MAKE WAY FOR DUCKS: THE EFFECT OF SPEED AND LIGHT ON MALLARD FLIGHT REACTIONS DURING REAL AND SIMULATED VEHICLE APPROACHES

by

SHANE GUENIN

(Under the Direction of Travis DeVault and James Martin)

ABSTRACT

Vehicle collisions with birds are financially costly and dangerous to humans and animals. To reduce collisions, we must better understand how birds respond to approaching vehicles. We used real and simulated vehicle approaches with mallards (*Anas platyrynchos*) to quantify flight behavior and probability of collision under different speed and lighting conditions. Mallards approached by a real vehicle had a delayed margin of safety; they are the first species found to use this strategy in response to vehicle approach. Nighttime lighting increased time before collision of flight in simulated trials but decreased likelihood of flight. Vehicle approaches at night might be perceived as less threatening than those during the day; alternatively, mallard visual systems might be incompatible with vehicle lighting in dark settings. Our findings suggest mallards might be unequipped to adequately respond to fast-moving vehicles and demonstrate the need for continued research into promoting avian avoidance behavior.

INDEX WORDS: Animal-vehicle collisions, Antipredator behavior, Avoidance behavior, Flight initiation distance, Video playback

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DEDICATION

To, for, and about my ducks

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CHAPTER 1

INTRODUCTION

Since the 19th century, humans have developed terrestrial, aquatic, and eventually aerial vehicles that could move at increasingly faster speeds, outpacing even the fastest animal predators. Some animals are susceptible to being struck by high-speed vehicles (DeVault et al. 2014, 2015), and the mechanisms governing animal responses to vehicles are poorly understood. Several hypotheses have been explored to explain why various taxa sometimes fail to evade vehicles (Lima et al. 2015). In some cases, animals might not perceive a vehicle as risky until a collision is inevitable; in others, animals might not initiate an evasive behavior in time to avoid the vehicle, even when the vehicle is perceived as a deadly threat (Blackwell et al. 2019b, 2020).

Animal-vehicle collisions (AVCs) are especially concerning for human safety when they involve collisions between animals (usually birds) and aircraft. During the last 30 years, these bird strikes were responsible for 292 human fatalities (FAA 2019) and are estimated to cause an average $205 million in damage to U.S. civil aircraft annually (Dolbeer et al. 2021). Although bird strikes at low altitudes have decreased in recent years due to intensive wildlife management at airports (Dolbeer et al. 2014), the rate of damaging collisions outside airports is increasing (Dolbeer 2011, DeVault et al. 2016). There is a clear need to better understand how birds perceive and respond to oncoming vehicles (Lima et al. 2015), which could inform measures to reduce the probability of strikes, especially at higher altitudes, where aircraft damage is more likely to result when strikes occur (Dolbeer 2006).

According to antipredator theory, animals assess perceived risk based on associated costs and benefits (Ydenberg and Dill 1986). Prey animals should make decisions which maximize fitness by reducing the likelihood of predation (Cooper and Frederick 2007) but might choose to delay or even avoid using antipredator behaviors in favor of other responses relative to the magnitude of the perceived risk (Helfman 1989). Animal responses to anthropogenic stimuli are expected follow principles like those followed when encountering predators (Frid and Dill 2002). Importantly, though, there is no theoretical framework describing how animals detect and respond specifically to approaching vehicles (Blackwell et al. 2016), which are different from predators in several ways, including size, speed, and directness of approach (Lunn et al. 2022).

Three potential escape strategies an animal could employ after alerting to a perceived, oncoming threat involve the use of a temporal, spatial, or delayed margin of safety (Cárdenas et al. 2005, DeVault et al. 2015, Lunn et al. 2022). Animals using a temporal margin of safety base the timing of their flight response on the estimated amount of time that will elapse before the threat reaches them. More specifically, they adjust their flight initiation distance (the distance between the animal and the oncoming threat at the onset of the flight response; FID) based on the speed of the oncoming threat to maintain a consistent time-to-collision (TTC). As a result, FID increases as approach speed of the threat increases when an animal uses a temporal margin of safety. During a spatial response, FID remains consistent regardless of the speed of the oncoming threat; as a result, TTC decreases as the speed of the threat increases. Temporal margins of safety have been observed in Thomson's gazelles (*Eudorcas thomsonii*; Walther 1969), broad-headed skinks (*Emece laticeps*; Cooper 1997), and desert iguanas (*Dipsosaurus dorsalis*; Cooper 2003), whereas spatial margins of safety have been seen in woodchucks (*Marmota monax*; Bonenfant and Kramer 1996), galahs (*Cacatua roseicapilla*; Cárdenas et al. 2005) and brown-headed cowbirds (*Molothrus ater*; DeVault et al. 2015). Likewise, other species fail to adjust FIDs for the speed of approaching vehicles, at least for a subset of vehicle speeds, including turkey vultures (*Cathartes aura*; DeVault et al. 2014), rock pigeons (*Columba livia*; DeVault et al. 2017), and white-tailed deer (*Odocoileus virginianus*; Blackwell et al. 2014). The delayed margin of safety, as proposed by Lunn et al. (2022), is hypothesized to result from an animal being distracted by other stimuli, allowing faster threats a closer approach to the animal than slower threats before the animal reacts. As such, a delayed margin of safety describes situations wherein FID and TTC both decrease as approach speed of the threat increases. To our knowledge, no previous studies have documented a delayed margin of safety in the context of predator or vehicle approaches.

Avian responses to perceived risk vary across species (Lima 1993, Stankowich and Blumstein 2005), although birds generally employ antipredator strategies in their attempt to avoid vehicles (Bernhardt et al. 2010). Species that use a spatial margin of safety often struggle to avoid vehicles approaching at high speeds (DeVault et al. 2014, 2015, 2017). For example, DeVault et al. (2015) found that brown-headed cowbirds consistently initiated a flight response when the oncoming vehicle was approximately 28 m away, regardless of its speed (a spatial response). This strategy became maladaptive once vehicles reached speeds of 120 km/h or higher, because cowbirds could not clear the path of vehicles traveling at those speeds in time to avoid collision (for a discussion of this “critical vehicle approach speed”, see Lunn et al. 2022). Additionally, smaller, more maneuverable bird species are often most likely to be struck by aircraft (Fernández-Juricic et al. 2018), although it is unclear whether this is due to a behavioral response by larger species, or a disproportionate management effort keeping larger species away from runways (DeVault et al. 2013). That said, large-bodied birds remain the most hazardous for aircraft (DeVault et al. 2018), and it is important to understand how they respond to vehicles approaching under a variety of conditions.

Although many flighted bird species pose serious risks to aircraft, one which consistently ranks among the top ten most costly is the mallard (*Anas platyrhynchos*; DeVault et al. 2011, Pfeiffer et al. 2018). Mallards accounted for nearly 1,300 bird strikes from 1990 through November 2022 with US civil aircraft, with an additional 945 strikes attributed to unknown duck species (FAA 2022). An estimated 68.2% of mallard strikes outside of airport environments between 1990-2014 caused damage to civil aircraft (DeVault et al. 2016). Few management options are available to mitigate bird strikes with aircraft outside of the airport environment. Although some bird species might initiate flight responses from aircraft noise (Harris et al. 2005, Lima et al. 2015), mallards and other dabbling ducks (*Anatinae*) are not typically flushed by low-flying aircraft (Conomy et al. 1998). With this in mind, understanding how mallards react to the visual stimulus of an approaching vehicle and being able to predict their behavior more accurately is integral to mitigating bird strikes in the future, especially with respect to the development of aircraft lighting as a visual deterrent (Blackwell et al. 2012, Doppler et al. 2015, Goller et al. 2018).

