2013

Cowbird Behavioral Responses to Lights Tuned to Their Visual System: Implications for Bird-Aircraft Collisions

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Recommended Citation

Doppler, Megan S., "Cowbird Behavioral Responses to Lights Tuned to Their Visual System: Implications for Bird-Aircraft Collisions" (2013). *Open Access Theses*. 25.
https://docs.lib.purdue.edu/open_access_theses/25

Graduate School ETD Form 9
(Revised 12/07)

PURDUE UNIVERSITY
GRADUATE SCHOOL
Thesis/Dissertation Acceptance

This is to certify that the thesis/dissertation prepared

By Megan S. Doppler

Entitled
Cowbird behavioral responses to lights tuned to their visual system: implications for bird-aircraft collisions

For the degree of Master of Science

Is approved by the final examining committee:

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Approved by: Peter J. Hollenbeck 12/02/2013
Head of the Graduate Program Date

COWBIRD BEHAVIORAL RESPONSES TO LIGHTS TUNED TO THEIR VISUAL SYSTEM: IMPLICATIONS FOR BIRD-AIRCRAFT COLLISIONS

A Thesis

Submitted to the Faculty

of

Purdue University

by

Megan S. Doppler

In Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

December 2013

Purdue University

West Lafayette, Indiana

ACKNOWLEDGEMENTS

I would like to thank the Lindburgh Foundation and Purdue Summer Research Opportunities Program (SROP) for funding this project and Dr. Esteban Fernandez-Juricic for his assistance and support during my graduate career. I would like to thank all the people who made this project possible by helping me create the stimuli and collect the data, specifically Patrice Baumhardt, Ron Needham, Corben Meyer, Chris Wall, Tom Snyder, Nathan Ikerd, Mollie Burkhard, Megan Nelson, and Lily Liang. I would also like to thank my family: my father and mother, John & Beth Doppler, for knowing exactly what to say and keeping me relaxed and focused on my end goal; my brother, for believing in my and all my “science stuff”; and my boyfriend, Andrew Saenger, for always being there for me throughout all the ups, downs, and late nights. I would not have been able to complete this project without my committee, lab mates, and undergraduates. And I would like to thank Monster Energy, Co. for keeping me energized through the late nights, early morning, and everything in between.

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ABSTRACT

Doppler, Megan S. M.S., Purdue University, December 2013. Cowbird behavioral responses to lights tuned to their visual system: implications for bird-aircraft collisions. Major Professor: Esteban Fernández-Juricic.

Collisions between birds and aircraft cause extensive monetary expenses and are a risk to human lives, as well as the lives of endangered and threatened birds. Birds are highly visual organisms with visual system substantially different from humans. Previously, studies show that the use of white broad-spectrum lights have the potential to enhance bird avoidance behavior; however, no study has investigated the effects of light colors that would be more salient from the avian perspective. The purpose of this project was to assess detection and avoidance responses of brown-headed cowbirds exposed to a radio-controlled (RC) aircraft with a lighting system with high visual saliency from their visual perspective (blue LED lights, 470 nm). In the first experiment (RC aircraft static), we found that birds showed alert behaviors more quickly in response to the RC aircraft with the lights on compared to that with the lights off. In the second experiment (RC aircraft approaching the animals), we found a significant speed effect. Cowbird alert responses were delayed at higher speeds when the RC aircraft had the lights off. However, the speed effect diminished with the type of light. We found a less pronounced (but still significant) speed effect when the lights were pulsing, but when the lights were steady, the speed effect was no longer significant. Time to "collision" at avoidance was only significantly affected by ambient noise. Our findings suggest that developed to maximize avian visual systems can attract their attention to the aircraft and potentially enhance the ability of birds to detect the aircraft even at high speeds, particularly when the lights are steady.

INTRODUCTION

Collisions between wildlife and moving vehicles (i.e., aircraft, cars, etc.) have been on the rise in recent years (Dolbeer 2011). For instance, over 100,000 bird and aircraft collisions (bird-strikes) have been documented in the last 22 years (Dolbeer 2011) and many more strikes have gone unreported (80-70%,Burger 1985; Blackwell & Wright 2006). Bird-strikes cause economic losses (i.e., $700 million annually in the US) and pose safety risks to passengers (e.g., 23 human deaths and 223 injuries from 1990 to 2011 in the US) (Dolbeer 2011). In addition, bird-strikes are a conservation concern, especially when threatened or vulnerable species are struck, such as the endangered Hawaiian duck, Newell's shearwater (Linnell et al. 1999), and Tasmanian wedge-tailed eagle (Bekessy et al. 2009). Airports have implemented multiple management strategies to reduce the density of species that can cause damaging strikes (Cleary & Dolbeer 2005). However, these strategies are limited because many strikes occur beyond airport jurisdiction (Dolbeer 2011). Recent research has enhanced our understanding of how birds interact with aircraft, which could potentially lead to some remediation techniques.

