of visual window treatments based on strategies used to prevent other types of collisions. Freestanding structures like cell towers or wind turbines are collision risks for birds. Such collisions are likely related to the previously discussed limitations of birds' visual systems (Martin 2011), and sound is being explored as a way to change birds' detection of the threat and deter these collisions (Swaddle and Ingrassia 2017; Boycott et al. 2021). Auditory warning signals are hypothesized to work by redirecting a birds' visual attention forward. We hypothesize that this same sensory redirection could be used to draw a birds' attention to a visual deterrent on a window. A collision mitigation strategy that taps into multiple sensory systems (in this case, auditory and visual) may be more likely to be noticed by a bird and will thereby increase its ability to avoid a hazard.

We explored this idea with the following question: will a multimodal signal improve a bird's ability to avoid a window? We utilized a repeated measures design, exposing zebra finches (*Taenopigya guttata*) to a series of 4 different treatments in a balanced order. The treatments included untreated control windows, a sound cue treatment, a visual cue treatment, and a combination multimodal treatment. We predicted that the unimodal treatments would decrease collisions, but the reduction would be even greater when both the sound and visual cues were present.

Materials and Methods

General housing

We used 24 adult zebra finches (*Taeniopygia guttata*) in this study. The birds had no exposure to the experimental conditions beforehand. When not in experimental trials, they were housed in a common aviary (add approximate dimensions) with ad libitum food (millet blend), drinking water, bathing water, cuttlebone, calcium-rich grit, and perches.

Flight trials and experimental treatments

We conducted experimental trials in an outdoor flight arena (Figure 1) from June to August 2021. The arena consisted of a short, darkened tunnel (7 x 1.2 x 1.2 m) that led to a larger, open and daylit area (7.5 x 2.5 x 3 m) in which we placed a wooden structure (2.3 x 2 m) that contained two commercially available double-glazed replacement windows (Pella 150 Series 35.5-in x 53.5-in x 4.688-in Jamb Vinyl New Construction White Single Hung Window Half) (Swaddle et al. 2020). The structure was angled back at approximately 5 degrees to increase the amount of sky in the reflection. We hung a gray drop cloth behind each window and illuminated the area with LED lights to create lighting conditions on the internal surface of each window that are typical of indoor lighting in our area (Emerson et al 2022 *in review*). This arrangement created a reflection, at least to experimenters' eyes, on both windows. Additionally, artificial greenery was hung above the end of the darkened tunnel. The resulting reflection contained mostly images of the sky and clouds, and the greenery became visible when approaching the window structure.

Individually, we released birds from the hand in the darkened tunnel and, with a vocal startle stimulus (shouting the word “go!”), encouraged them to fly into the daylit area and toward the windows. This approach differs from other flight tunnel studies because the obstacle of interest is lit by ambient daylight rather than being backlit, while still taking advantage of the birds’ instinct to fly from dark to light. In almost all flights, birds flew directly toward the windows. We strung a fine mist net (70 denier 2 ply) across the width of the tunnel 0.5 m in front of the windows to prevent actual collisions. We placed a small directional speaker (Holosonics audio spotlight) at the base of the structure between the two windows so that we could project a narrow beam of sound directly from this location toward the release point of the bird. We also placed three GoPro Hero7 cameras in fixed places to video record (60 frames per second) each flight for later analysis. We began experimental flight trials at 09:00am each day to ensure some consistency of lighting conditions among days. We did not conduct flight trials during rain or if the wind exceeded approximately 12kph, as anything more than a light wind produced noticeable movement of the mist net.

We exposed each bird to four treatments: control, visual, sound, and multimodal. In control trials, we did not alter the appearance of the windows and did not play a sound cue. In visual trials, we presented windows that had been treated with a Solyx SX-BSFH horizontal bird-safety film, which is a product endorsed by the American Bird Conservancy (“Products & Solutions Database” n.d.). In sound trials, we used non-treated windows and played a 4-6 kHz sinusoidal, frequency-modulated sound from the directional speaker. This frequency was selected based on previous work in the lab (Thady, Emerson, and Swaddle 2022). In multimodal trials, we used Solyx-treated windows and played the 4-6 kHz sound from the directional speaker. All birds were exposed to all the treatments in a balanced order; the four treatments were evenly distributed with respect to birds' repeated exposures. Hence, order effects were avoided, and each bird served as its own control.

Flight Analyses

We analyzed the video from each flight to evaluate qualitatively whether birds would avoid or collide with the windows. Specifically, we assigned each flight to three flight outcome categories: early avoid, late avoid, and collision. A flight was designated and early avoidance if the bird made a small adjustment in their flight trajectory at the beginning of their flight, such that they flew clear of the structure. A late avoidance described flights where the bird made a large change directions in the middle or end of their flight to avoid the structure. Lastly, a flight was considered a collision if the bird would have hit the windows of the structure if not for the mist net.

In addition, we analyzed each video quantitatively in Python version 3.8.3 (Van Rossum and Drake 2009) using the open-source software package, Argus. Specifically, we reconstructed the flight path of each bird in each treatment in three dimensions (Jackson et al. 2016). To synchronize the videos, we used rings from walkie talkies and a flashlight. A tone played simultaneously from walkies positioned at each camera helped the software line up the videos using the WAV files. From there, we used the on and off flashing of the light to sync the videos exactly. In order to reconstruct 3-D flight in real space, we calibrated the air space in the flight arena using a 0.46m wand with two brightly colored polystyrene orbs on each end. The wand was slowly moved through the whole flight area, and points were selected so that a large variety of positions and orientations were visible in all 3 cameras. An “L” shaped PVC structure served as a reference to determine the spatial origin and direction of the x and y axes, and the z axis was calculated automatically by the software. To digitize each flight, we clicked on the centroid of the bird in every frame, beginning from when the bird was visible in all three cameras and ending when the bird either made contact with the mist net, landed, or turned around completely.