Although salient aircraft lighting has been shown to enhance alert behaviors for several bird species in response to oncoming vehicles (Blackwell et al. 2009b, 2012; Doppler et al. 2015), no such data exist for nighttime conditions. In fact, we are unaware of any previous empirical studies exploring bird reactions to vehicles at night, irrespective of onboard lighting. However, such data are critical for reducing bird strikes with aircraft, given that many species, including mallards and other migratory waterfowl, generally navigate at night (Korner et al. 2016). Bird strike data from the USA indicate that strikes with mallards are more frequent at dusk and night than during the day, even though there are fewer aircraft flights during this period (FAA 2022). Furthermore, per aircraft movement, 1.8 × more bird strikes occur at night versus day; above 152 m in altitude (i.e., outside of the airport environment), approximately 7 × more bird strikes occur per aircraft movement at night compared to day (Dolbeer 2006).

The goal of this study was to increase our understanding of avian reactions to approaching vehicles using mallards as a model species, incorporating aspects of perceived risk when conditions change from day to night. In doing so, we hoped to provide information that can be used to develop mitigation strategies for reducing collisions with vehicles, thus increasing human and animal safety while reducing damage to vehicles. We predicted that, similar to previously studied bird species, mallards would exhibit a spatial margin of safety (Cárdenas et al. 2005, DeVault et al. 2015). As such, we expected FID to remain constant and TTC to decrease as vehicle speed increased. Furthermore, we predicted that mallards would exhibit shorter FIDs and be less likely to flee during nighttime vehicle approaches, given mallards' relative ease of capture (Buchanan et al. 2015) and decreasing vigilance (Javůrková et al. 2011) during dark conditions. We also evaluated whether individuals would have survived an experimental vehicle approach based on the timing of their flight initiation and predicted that probability of survival (hereafter, "successful avoidance") would decrease as vehicle speed increased. We used two types of experimental approaches: simulated (i.e., video playback) vehicle approaches, which allowed for high experimental vehicle speeds unsafe to test in the field (DeVault et al. 2015), and field vehicle approaches, which quantified how mallards reacted during a genuine vehicle encounter.

CHAPTER 2

METHODS

In this study, we conducted two experiments at the Savannah River Site (SRS), an 803 km^2 federal property adjacent to the Savannah River near Aiken, South Carolina, managed by the United States Department of Energy (Savannah River Site 2020). All animal care and use for this study was approved under the University of Georgia's IACUC Protocol A2021 07-001-Y1-A3.

For both experiments, we used a single captive population of domestically-raised, wild-type mallards as a model organism for ducks involved in vehicle encounters. These birds were raised to be released into hunting preserves, thus remained flighted and were reared with minimal human contact. Flighted birds were necessary to represent realistic vehicle approaches, because birds whose flight feathers had been clipped and rendered incapable of flying might have behaved differently than flighted birds (Blackwell et al. 2019a). We used 97 birds in this study (30 female, 67 male). From arrival to release, 77 birds were kept for four months, and 20, which arrived later in the study, were kept for two months. While in our care, ducks were housed in a brooder house grouped in pens by sex with continual access to flowing water, which pooled in a 36 cm trough on one end of the pens. They were fed Purina® brand duck feed pellets, ad libitum.

Video Trials

We used video playback to expose mallards to high-speed vehicle approaches in a controlled, safe environment. Video playback is effective in assessing animal response to various stimuli (D'Eath 1998) and has been used in previous studies involving birds (Lea and Dittrich 1999), including those evaluating behavior in response to oncoming vehicles (DeVault et al. 2015, 2017, 2018). A white 2018 Ford F-150 pickup truck with its high-beam, halogen headlamps on was used for all vehicle approaches. A 3-m long, 2.5-cm wide, black, steel, square tube was fixed to the top of the cab (approximately 2 m from the ground), and two 4950 lumen Sunspot 36 LX airplane landing lights (AeroLEDs, Boise ID) were attached on either end of the bar (Figure 1). This lighting arrangement was chosen to mimic the lighting array of a small passenger aircraft traveling down a runway (Blackwell and Bernhardt 2004). Vehicle approaches at three speeds (30, 60, and 120 km/h) were recorded in 4k resolution (2160×3840 pixels) at 30 frames per second (fps) during the day on 27 October 2021 and night on 2 November 2021 (six videos total) using a Sony Handycam model video camera. The speeds were later doubled during video editing to 60 fps to achieve vehicle playback speeds of 60, 120, and 240 km/h to reduce the likelihood of the mallards perceiving flicker in the video (D'Eath 1998). Cameras were placed on the centerline of the road to record the vehicle approach from the approximate height of a mallard. The vehicle began its approach 550 m from the camera and was visible to the mallard throughout the duration of the approach. One of the limiting factors in the ability of mallards to detect a vehicle is the distance at which their visual system can resolve the vehicle. Using the visual acuity of mallards (12.8 cycles per degree; Fernandez-Juricic et al. unpublished data), we estimated the distance the vehicle used for the approaches (relative to its 1.9 m width) would fit in the same angle or retinal space was 1 cycle at the threshold of resolution (assuming optimal light conditions). We used the formula $d = \frac{r}{tan\frac{\alpha}{2}}$; where r represents the radius of the object (approaching truck), and α = $\frac{1}{visual\ acuity}$ (for a similar approach see Tyrrell et al. 2013), and determined the 550 m approach distance was well within the range of a mallard's visual acuity.

Figure 1. The experimental vehicle with airplane landing lights attached.

Video-simulated trials were run between 10 November 2021 – 18 January 2022. In the video lab, each individual mallard was exposed to one of the six treatment videos. Each treatment video was played for 16 individuals (5 female, 11 male), with 96 birds total used for the experiment. Following DeVault et al. (2015), we began a video trial by placing an individual mallard in the video box, a 108×157×116 cm box comprised of a plywood ceiling and three walls, a 2.5 cm mesh front wall separating them from a 83×145 cm Samsung RU8000 Series television screen, and a wire mesh floor. Three cameras recorded mallard responses in the box from the sides and back, and video feeds from each camera were recorded for later analysis and livestreamed to an adjacent room for real-time observation. During all trials, the box was illuminated from above by two 15-watt LED bulbs (1600 lumens) and sealed from all other external light. Each mallard was captured in the holding facility using a net, transferred to the video box in a small pet carrier, and given a five-min acclimation period in the box before the vehicle approach video was played. Before the mallard was placed into the video box, the approach video was loaded, and remained paused on the first frame during acclimation. Approach videos lasted between 10 – 30 sec after start, depending on vehicle speed. After each trial, individuals were banded before being returned to the holding facility to ensure none were repeated in future trials.

To determine the hypothetical outcome of avoidance responses to simulated vehicle approaches (i.e., collision or successful escape), we calculated the mean time required for mallards to move from the path of the vehicle (i.e., the minimum TTC required for vehicle avoidance) by conducting a field experiment to quantify the time necessary for mallards to travel 3 m (the width of a standard road lane) from a stationary position (DeVault et al. 2015, 2017). To do so, we constructed an 8-m-long chute from snow fencing in a 15×10 m flight cage. The distance of the chute was marked at 0.5 m intervals. Mallards (n = 20; 10 male, 10 female) were placed into a net and held above the ground by a researcher in a blind, and once lowered onto the ground, the researcher jumped from the blind and shouted, prompting an escape response. These responses were video recorded, and the time from flight initiation until the birds reached the 3 m line was noted. We found that mallards required 1.0 ± 0.14 sec to cover 3 m.

Field Trials

We conducted a field experiment on an unused road on the Savannah River Site, 15 km from our holding facility, to quantify mallard responses to a real vehicle approach. The road corridor was 12 m wide, including two lanes and a grass shoulder, and was heavily forested on each side. Albeit relatively narrow, we do not believe the wooded edge influenced escape behavior, given that many ducks chose to flee into the cover of the trees.

Following Blackwell et al. (2019a), ducks were released during the field portion of the study, due to (1) the difficult nature of recapturing flighted birds once they take flight and (2) the necessity of not impeding their flight so we could be confident their responses were not affected by any imposed barrier. During the field experiment involving a real approaching vehicle, there was a risk of collision. However, we took multiple steps to avoid this possibility including using an experienced driver, a mandatory braking zone, a passenger observer who monitored the entire encounter on a forward-looking infrared (FLIR) camera (i.e., at night) and alerted the driver to the approximate distance to, and any movement of, the individual. During the field experiment involving a real approach by a vehicle, one individual was struck at a low speed and flew away before any evaluation could take place, which led us to believe its injuries, if any, were minor.

Approaches in the field occurred during the day (10:00 – 14:00) and night (30 min after sunset – 23:00), using the same vehicle and aircraft landing light setup described above. Daytime trials were conducted on 15 – 17 February 2022. During nighttime trials, we conducted the experiment on clear nights on or around the full moon (>90% illuminance), on 14 –16 February 2022. Field approaches were conducted at 40 and 60 km/h. These two speeds (compared to 60, 120, 240 km/h during simulated approaches) were chosen to allow the driver to safely brake prior to any actual collisions, and to reduce the overall number of treatments, given that we anticipated some individuals would escape the experimental arena immediately upon release (i.e., before the vehicle approach began).

We measured our truck's braking distances at both speeds prior to approaches with live birds and determined we could stop within 10 m at 40 km/h and 15 m at 60 km/h. We used this information to mark mandatory braking points on the road at 10 and 15 m from the mallards' release point to reduce the chance of striking a live bird. Additionally, during nighttime approaches, a forward-looking infrared (FLIR) camera was mounted on the vehicle and monitored by a passenger to provide the driver real time updates on an individual's location during each trial. Given that during 1.0 s (time required for a successful avoidance; see above) a vehicle travels 11.1 m at 40 km/h and 16.7 m at 60 km/h, individuals failing to initiate avoidance by the time braking was necessary could generally be considered as high collision risks. Also, birds that responded while the truck was braking did so at slower approach speeds (i.e., received a different visual stimulus prior to reaction) which we considered in our analysis (see below).

For each day or night of data collection in the field, 16 trials, each with a unique individual mallard, were conducted in succession. Mallards were corralled 50 m beyond the experimental arena and behind opaque tarps to minimize visual exposure to the vehicle prior to their trial. During each field trial, an individual was moved from the holding area and positioned 550 m from the vehicle's starting point in an animal carrier in which all openings except the forward-facing door were covered. Next, the door was opened remotely by a researcher behind a blind, and the individual was allowed to walk into the roadway (see also Blackwell et al. 2019a). If, after 30 s, the individual had not left the carrier, it was nudged out using a plunger. A 4×4 m grid was drawn onto the road surface with chalk so that the position of the individual throughout the approach could be ascertained on video (see below) relative to its release point. Once the individual stepped out of the animal carrier, a second researcher, concealed within a second blind approximately 30 m away, indicated to the driver via cellular phone to begin the approach. The driver of the vehicle then quickly accelerated to the treatment speed, set the cruise control, and approached the location of the mallard following the centerline of the road. The driver stopped the vehicle at the predetermined braking location if the bird remained in the path of the vehicle. If the bird moved beyond the path of the vehicle, the driver did not change speed or direction until it was approximately 25 m beyond the release location or the duck's current position, whichever was further. In situations during which the driver was compelled to brake, a confounding factor was introduced for those individuals whose flight response occurred after braking. This potential confounding variable, (i.e., braking) was considered during data analysis (see below).

All vehicle approaches and mallard behaviors were video recorded by two cameras – a Sony Handycam video recorder positioned perpendicular to the release point on the road, and a Canon EOS 77D camera positioned 15 m from the release point, facing along the roadway to record the entire approach (Figure 2).

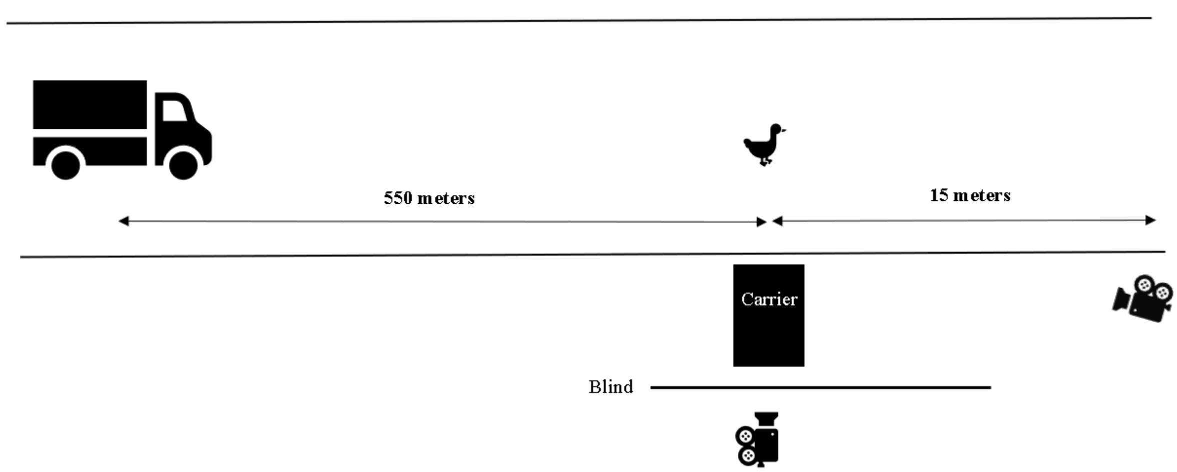

Figure 2. The location of the vehicle, mallard, and cameras at the beginning of an approach in the field.

Analyses

For both experiments, we extracted the FID and TTC values from the videos, following DeVault et al. (2015) and Blackwell et al. (2019a), and corrected for duck movement after release when necessary in the field (Figure 3). In the field experiment, we collected a third metric, the ultimate distance from the road's centerline to the location of the bird at the time of its flight, or collision (had the vehicle not braked) if no flight response was observed (distance to the vehicle path, VP_Dist; Figure 3). All analyses were performed using R Statistical Software (v4.1.2; R Core Team 2021). All samples analyzed for our models were checked for outliers using a Grubbs test (Grubbs 1969) using the "outliers" R package (Komsta 2022); regressions and generalized linear models were performed using the "car" (Fox and Weisberg 2019), "sjstats" (Lüdecke 2021), and "emmeans" (Lenth 2022) R packages.