We used the 3-D coordinates generated by Argus to reconstruct each flight and compute four metrics: instantaneous velocity (average and end of flight velocity), minimum distance from the structure (i.e., how close the bird flew to the structure), and distance of greatest angle of inflection (i.e., at what distance from the structure did the bird make its largest change in direction of flight path).

Flight Metrics

We calculated instantaneous velocity (v_n) by subtracting the value of the previous frame’s (*n-1*) coordinates from the current (*n*) (Figure 2). We multiplied the resultant vector magnitude by 60 to yield velocity in m/s (equation 1). We calculated the average velocity and the velocity at the end of flight, for each trial.

Equation 1: Instantaneous velocity

$$v_n = \sqrt{(x_n - x_{n-1})^2 + (y_n - y_{n-1})^2 + (z_n - z_{n-1})^2} * 60$$

We calculated distance from the centroid of the structure (d_n) for each frame by taking the square root of the squared distances between the xyz coordinates of the bird in each frame, and the coordinates of the structure's centroid (equation 2). We found the minimum d_n for each flight and assigned that as the minimum distance from the structure for the given flight.

Equation 2: Distance from structure

$$d_n = \sqrt{x_n^2 + y_n^2 + z_n^2}$$

We calculated angle of inflection (Θ_n), or the greatest change in direction, by predicting the bird's position in the next frame based on its position in the previous frame (assuming linear forward movement) and compared the difference between the predicted and actual positions (equation 3). We omitted the *y* axis in these calculations, as this axis corresponded to the bird's forward motion toward the windows, and we wanted to isolate left-right (*x*) and up-down (*z*) deflections in each flight path. The angles between the actual and predicted vectors were smoothed using a five-frame moving average and graphed as a function of time. The largest value corresponded to the frame with the largest angle of inflection. We noted the distance between the bird and the structure in that given frame and defined it as the distance of greatest angle of inflection.

Equation 3: Angle of inflection

$$\Theta_n = \cos^{-1} \frac{\left(x_{n+1_{expected}} - x_n\right) * \left(x_{n+1_{actual}} - x_n\right) + \left(z_{n+1_{expected}} - z_n\right) * \left(z_{n+1_{actual}} - z_n\right)}{\sqrt{\left(x_{n+1_{expected}} - x_n\right)^2 + \left(z_{n+1_{expected}} - z_n\right)^2} * \sqrt{\left(x_{n+1_{actual}} - x_n\right)^2 + \left(z_{n+1_{actual}} - z_n\right)^2}},$$

where $x_{n+1_{expected}} = x_n + (x_n - x_{n-1})$ and $z_{n+1_{expected}} = z_n + (z_n - z_{n-1})$

Statistical analysis

We conducted all statistical analyses in R version 4.1.2 (R Core Team 2021). We performed a principal components analysis (PCA) using the following metrics: average velocity, end of flight velocity, the minimum distance to the structure, and the distance of greatest angle of inflection. Further, we ran a PERMANOVA on the PCA products to determine if the qualitative flight outcome categories (i.e., early avoidance, late avoidance, collision) were distinguishable based on the component scores generated by this PCA (Oksanen et al. 2013). We used the Adonis test assessed differences in location, and the BetaDisper test to assess differences in dispersion.

Based on interpretation of the PCA results (see below; figure 4) we grouped the late avoidance and collision flight outcomes into a single category and compared those to flights where we observed early avoidance. This created a comparison of riskier flight behaviors (late avoidance plus collisions) compared with safer flight behaviors (early avoidance). Specifically, we created a generalized linear mixed model to explore whether the treatments (control, visual, sound, multimodal) could predict the qualitative flight outcomes (early avoid vs late avoid + collision). In this analysis, we coded early avoidances as “0”, and late avoidances plus collisions were coded as “1”, resulting in a binary response variable. As such, we used a binomial error structure with the logit link function. Because this experiment utilized a repeated measures design, a mixed model was appropriate to account for the effect of individual birds (Brooks et al. 2017). We used a random intercept structure. While a random slope and intercept structure would have been appropriate, there were not enough data for that model to converge. The predictor variables were selected based on a priori hypotheses. We assessed the residuals based on the “DHARMa” package (Hartig 2022). We calculated the pseudo r-squared value (theoretical method) using the r.squaredGLMM function in the MuMIn package (Bartoń 2020). The treatments were evaluated by whether the 95% confidence intervals (CI) of their effect sizes overlapped with zero, relative to the control.

Results

We did not analyze flights where a bird was not visible in at least two of the three cameras (5 flights over all 4 trial days). This was most often the case when a bird did not leave the dark portion of the tunnel. In addition, we excluded birds if they had only one viable flight out of their possible set of four (one for each treatment). In our final sample size, we analyzed 71 flights from 19 individuals. Figure 3 shows the proportion of qualitative responses for each treatment.

Defining risky flight behavior

The first principal component (PC1) explained 49.3% of the variation in the total data set and loaded negatively with both velocity metrics (average velocity, end velocity) and positively with both distance metrics (minimum distance, turn distance) (Table 1).

Hence, as PC1 increased birds flew slower. PC2 explained a further 34.3% of the original variation and loaded positively with both distance metrics and negatively with both velocity metrics (Table 1). Thus, as PC2 increases the birds flew at a greater distance from the windows. To aid in the interpretation of the principal components, the vectors of the flight metrics and the centroids of the qualitative categories were visualized in figure 4.

The pairwise Adonis PERMANOVA indicated that the "early avoid" group was locationally distinct from both the "late avoid" (early vs late: $df = 1$, $F.Model = 4.98$, $p = 0.0092$) and "collisions" (early vs collide: $df = 1$, $F.Model = 7.74$, $p = 0.0014$). However, "late avoid" and "collisions" flights did not cluster separately in the PC plot ($df = 1$, $F.Model = 0.42$, $p = 0.65$); consequently, we combined these two categories in further analyses. The BetaDisper test was not significant overall (df = 2, $F = 1.61$, $p = 0.21$), indicating that the dispersion of the three groups is comparable.

Given the outcomes of the PCA and clustering of flights according to PC1 and PC2 (which collectively explained 83.6% of the variation in flight metrics), we defined flights into two categories: lower risk ("early avoid" flights, indicated in blue on Figure 4) and higher risk ("late avoid" and "collisions", indicated in yellow and red respectively, on Figure 4). We used this categorization of flight risk (lower vs higher) as the binary response variable for a generalized linear mixed model.

Generalized linear mixed model to explain risky flight behavior

The predictors for high-risk flight behavior were treatment, previous exposure (fixed effects) and band number (random effect) (Table 3). Figure 5 shows the probability of higher risk flight behavior (combination of "late avoid" and "collision") as predicted by the final model. The DHARMa package did not flag any issues with respect to overdispersion or heteroscedasticity. The pseudo r^2 value of the final model was 0.269 (theoretical method). Without band number as a fixed effect, the r^2 value dropped to 0.1566, and the standard deviation of the intercepts of each band number was 0.712.

This final model indicates that treatment groups influenced the probability of higher risk flight (Table 3). With the control condition as the reference factor, the visual and the multimodal treatments were negatively related to increasing risk of collision (Table 3). This means that the presence of visual or multimodal cues was associated with lower risk of collision with the windows (Figure 5). The sound treatment was also somewhat negatively related to high-risk flight behavior (Table Y) but this relationship was not statistically supported to the same degree as the 95% confidence interval associated with this coefficient overlapped with zero (Figure 6).

Discussion

The results of this study did not support our original hypothesis but still yielded interesting results, as well as offering an alternative to the current collision research paradigm. Both the visual and the multimodal cue reduced the probability of risky flight behavior, but the multimodal was not necessarily any better in this situation. Though the effect of the sound lacked strong statistical support, there was a trend of risk reduction when compared to the control. This is interesting, because if a reflection is acting purely as an attractant, then the sound cue alone would be expected *increase* risky flight behavior. This is not the case, which may suggest that our conception of how birds perceive windows is incomplete. This study serves as a proof of concept for a more nuanced way to study collisions in a lab setting. Looking at a series of relevant flight metrics rather than a binary result provides more insight into bird flight behavior when confronted with an obstacle. Additionally, the open-air flight corridor utilized in this study yields more biologically relevant data than studies that utilize traditional flight tunnels.

The multimodal treatment in the context of this study

Our research does not provide conclusive evidence that multimodal cues are better at preventing window collisions than either unimodal cue, but this strategy still warrants further investigation. All the non-control treatments reduced the probability of high-risk flight behavior to some degree, but the multimodal treatment had the largest effect size in the model. This fact alone does not support the stated hypothesis, because the CI of the three treatments overlap with each other so much; as such, it is not possible to make meaningful comparisons between them. Ultimately, multimodal strategies should be investigated further, as they may be useful in situations where the efficacy of a visual cue is compromised. Additionally, future studies should aim to understand how different sensory modalities are influencing birds during flight.

Sound signals as a potential alternative to visual signals

Sound reduced the probability of high-risk flight behavior, but the data do not provide strong statistical support as the 95% CI overlapped with zero. However, this trend should not be discounted, as our current assumptions about how birds perceive windows would lead us to predict that sound alone should increase risky flight behavior in the presence of windows. If reflections are acting purely as an attractant, then sound (which directs a bird's visual attention forward) should amplify this effect. The fact that the sound signal improved flight outcomes at all might suggest that birds *can* differentiate between reflections and reality but require more time to fully process what they are seeing. Previous work suggests that sound in combination with a visual obstacle can prompt a bird to increase its angle of attack, thereby making it slower and more maneuverable (Swaddle and Ingrassia 2017). This slower speed could allow the bird to better process visual information, and the increased maneuverability could aid in avoidance. Sound cues are already a promising option for preventing collisions with freestanding structures but, could also be useful tools for preventing window collisions.

If sound is in fact effective at reducing collisions with windows, there are some applications where a sound treatment would be more practical than a visual one. Retrofitting a building with window film is a costly solution, as many films are $30 per square foot or more. Additionally, many alter the visual appearance of the windows to people in addition to the birds. Therefore, a series of directional speakers could be a good alternative. The primary drawback, of course, is the sound itself. This strategy would undoubtedly be inappropriate for a residential setting. Instead, a commercial area would be more appropriate, where the directional speakers could direct sound up and away from pedestrians. Additionally, the sound signal could be restricted to peak collision hours. Some work suggests that window collisions peak in the early morning hours then taper off until noon (Kahle, Flannery, and Dumbacher 2016). Unfortunately, there are not many robust field studies on collisions, and this gap in knowledge is a barrier to potential innovation.

It is widely recognized that collisions are a consistent source of anthropogenic mortality, but our understanding of the mechanisms that drive collision is lacking. Most of what is known comes from carcass collection studies, which are unable to account for scavenging and more importantly, sub-lethal collisions. An unknown number of birds suffer injury from collisions that they may or may not survive later. Knowing when, where, and why collisions are happening is necessary for optimizing mitigation strategies.

The value of a multivariate approach

Like many other behaviors, flight is complex. As such, can be challenging to translate observed behaviors into usable data. Research on collision mitigation typically utilizes a binary forced choice setup, wherein a bird flying down a dark tunnel must choose between a control window and a treated one. This technique is an effective way to determine what visual deterrents are most conspicuous to birds, but the results of such studies are not intended to directly translate to real-world situations. These experimental setups do not simulate realistic conditions, and do not allow for the spectrum of responses that might occur when a bird interacts with a window. For example, avoidance behavior initiated too late in a flight path could still result in a collision on a large glass facade, despite that same behavior appearing as a successful avoidance in an experimental flight tunnel. In addition to the arguably more ecologically relevant flight corridor utilized in this study, we used qualitative and multivariate approaches to gain more insight that might have been lost in a collide/avoid binary.