Figure 3. Metrics of FID, TTC, and distance to vehicle path (VP_Dist) illustrated on a schematic of an experimental vehicle approach.

Video Analysis

We first evaluated the probability of flight of individuals in response to simulated vehicle approaches in the video lab setting. During some animal-vehicle encounters, birds might not exhibit a flight response (Blackwell et al. 2012, 2019a), which was evident in our experiments. We used a generalized linear model with a logit link function to evaluate the binary flight response (1) or no flight response (0), with independent variables of vehicle speed, lighting treatment (night vs. day), the interaction of speed and light, and body mass (log transformed). A duck that initiated flight after a collision would have occurred was considered to have no flight response, as it would have been struck by the vehicle in a real-world scenario.

To evaluate which, if any, margin of safety (spatial, temporal, delayed) mallards employed during animal-vehicle interactions, we used general linear regression models of FID and TTC. For the video lab analysis, independent variables were body mass (log transformed), speed, lighting condition (day or night), and the interaction of speed and light. Using an ANOVA, we found that males were larger than females ($\bar{x}_{Male}$ = 1.16 ± 0.031 kg, $\bar{x}_{Female}$ = 0.99 ± 0.015 kg; $F_{60, 1}$ = 22.57, P <0.001); we chose to use the continuous variable (body mass) rather than sex to maximize degrees of freedom. In addition, we log transformed body mass to improve the normality of residuals. Vehicle speed and ambient lighting (i.e., as categorical variables) were treated as an interaction because the visual stimulus of an approaching vehicle is different at night compared to day (Verheijen 1985), and the looming qualities of this stimulus used by birds to determine speed may be altered in different ambient lighting conditions, causing the effective speed to vary (Kim et al. 2017). For those linear models, only ducks which initiated a flight response were included in the sample. To better meet the assumptions of homogeneity of variance and the normality of residuals, FID was square root transformed and TTC was log transformed.

For the individuals which had flight responses, we next analyzed whether speed or lighting condition affected successful escape among individuals that initiated flight. In the video lab, a duck's flight path was limited by the walls of the video box. Therefore, to determine whether a duck would have "succeeded," in avoiding the vehicle, we compared each individual's TTC to the minimum time required for a mallard to escape along the ideal escape path (perpendicular to the vehicle) for 3 m (see DeVault et al. 2015), which we determined was 1.0 sec (see Video Lab Trials, above). As such, any individual that initiated flight less than 1.0 sec before collision was deemed unsuccessful (i.e., a virtual collision occurred). To determine the effect of speed and lighting condition on escape success, we fit a generalized linear model with a logit link function to a binary response – all birds with TTC > 1.0 sec were considered successful (1), and those with TTC values < 1.0 sec were considered unsuccessful (0). Independent variables were vehicle speed, lighting treatment (night vs. day), the interaction of speed and light, and body mass (log transformed).

Field Analysis

Our analyses for the field experiment were similar to those for the video experiment, with a few minor differences. First, we included ambient air temperature as an independent variable in models for FID, TTC, probability of flight, and probability of successful escape because of its potential influence on avian FID (Møller 2014). Also, as mentioned above, a confounding factor was introduced for individuals whose flight response occurred after braking when the driver was compelled to do so to avoid collision. Individuals which initiated a flight response after the vehicle braked, but before it came to a stop, were omitted from analyses on FID and TTC, as the change in stimulus caused by braking might have affected their avoidance behaviors. To better meet the assumptions of homogeneity of variance and normality of residuals, we log transformed FID and TTC values.

We also evaluated the effect of the approaching vehicle on the position of the individual at the time of flight, or collision if no flight occurred (VP_Dist). We analyzed VP_Dist as a dependent variable because a mallard theoretically could see the vehicle for the entire approach distance (550 m; see justification above), and therefore any movements during the trial could have been related to the approaching vehicle. We fit linear models of VP_Dist using the same variables as models for FID and TTC. VP_Dist was square root transformed to better meet the assumption of homogeneity of variance.

To determine whether a flight response was successful in avoiding a vehicle collision, we had more information available to us in the field than in the video lab, where we relied only on a TTC threshold of 1.0 sec. More specifically, an individual with a TTC indicating a successful avoidance (>1.0 sec) in the video lab might not actually escape collision in a real-world scenario, depending on their direction of flight. Additionally, a bird with a TTC < 1.0 sec might still be successful in its escape in the field should its path to escape require less than 3 m of movement. As such, our criteria for success in the field considered the bird's position on the road and its flight trajectory and velocity. To have avoided collision, the bird must have removed itself from the path of the vehicle (1 m on either side of the centerline, given the vehicle's width of 2 m, or alternatively vertically clearing the vehicle's height of 2 m) by the time of collision. Birds which initiated flight after braking were universally considered to have "failed", as presumably none would have removed themselves from the path of the vehicle had braking not occurred.

Additionally, some birds, including those with TTC values of greater than 1.0 sec, failed due to their flight path (i.e., they had an adequate flight time, but flew directly toward the vehicle at an inadequate angle to vertically clear it). Other birds were successful, even with TTC < 1.0 sec, because of their location nearer to the edge of the vehicle path, requiring less than 3 m of movement to avoid the vehicle. We used a generalized linear model with a logit link function to evaluate the role of vehicle speed, lighting treatment, the interaction of speed and light, body mass (log transformed), and temperature on successful escape (outside the vehicle's path at collision; 1) or failed escape (inside the vehicle's path at collision; 0).

Finally, we investigated whether flight reactions in the field were comparable to those observed in the video lab. To do this, we analysed FID and TTC values of individual mallards that exhibited flight reactions during the 60 km/h treatment, the only speed treatment shared among the experimental arenas (video and field). Individuals in the field that flew after braking were omitted from this analysis. We used a linear regression to evaluate the effect of experimental arena, lighting condition, the interaction of experimental arena and light, and body mass (log transformed) on FID, TTC, and the probability of flight.

CHAPTER 3

RESULTS

Video Results

Individual mallards were generally calm after placement in the video box and throughout the five-minute acclimation period, but one individual continually attempted to escape the box during acclimation and was removed from our analyses. Across treatments for birds exhibiting flight responses, mean TTC was 2.15 ± 2.27 SD sec, (range = 0.11 – 14.73), and mean FID was 64.0 ± 53.8 m, (range = 3.5 – 245.5). One TTC value was identified as an outlier (TTC = 14.73 s, $P = 0.01$) and with this outlier excluded, mean TTC was 1.88 ± 1.32 sec (range = 0.11 – 4.86).

Of the remaining mallards after the removal of the flighty individual, 48 (50.5%) displayed a flight response, although the presence of a flight response varied across treatments (Figure 4; range = 31.6% – 67.8%). The probability a mallard exhibited a flight response in the video lab was affected by lighting condition ($\chi^2 = 10.66$, df = 1, $P = 0.001$; Figure 4); mallards at night were less likely to have a flight response (estimated marginal mean probability of flight at night = 31.6 ± 7.6%; day = 67.8 ± 7.1%). No other variables affected the probability of flight in the video lab.