To avoid this oversimplification, we calculated four different metrics for each flight. The challenge, however, with analyzing any single flight metric in isolation is that interpretations of the values are context dependent. For example, high velocity at the end of a flight would be bad in the context of a collision, but benign during an early avoidance flight. An early turn distance is desirable in the context of an avoidance, as we can infer that the bird detected the obstacle early and adjusted its flight path accordingly. During a collision, an early turn might mean that the bird was immediately fooled by the reflection and never realized the glass was an illusion. For this reason, it is difficult to meaningfully interpret individual flight metrics, and instead more useful to take a multivariate approach.

Conducting the PCA yielded axes that were straightforward to interpret, and further analysis revealed that the initial qualitative categorizations were grouped in interesting ways. Based on the variable loadings seen in Table 1, an increasing PC1 score meant the flight was slower, and an increasing PC2 score meant the bird stayed further away from the structure. This meant that the top right quadrant of the PCA were the slower flights with the greatest distance and could be considered the “low-risk” quadrant. This is where the early avoidances where centered. The late avoidances and collisions on the other hand were centered in the opposite quadrant, which was characterized by fast flights that came close to the windows. The PERMANOVA analysis revealed that, not only were late avoidances and collisions located in the “high-risk” quadrant, but they were also not distinct from each other with respect to the four flight metrics. This means that, although the flights have different outcomes, little separates the two. For this reason, an ideal mitigation strategy should not merely illicit avoidance, but *early* avoidance.

Window film was less effective than initially expected

The Solyx website claims that buildings with this film installed saw a 94% reduction in collisions, but we only observed 50% when comparing control and visual flights. This discrepancy makes sense because we observed a series of bird window interactions with a variety of outcomes, while buildings can only record lethal collision events. While the claimed reduction in collisions is promising, it would be more accurate to describe this as a reduction in *fatalities*, as there are likely still sub-lethal events occurring. This discrepancy emphasizes the need for more direct observational data, as the number of sub-lethal collision, and therefore the magnitude of the issue, is unknown.

Additional Considerations

Potential variables that impacted the data in this study include but are not limited to handling stress, wind, and variable lighting. Firstly, the release method used (from the hand) meant that each flight was a predator escape flight, and the finches were experiencing at least some degree of stress. This is desirable in some ways, because this is a reliable strategy for inducing a prompt exit from the tunnel and making the bird react quickly to the object of interest. However, this is likely not the case for all natural interactions between birds and glass. It is also logical to assume that the increased stress of the birds is artificially increasing the instance of risky flight behavior. This is not a flaw per se, but it does need to be considered when extrapolating results from controlled studies to the real world. Secondly, wind was an occasional issue when running the trials, as it resulted in movement of the mist net. We delayed releasing the birds during any sustained gusts, but sometimes there was movement of the net after the bird had been released. Any movement of the net can reveal its presence, making it impossible to know if the bird is reacting to the structure or the net itself. Lastly, trials were conducted at the same time each day to control the angle of the light, but cloud cover was variable. Trials were only conducted when clear weather was forecasted, but over the course of several hours cloud cover changed drastically. This had a visible effect on the windows, where increased cloud cover made the reflections weaker. We suspect that the variables of wind and light in particular are adding noise to the data, and either controlling these variables or accounting for them statistically would greatly benefit future studies. However, knowing precisely what to control for is difficult when the mechanisms driving collisions are not clearly understood.

Complicating matters further, it seems not every bird reacted to the treatments in the same way. The inclusion of band number in the GLMM was necessary given the repeated measures design of this study but was also helpful for understanding the variation in the data. The standard deviation of the individuals' intercepts suggests there is some innate differences in flight behavior. However, our model only used random intercept, even though a random slope + intercept model likely would have been more biologically appropriate because a wide range of behavioral reactions were observed. Some birds avoided early every time, and some collided every time. Some birds steadily improved with repeated exposure to the tunnel, while others seemed to respond most to certain treatments. Unfortunately, there were not enough data for that more complicated model to converge. When the control flight metrics were subtracted from the treatments no strong patterns emerge, which may be partially attributable to the variety of individual responses (Figure 7). A larger sample size might allow a more sophisticated model to parse out the effects of the treatments when several behavioral and environmental factors are present.

Conclusion

The results of this study do not provide definitive support for alternative window collision deterrents, but do raise more questions that could guide future collision research. Could a multimodal approach be useful in situations where a visual cue is compromised? Could a sound cue alone be an effective collision deterrent when a visual cue isn't logistically possible? Expanding the possibilities when it comes to preventing collisions will only make bird friendly practices easier to adopt.

Additionally, this study highlights the gaps in current collision research. Traditional tunnel testing is useful for quickly assessing a large volume of anti-collision products, but they do not translate to real world performance or provide insight into birds' avoidance behaviors. This project, as well as previous work in the Swaddle lab, are proof of concept for a more biologically relevant way to study collisions in a lab setting. Our approach addresses both issues by simulating more realistic window obstacles and looking at flights in a more holistic way. Gaining a deeper understanding for how and why collisions are happening is critical for building a more bird friendly world.

APPENDIX

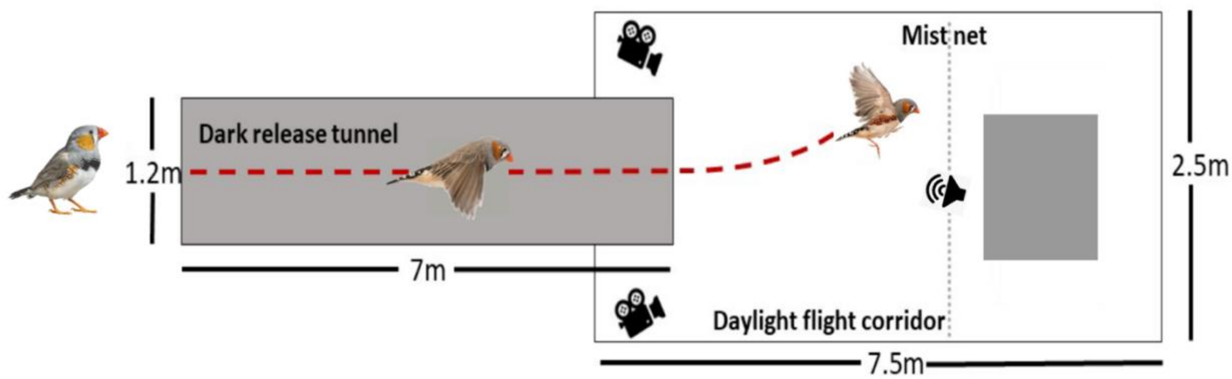

Figure 1. Schematic representation of the outdoor flight tunnel. Zebra finches (*Taeniopygia guttata*) were released from the dark, enclosed portion of the tunnel. Birds were flown towards the structure, which contained a frame holding commercially available windows. A utility blanket was hung behind the windows to create a reflection, and small artificial lights lit up this back area to ensure the reflection was not too strong. A mist net in front of this structure prevents any collisions from occurring. Three GoPro Hero 7 cameras filmed each flight. Windows with and without the Solyx film were switched out according to the treatment being tested. A directional speaker panel was centered at the base of the structure, and a 4-6kHz oscillating frequency was played for the sound and multimodal treatments.

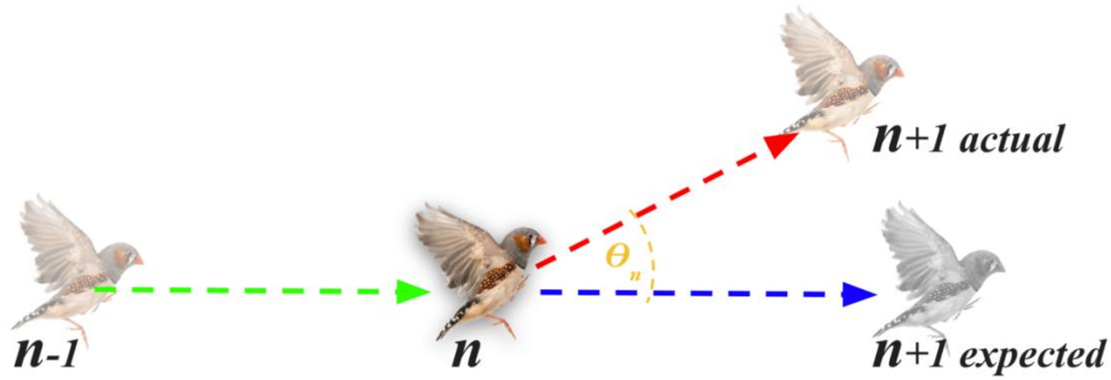

Figure 2. Visualization of the angle of inflection, where *n* is the current position of the bird, *n-1* is the previous position, *n+1 expected* is the position the bird would be in if it continued in the same direction, and *n+1* actual is the bird's position in the next frame. The angle of inflection is found by treating *n* to *n+1 actual* and *n* to *n+1 expected* as two vectors sharing the same origin and using equation 3 to calculate the angle in between them.