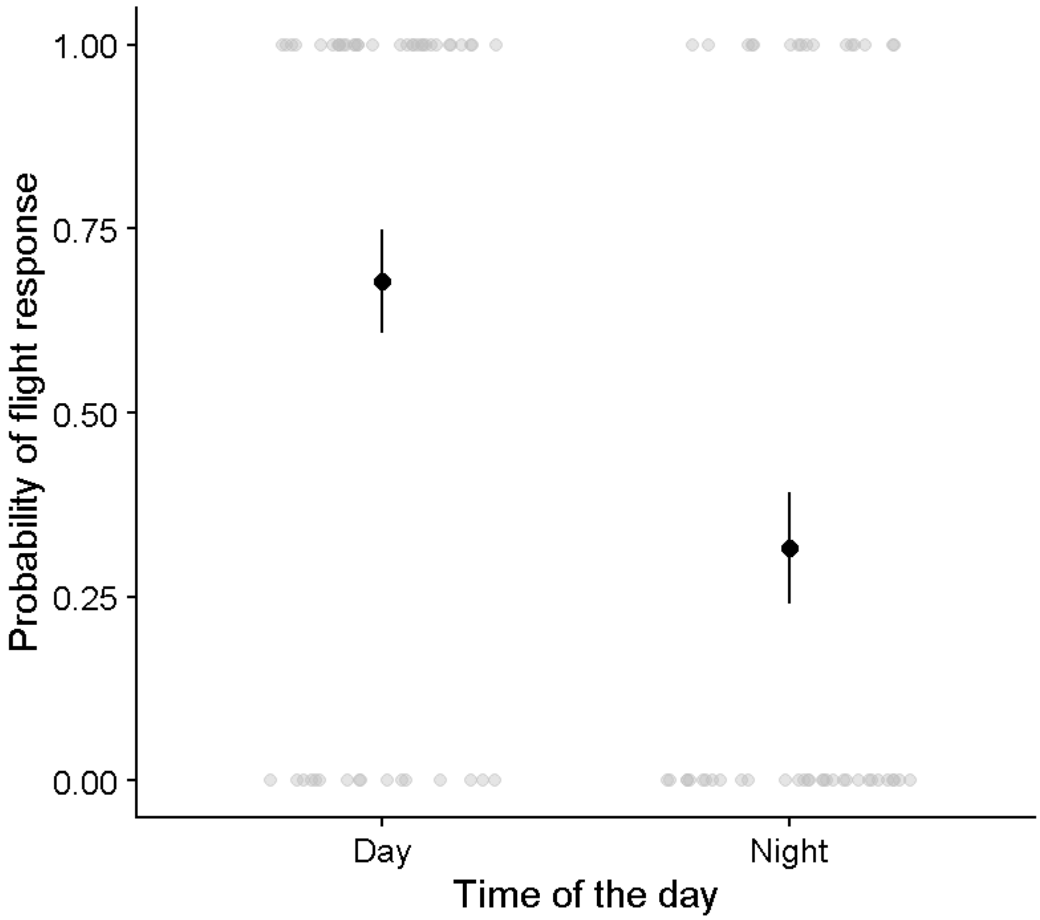

Figure 4. Marginal means of the probability of a flight response between lighting treatments when a mallard was exposed to a simulated vehicle approach.

Flight initiation distance in simulated approaches was not influenced by any of the variables we tested (all *P* >0.2). Our models investigating the effects of vehicle speed and light on TTC were more equivocal. With the outlier included, we found no evidence for the influence of any variables on TTC (all *P* >0.2). However, with the outlier removed, TTC was higher at night compared to day ($F_{1, 40}$ = 5.15, *P* = 0.03; Figure 5). We found no evidence for influence of other variables on TTC with the outlier removed (all *P* >0.529).

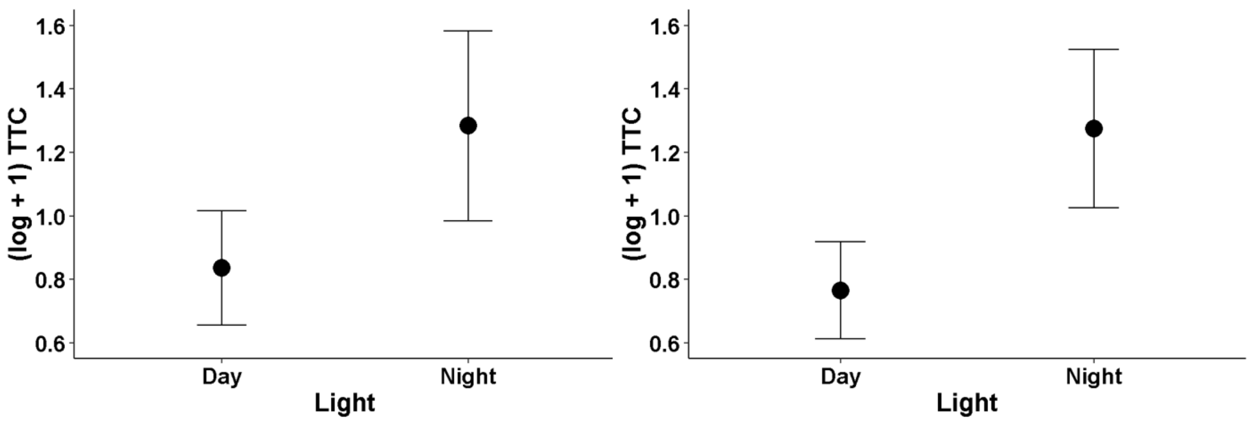

Figure 5. Marginal means of log(TTC) among mallards exposed to a simulated vehicle approach across lighting treatments. No strong influence was noted when an outlier was included (left) but an influence from light was seen with the outlier excluded (right).

Probability of successful avoidance in the video lab was strongly influenced by vehicle speed (χ^2 = 9.65, df = 2, *P* = 0.01), with nominal probabilities of 42.1 ± 9.0%, 50 ± 9.2%, and 15.2 ± 6.4% at 60, 120, and 240 km/h, respectively. A post-hoc Tukey test indicated that mallards were more likely to successfully avoid the vehicle at 120 km/h than at 240 km/h (z = 2.78, *P* = 0.02), although success at 60 km/h did not differ from 120 km/h (z = -0.62, *P* = 0.81), nor did success at 60 km/h statistically differ from 240 km/h (z = 2.26, *P* = 0.06; Figure 6). We found no evidence that other variables affected the probability of successful avoidance (all *P* >0.34).