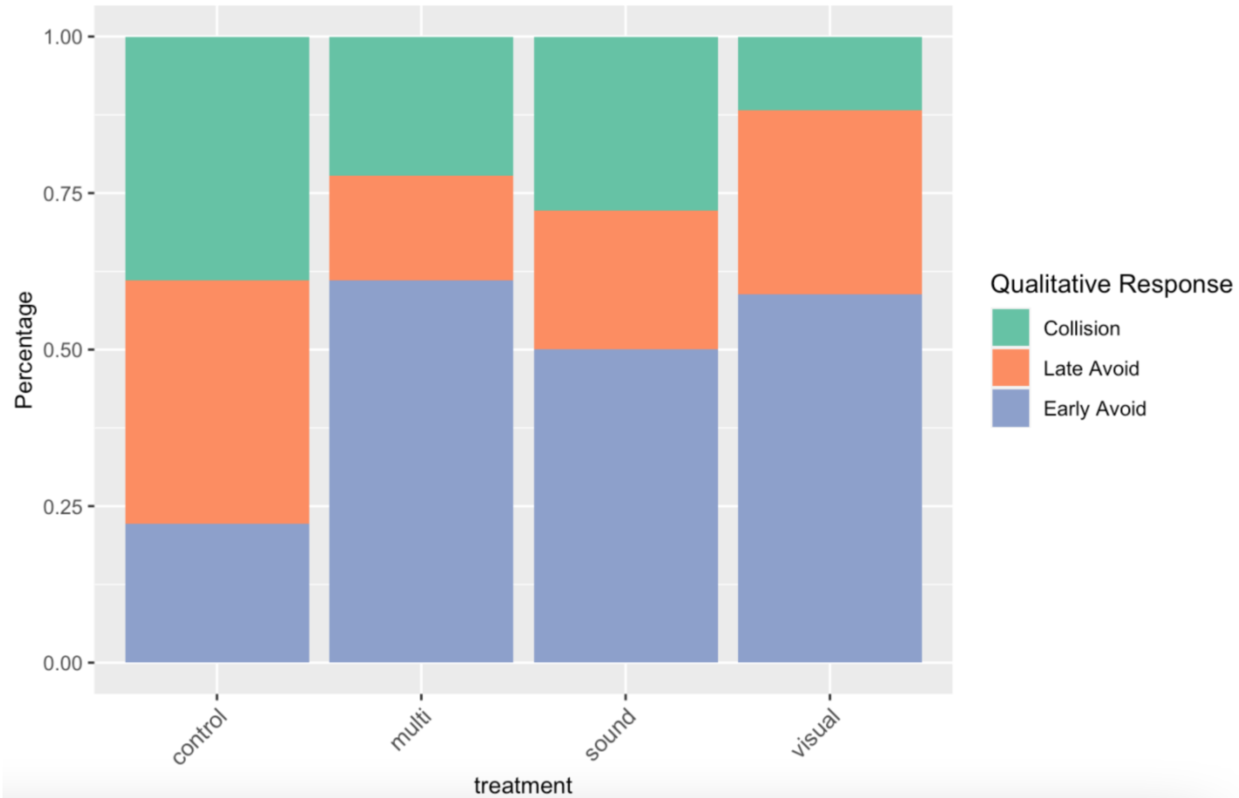

Figure 3. Percentage of qualitative responses broken down by treatment. Zebra finches (*Taeniopygia guttata,* n = 19) were flown at an obstacle in an open-air flight tunnel, and their flight behaviors were categorized as either “collision”, “late avoidance”, “early avoidance”, or “does not engage”. Each bird flew 4 times, each time being exposed to a different treatment (control, visual, sound, and multimodal). The number of each flight response type was summed. Flights that fell into the “does not engage” category were not included in this figure, and the remaining flights were converted to a percentage in order to more easily make comparison between treatments. (Wickham 2016)

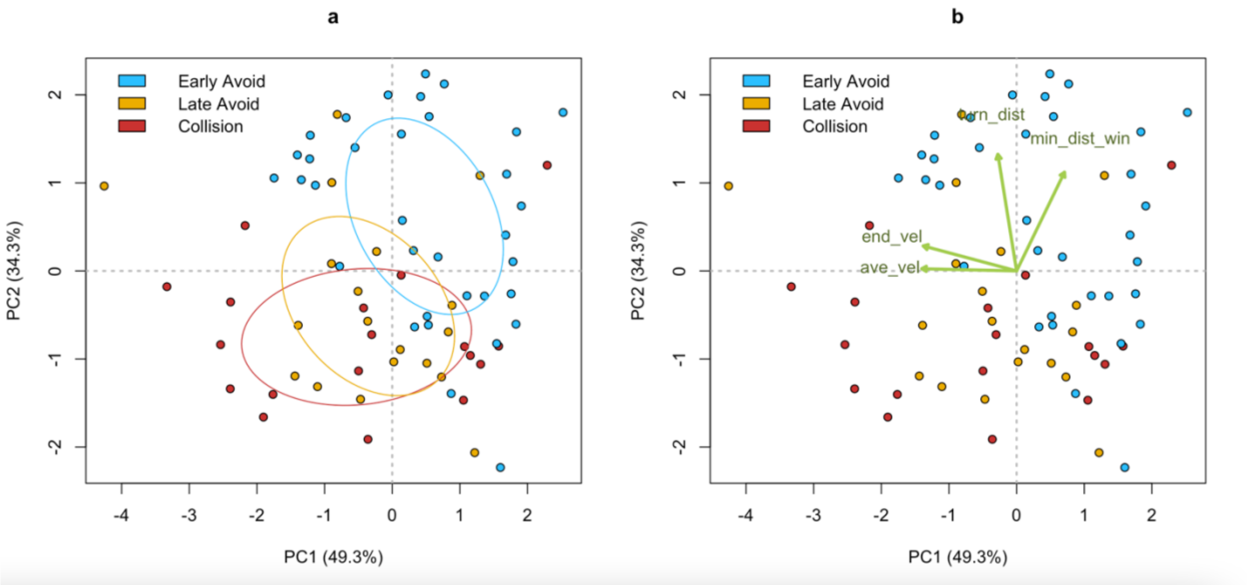

Figure 4. PC1 and PC2 relate to velocity and distance respectively. A principal components analysis was run for the following flight metrics; minimum distance from window, average velocity, end velocity, and change in velocity. The first principal component explains 63% of the variation in the data, while the second explains 19%. The top panel displays the standard deviation around the centroid for each of the three qualitative responses (collision, late avoid, early avoid), and the bottom panel shows how each variable relates to the first two principal components. Higher PC1 scores generally correspond to less risky flight behavior, and future analyses could utilize this principal component as a response variable in a GLMM.

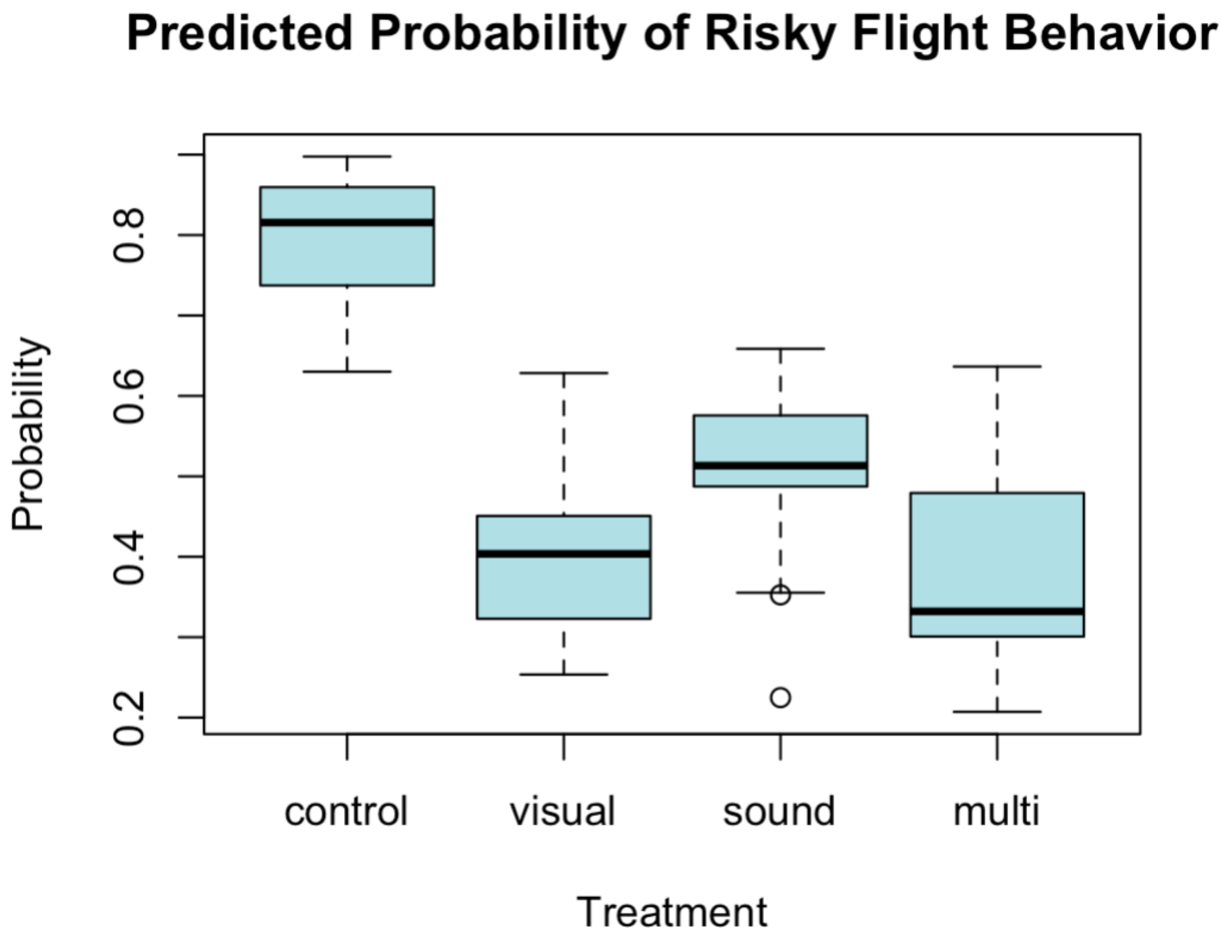

Figure 5. Predicted probabilities of risky flight behavior**.** The qualitative responses were divided into two categories: risky flight behavior (collision, late avoidance) and non-risky flight behavior (early avoidance). A binomial GLMM was fitted to the data, with band number as the random effect and treatment as the most significant fixed effect. The probability of high-risk flight behavior as predicted by the model for a given treatment is shown above. All 3 of the non-control treatments are predicted to have lower risk (although the sound treatment was not significant), and the multimodal treatment is slightly lower risk than both unimodal treatments.

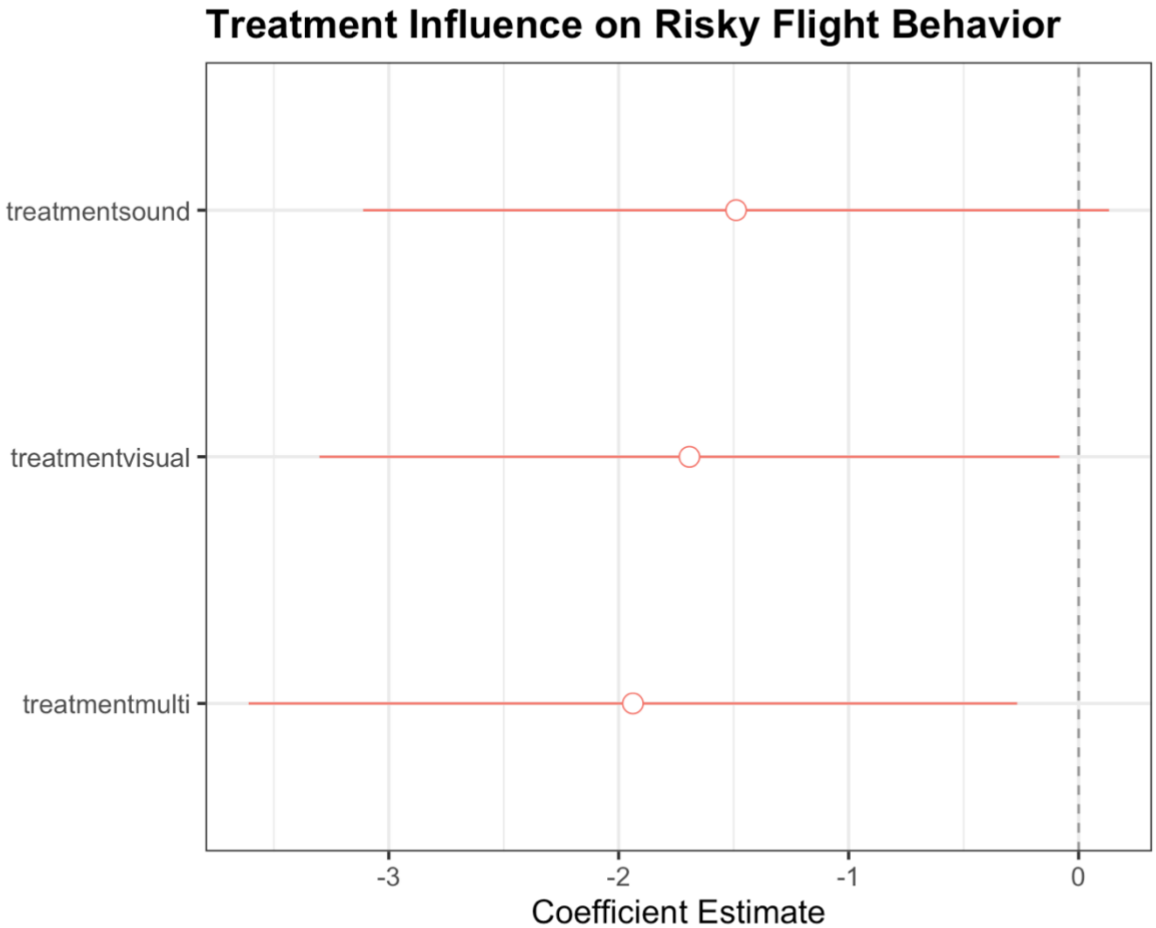

Figure 6. The confidence intervals for the visual and multimodal treatments do not overlap with zero. The estimates for the coefficients of each treatment are represented on the x axis, with the bars representing the 95% confidence intervals. The CIs do not overlap with zero for the visual and multimodal treatments, which is strong statistical support that they reduce the probability of high-risk flight behavior.