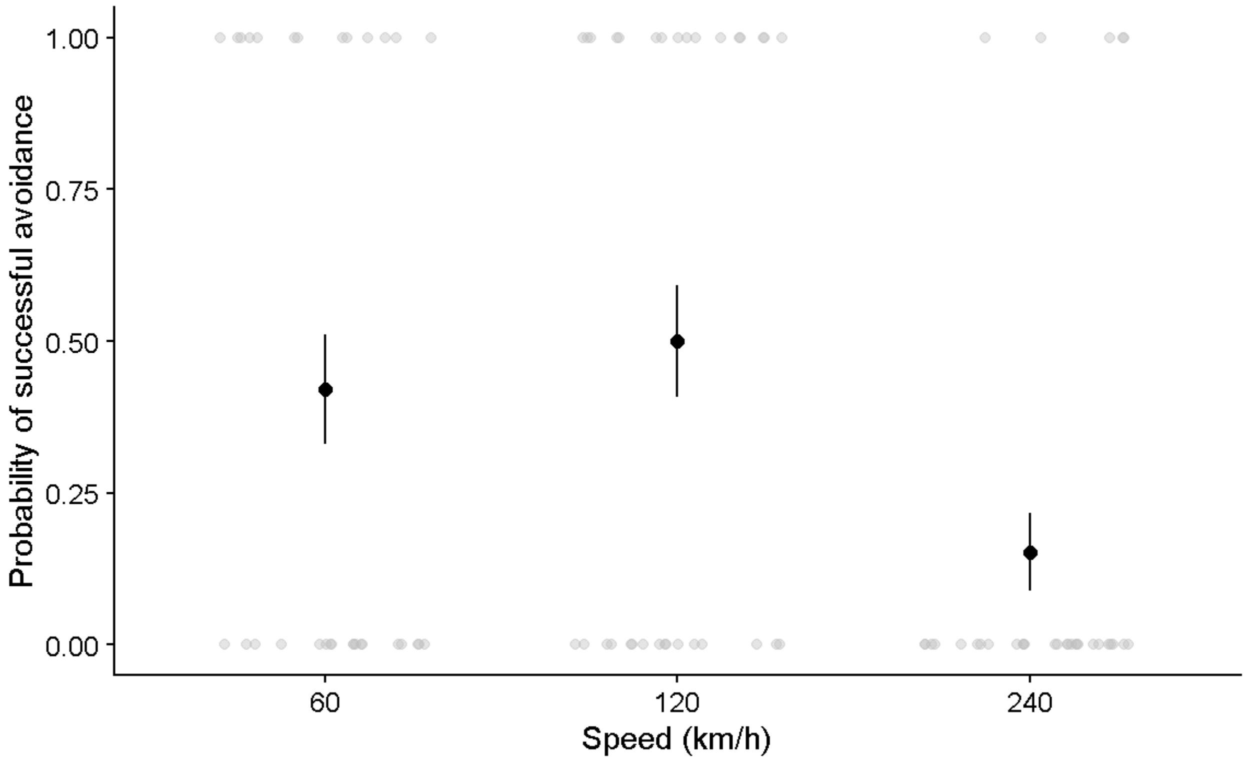

Figure 6. Marginal means of a mallard's probability of successful avoidance (TTC >1.0 sec) at three experimental speeds during simulated vehicle approaches.

Field Results

As expected, some individual mallards flew away immediately upon release; 62 (64.6%) remained on the road after release long enough to be scored. Of the mallards that flew before the approach, 18 (52.9%) were female, which comprised 60.0% of our total female mallards. Across treatments for birds exhibiting flight responses, mean TTC was 7.03 ± 9.57 sec (range = 0 – 34.02 sec). Mean FID was 84.1 ± 111.3 m, range = 0 – 378 m.

Of the scorable birds, 41 (66.1%) displayed a flight response, although 7 of the 41 initiated flight after braking. In the field, braking was the only significant variable in the model for probability of flight ($\chi^2 = 28.88$, df = 1, $P < 0.001$). This result was expected; 17 of 21 mallards without flight responses required braking. However, it is unlikely that these mallards opted not to fly *because* they were braked for. If braking was removed from the model (that is, to assume the change in stimulus caused by braking did not affect whether or not a mallard chose to flee), no variables affected the probability of flight. However, there was a nominally lower probability of flight at higher speeds, with a marginal mean probability of flight of 76.5 ± 7.9% at 40 km/h, and 56.1 ± 9.0% at 60 km/h.

In the field, both FID ($F_{1,28}$ = 9.81, P = 0.004) and TTC ($F_{1,28}$ = 11.03, P = 0.003) decreased with speed (Figure 7). No other variables affected either response (FID, all P >0.08; TTC, all P >0.189). VP_Dist increased at 60 km/h ($F_{1,32}$ = 9.29, P = 0.005), and was also higher during the day at this speed than during the night ($F_{1,32}$ = 6.87, P = 0.01; Figure 7) Light, the log of body mass, and air temperature did not affect VP_Dist (all P >0.284).

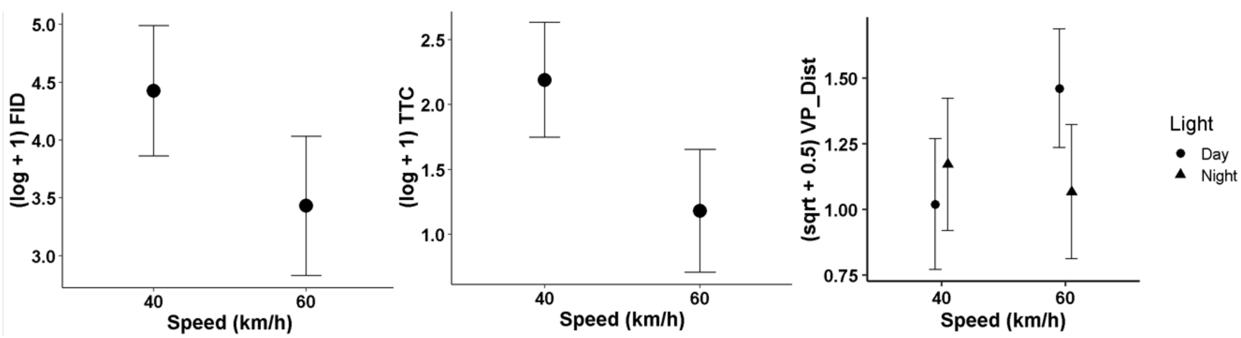

Figure 7. Effects of vehicle speed on log(FID) and log(TTC), and the interaction of vehicle speed and light on sqrt(VP_Dist) of mallards during vehicle approaches in the field.

Successful avoidance of the vehicle in the field, as determined by whether the individual remained in the path of the vehicle at the time of collision, was not affected by any independent variable (all P >0.147). However, after applying the theoretical success metric we used in the video lab (successful avoidance requires at least 1.0 sec TTC) in the field, this theoretical probability of success decreased as speed increased, with marginal means of success dropping from 55.8 ± 12.9% at 40 km/h to 14.6 ± 8.6% at 60 km/h (χ^2 = 7.95, df = 1, *P* = 0.005; Figure 8).