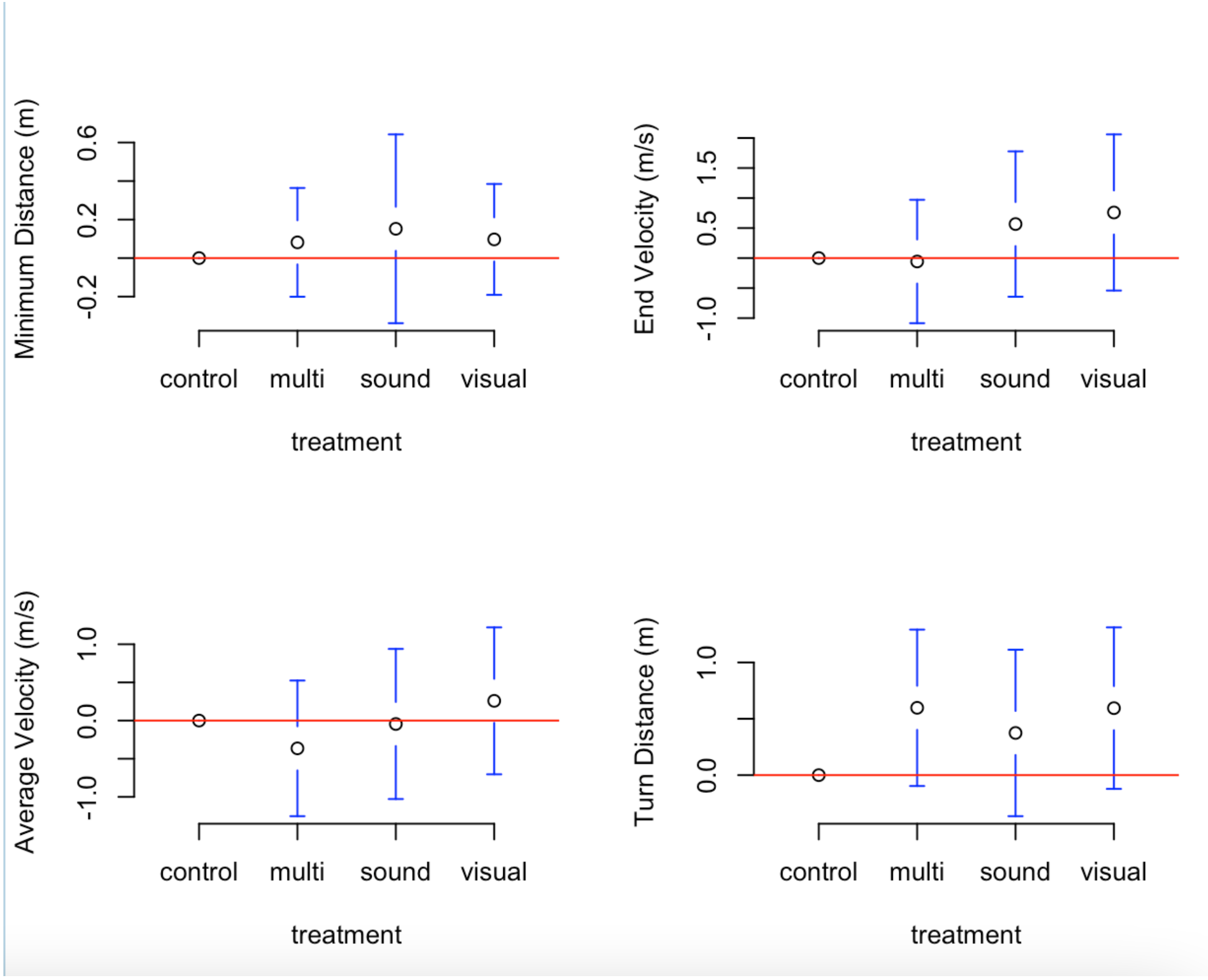

Figure 7. No clear pattern emerges when control flight metrics are subtracted from the other three treatments. Each panel shows one of the four flight metrics. For each bird, the control value for each metric was subtracted from the treatment values seen on the x axis. These differences were averaged among all the birds by treatment. The blue bars represent the 95% CI.

Variable	PC1 (49.3%)	PC2 (34.3%)
Turn distance	-0.6723125	0.60259248
Minimum distance from window	0.1738067	0.92350029
End velocity	-0.911702	-0.04731147
Average velocity	-0.8831342	-0.22814869

Table 1. The individual variable loadings for the first and second principal components (PC). The percentage of variation explained is listed next to each. PC1 is negatively associated with both velocity metrics, and PC2 is positively associated with both distance metrics.

avoid ~ treatment + previous_exposure + (1|band_number)		
	Coefficient	Std Error
(Intercept)	1.8293	± 0.7860
Visual treatment	-1.6923	± 0.8211
Sound treatment	-1.4893	± 0.8275
Multimodal treatment	-1.9382	± 0.8529
Previous exposure	-0.281	± 0.2550

Table 2. Only the visual and multimodal treatments have strong statistical support for reducing the probability of high-risk flight behavior. This determination is based on whether the 95% confidence intervals of the various coefficients overlap with zero. See figure 6, where this is visualized for the three non-control treatment.

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