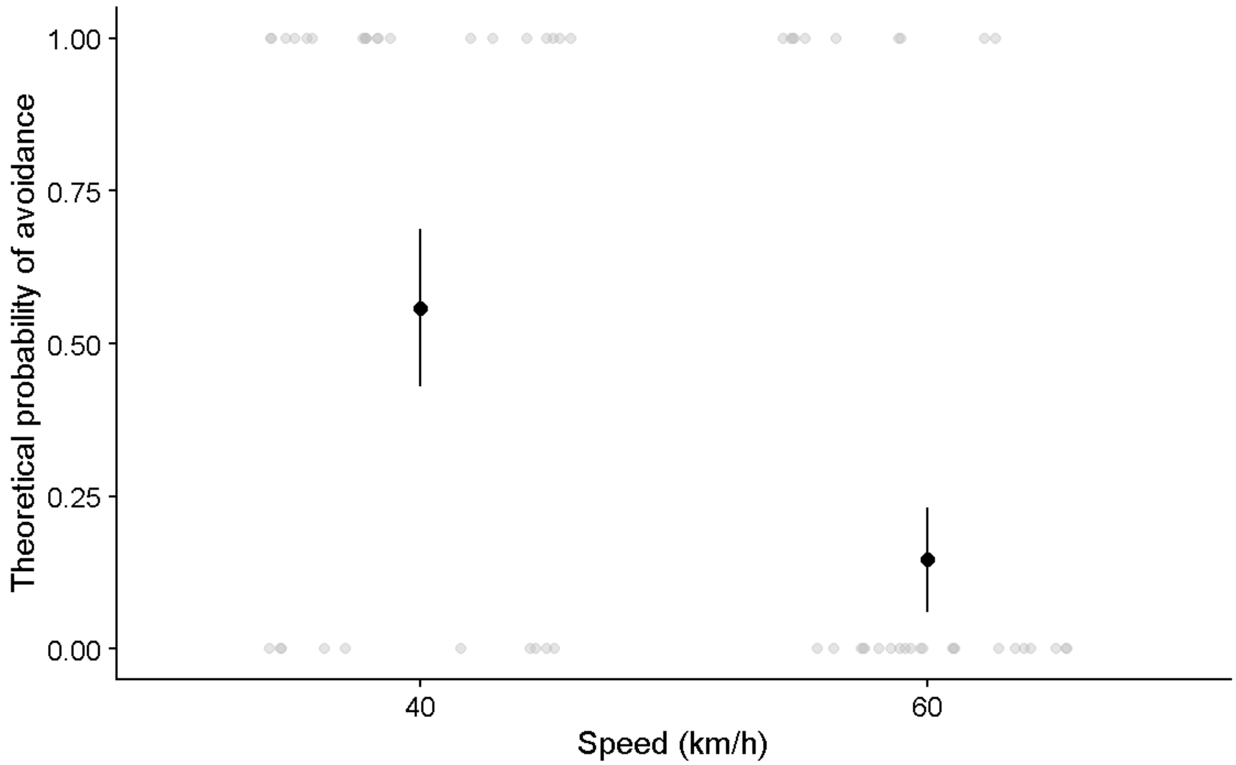

Figure 8. Probability of a mallard's successful avoidance of the vehicle (TTC >1.0 sec) at two experimental speeds during field vehicle approaches.

Experimental arena (i.e., video lab or field) did not affect FID ($F_{1,28}$ = 0.22, *P* = 0.64) or TTC ($F_{1,28}$ = 0.03, *P* = 0.86) values for the 60 km/h treatment. These values are nearly identical between the two arenas, with marginal means for log(FID) at 3.45 ± 0.26 in simulated trials, and 3.42 ± 0.27 in field trials, and log(TTC) at 1.14 ± 0.18 in simulated trials and 1.17 ± 0.18 in field trials. The probability of flight also did not differ between experimental arenas (χ^2=0.01, df = 1, *P* = 0.92) with a marginal mean probability of flight of 13.1 ± 37% in the field and 20.5 ± 36.3% in simulated trials.

CHAPTER 4

DISCUSSION

Ours is the first study to assess reactions of individual birds to vehicle approach using both video playback and real vehicles, allowing us to ask questions regarding vehicle speed and lighting, and to compare behaviors between the two experimental contexts. This comparison is critical for accurately discerning bird response to vehicle approach, particularly for approach speeds that exceed those possible for use in seminatural experiments. Additionally, our study is the first to explore avian reactions to oncoming vehicles at night, when collisions per flight are 7× more likely (Dolbeer et al. 2006) and are especially concerning during migratory periods (FAA 2020). We found the first evidence for a delayed margin of safety in response to vehicle approach, although limited to the lower vehicle speeds tested in the field. Furthermore, we found that nighttime lighting during simulated approaches reduced the likelihood a mallard would respond to a vehicle approach, but when they reacted, they did so with more time to spare until a potential collision occurred than their counterparts under daytime conditions. Below, we discuss these findings in the context of antipredator behavior, as well as the future methodological implications.

There are two previously reported mean FID values for mallards in the literature, one in response to approach by a motorized boat at 25 km/h (92.2 ± 60.2 (SD) m; Mayer et al. 2012), and the other in response to a walking human approach (9.9 m; Jiang and Møller 2017). Our mean FID values of 64.0 ± 53.8 m in simulated trials and 84.1 ± 111.3 m in field trials were more comparable to those found in Mayer et al.'s (2012) study. Even so, as we might expect given the delayed margin of safety observed during field approaches at 40 km/h and 60 km/h in our study, the FID observed by Mayer et al. (2012) was slightly longer using a 25 km/h approach. The much lower FID observed from a human approach (Jiang and Møller 2017) could be due to 1) urban mallards being more habituated to humans and therefore displaying very short FIDs relative to those with less human contact (Møller 2008), or 2) the possibly that at the very slow speeds used in human approach experiments (~1.8 km/h; Blumstein 2006), perceived risk is lower than approaches closer to the hunting speeds (90 km/h, northern goshawk (*Accipiter gentilis*) & peregrine falcon (*Falco peregrinus*); Alerstam 1987) of a mallard's traditional predators (Stankowich and Blumstein 2005; Cooper 2006). Additionally, human approaches resulted in longer mean FIDs (47.9 m – 111.5 m) in other members of the *Anatidae* family (McLeod et al. 2013), indicating the results from Jiang and Møller (2017) may have come from a population of mallards habituated to humans.

Mallards tested in the field experiment had decreased FIDs and TTCs as speed increased, indicating a delayed margin of safety. In contrast, a spatial margin of safety has been observed in other bird species (Cardenas et al. 2005; DeVault et al. 2015). As noted by Lunn et al. (2022), a delayed margin of safety can result from distracted monitoring of a potential threat. Unlike in the video experiment, in which the mallards were allowed five minutes to acclimate to the arena, field approaches began immediately upon their release to reduce the probability of the mallard escaping prior to the approach. This method gave them little time to take in their surroundings after being held in a dark environment, and subsequently provided potentially distracting visual stimuli which might have reduced their assessment time of the approaching vehicle. Alternatively, the daytime increase in VP_Dist with speed might not indicate distraction, but difficulty processing potential risk at the higher speed. Specifically, the period of low-quality assessment (between object detection and alert response) and high-quality processing (from alert to flight) (Tyrrell and Fernández-Juricic 2015) decreases with increasing approach speed (DeVault et al. 2015). It should be noted, as well, that neither of our experimental arenas represented a mallard's typical habitat, and their preferred predator escape strategies of diving underwater or flushing into herbaceous vegetation (Lima 1993) were not possible. Perhaps a delayed margin of safety was representative of a period of confusion given a relatively contrived scenario for an obligate waterbird.

It is difficult to come to a definitive conclusion when interpreting patterns of FID and TTC in the video lab with regard to vehicle speed. During simulated approaches, the vehicle could have been approaching too quickly (up to 240 km/h) for the mallards to use traditional antipredator strategies, a phenomenon which was observed in brown-headed cowbirds (DeVault et al. 2015) and turkey vultures (DeVault et al. 2014). What seems clear from the simulated experiment, however, is that lighting influences both the likelihood and timing of mallard flight responses. Further, the combined analyses indicate that the video context yields data on par with the seminatural context and, thus, we can increase our approach speeds in the virtual context and infer how birds respond to this threat.

In the video lab, mallards were less likely to exhibit avoidance behavior in reaction to videos filmed at night. However, when flight was provoked by nighttime videos, this response began with more time before a potential collision than flight reactions to videos filmed during the day, a result not observed in the field. Without accompanying audio cues, perhaps this abstract stimulus was not perceived to be as threatening as it would be in a real setting. This binary response also could result from differences in individual thresholds of risk. Intraspecies variability in avian fear responses to humans was demonstrated by Carrete and Tella (2011), and perhaps this intraspecies variability in fear is also present as a response to anthropogenic stimuli like vehicles. For example, potential differential behavior in response to vehicle disturbance by vehicle type is not unrealistic (Hardy and Crooks 2011; but see also DeVault et al. 2018). The immobility shown by many of the individuals during nighttime trials also could reflect a period of assessment (DeVault et al. 2015). Given the change in effective speed caused by bright headlights in a dark setting (Kim et al. 2017), it is possible the looming stimulus would not be seen as threatening until it is too late to react to avoid collision (Blackwell et al. 2019b, 2020).

The effects of lighting were also present during field approaches. We found that mallards located themselves farthest from the vehicle's path of travel (VP_Dist) at the time of flight or collision at the higher speed, but only during the day. The birds appeared to position themselves farther from the vehicle when the visual stimulus loomed more quickly in daytime conditions. This could potentially indicate the mallards perceived the vehicle as something other than a predation threat (Lunn et al. 2022); rather, their perception of risk depended on the directness of the vehicle's approach to their position, a response previously found in other bird species (Wang and Frost 1992; Møller & Tryjanowski 2014; Lima et al. 2015). It is worth noting, however, that only ducks with flight responses were included in the analysis of VP_Dist. The evident lack of perceived risk in those which did not fly is not explained by this finding.

The sizable minority of mallards which did not exhibit any reaction to the approaching vehicle was puzzling. Non-flights to vehicle approach have been observed in previous vehicle-approach experiments with some bird species (Blackwell et al. 2012, 2019a; DeVault et al. 2017), but not in others (DeVault et al. 2014). Our mallards were raised on a farm and were received by us between the ages of 3 – 6 months. Given their life history, it is plausible that the simulated vehicle observed in our experiments was their first experience with the visual stimulus of any vehicle. In a review of predator neophobia, birds, captive-raised animals, and animals with a trophic role lower than tertiary consumers all displayed significantly higher levels of neophobia than other taxa, wild-caught animals, and predators (Crane and Ferrari 2017). The mallards used in our experiment possess all three of these qualities, although half (50.5%) in the simulated experiments and one third (35.4%) in the field experiments apparently did not regard the vehicle as threatening enough to actively avoid. Irrespective of whether a bird flees from an oncoming vehicle, the likelihood of collision should be investigated.

In both simulated and field experiments, the probability of successful avoidance (>1.0 s TTC) decreased as vehicle speed increased. Low TTC values at high speeds seem reasonable given the temporally shorter approach at higher speeds, delayed margin of safety observed in the field, and the possibility of a spatial margin of safety during simulated trials. During field approaches, the probability of successful avoidance decreased dramatically as speed increased from 40 km/h (55.8%) to 60 km/h (14.6%). This apparent sensitivity to relatively small changes in speed is concerning, given that modern cars on highways and aircraft on runways are generally much faster. Notably, whether a bird would have avoided a collision in the field was not affected by speed, or any other variables, demonstrating a need to consider additional variables in animal-vehicle collision studies beyond the time of flight to determine whether a collision would occur.

Flight initiation time and distance are just one component of an animal's total flight response, along with the direction and angle of flight, the sustained velocity of the flight, and the distance needed to clear the vehicle's path (Blackwell et al. 2019a). Our results indicate that at higher vehicle speeds, mallards will initiate avoidance responses with very little time available to avoid collision (*sensu* Bernhardt et al. 2010), and whether this short escape time allows the mallard to clear the path of the vehicle or not, any TTC <1.0 sec results in a hazardous scenario, especially when the reaction of the vehicle operator may be to swerve, creating an even more hazardous situation, or when there are additional forces acting on the area around the vehicle, like the intake of an engine. Lastly, the assumption used in this study (and in DeVault et al. 2015, 2017), that a 3 m flight is needed to avoid collision, is a useful tool for analyzing factors contributing to a hazardous encounter. However, this assumption is not always conclusive in terms of whether a collision would occur. In simulated vehicle encounters, however, it remains the best available proxy, as the ability to analyze subsequent flight characteristics is limited.

One of the goals of this study was to evaluate the comparability of the results of animal-vehicle collision studies conducted using simulated approaches (DeVault et al. 2015, 2017, 2018) to animal responses to actual vehicle approaches (Blackwell et al. 2009b, 2012, DeVault et al. 2014, Doppler et al. 2015). At low speeds (i.e., 60 km/h) video-simulated vehicle approaches appear to elicit similar FID and TTC values as real vehicle approaches in the field. We found no difference in the FID, TTC, or probability of flight between experimental arenas when speed was consistent. Although this comparison was made with a small sample of our birds (52 individual mallards, 61 total data points), it suggests that patterns found in the video lab could be applicable to those observed in the field, when treatments are held constant across arenas. This provides additional support for the efficacy of the use of video-simulated vehicle approaches when studying wildlife-vehicle interactions, further confirming the pattern seen comparing the mean FIDs (roughly 30 m) found in brown-headed cowbirds between Blackwell et al.'s (2009b) field approaches and DeVault et al.'s (2015) simulated approaches. This is an important finding for future studies as well, as video-simulated approaches are safer for test subjects, have lower likelihood to introduce confounding variables, and do not require the release of animals.

However, field approaches allow us to quantify characteristics of the avoidance response and other contributing factors (e.g., Blackwell et al. 2019) and how those behaviors might be exploited to enhance avoidance behaviors.

Beyond the confirmation of the efficacy of video playback in generating realistic responses from birds, these results have immediately applicable implications. Like brown-headed cowbirds (DeVault et al. 2015), vultures (DeVault et al. 2014), and mourning doves (Blackwell et al. 2009b), our results indicate mallards will often fail to avoid vehicles when they approach at the takeoff speed of most aircraft (~240 km/h). To reduce collisions, the presence of waterbirds around airfields should be discouraged (Blackwell et al. 2009a; DeVault et al. 2011). Separation in space between these birds and vehicles is necessary, because the faster the vehicle, the more likely a collision is to occur. However, it is often impractical to completely remove wildlife from these areas, especially in the case of birds like mallards, which thrive in human-dominated environments (Figley and VanDruff 1982). In recognizing that a complete separation in space between mallards and aircraft in impossible, our results provide a few, more moderate suggestions. Firstly, the riskiest time to encounter a mallard is at night, during which they are frequently active (Korner et al. 2016). However, mallards typically only fly long distances (>200 km) when migrating (McDuie et al. 2019). Mallards are one of the most hazardous bird species to aviation, causing damage in 68.2% of collisions – 41.1% of these collisions occurring with multiple individuals (DeVault et al. 2016). We suggest, then, that during the months of migration, flight should be minimized at the altitudes used most by migrating birds as much as is practical. Although mallards have been struck by aircraft at altitudes up to 6400 m (Manville 1963), most individuals migrate at altitudes less than 915 m (Lincoln and Peterson 1979). An approximate “danger zone” for mallards therefore could be described as ground level to 1000 m.

Additionally, we found that mallards appear to stay farther outside the path of a vehicle when it is moving quickly and during daytime conditions. Future research should focus on improving the visual saliency of high-speed vehicles to birds (Blackwell et al. 2012; Goller et al. 2018), to increase the likelihood birds will detect and avoid oncoming aircraft sooner, before collisions are imminent.

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