Birds engage in avoidance behavior when encountering aircraft in their flight path in a way similar to that displayed during anti-predator behavior (Frid & Dill 2002; Bernhardt et al. 2010; Blackwell et al. 2012). For instance, birds performed evasive maneuvers prior to collisions with aircraft (Bernhardt et al. 2010). Therefore, we can use the framework of anti-predator theory to help identify the key factors involved in a bird-aircraft collision course (Blackwell et al. 2013). To avoid collision, birds must detect the presence of the aircraft, recognize it as a potential threat, and change their flying path quickly (Blackwell et al. 2012).

Establishing when birds respond to aircraft can help predict potential outcomes of bird-aircraft interactions. This is especially important given that aircraft speeds are faster than the typical predator that birds have evolved to detect and avoid. It is then essential to determine which conditions would allow birds enough time to veer away from the approaching object. Time to “collision” at alert is the time between aircraft detection and potential collision, with higher values indicating a quicker alert response (Blackwell, Fernández-Juricic, et al. 2009; Blackwell et al. 2012). The time between the bird initiating avoidance behavior (e.g., flight, rapid movement away from the approach, etc.) and potential collision is the time to “collision” at avoidance (Blackwell et al. 2012). Finally, the difference between time to “collision” at alert and at avoidance is the buffer time, which is a proxy of how quickly a bird can initiate avoidance behavior after detection. Shorter buffer times indicate a greater ability of a bird to respond to aircraft by engaging quickly in avoidance maneuvers. From a safety perspective, increasing the probability of detecting the aircraft might provide birds with the extra time necessary to reduce the chances of collision. This could be accomplished by making aircraft more visually conspicuous to birds (Blackwell et al. 2013).

Aircraft lights may increase visibility to birds (Lustick 1973; Larkin et al. 1975). For instance, brown-headed cowbirds and Canada geese respond sooner to approaching vehicles with pulsing white lights on than with the lights off (Blackwell & Bernhardt 2004; Blackwell et al. 2012). However, birds have different visual systems from humans and white lights may not necessarily be a salient cue from an avian visual perspective. Birds have four single cone photoreceptors (Hart, 2001a), allowing them to have a wider color space than humans. They also have oil droplets, caretenoid-filled lipid-based organelles in their photoreceptors, which filter light as it enters the retina, enhancing color discrimination (Goldsmith et al., 1984; Partridge, 1989; Hart, 2001b). Adding lights tuned to the avian visual system may enhance alert and avoidance behaviors.

However, bird responses to approaching objects can be influenced by the properties of the object (e.g., speed) as well as the visual environment (e.g., ambient light conditions). For instance, approach speed affects the perception of a looming stimulus, with an increase in speed decreasing the perceived looming (Wann et al. 2011). Consequently, birds are more likely to be struck on roadsides with higher speed limits (Farmer & Brooks 2012; Legagneux & Ducatez 2013). This suggests a perceptual constraint on the ability of birds to determine time to contact with a fast approaching object. Additionally, ambient light conditions can influence the probability of detecting an approaching object (Blackwell, Fernández-Juricic, et al. 2009). At higher ambient light intensities, brown-headed cowbird alert responses quickened when exposed to an approaching truck with steady lights; however, this effect was reversed when the light was pulsing (Blackwell, Fernández-Juricic, et al. 2009).

It is unknown whether lights *specifically* tuned to avian visual systems are effective at capturing birds' attention, leading to detection and avoidance behaviors. Therefore, the goal of this study was to determine the responses of brown-headed cowbirds (*Molothrus ater)* to an approaching aircraft with lights that maximize their color visual sensitivity. Cowbirds are an appropriate model species because their visual systems have been thoroughly described (Blackwell, DeVault, et al. 2009; Dolan & Fernández-Juricic 2010) and they show avoidance behavior when exposed to approaching objects (Blackwell et al. 2012). Specifically, we (1) determined the wavelength of light that would be more salient to cowbirds using perceptual modeling (Vorobyev & Osorio 1998), (2) tested the assumption that cowbird behavior would change when presented with these lights tuned to their visual system compared to their baseline behavior, and (3) measured time to "collision" at alert, time to "collision" at avoidance and buffer time in response to an approaching radio-controlled (RC) aircraft with lights off, and lights on steady and pulsing. We also considered other factors that could be affecting the perception of the aircraft: speed, ambient light conditions, and ambient noise (i.e., faster speeds would increase engine noise). Understanding the responses of birds to lights tuned to their visual systems can open up new possibilities to develop in the future systems that enhance the detection of approaching vehicles, which can have important management implications to minimize wildlife-vehicle collisions.

METHODS

Brown-headed cowbirds were captured in Erie County, Ohio in collaboration with the U.S. Department of Agriculture, Animal and Plant Health Inspection Service. We transferred individuals to West Lafayette, and color banded them. Cowbirds were housed in 0.61 m x 0.61 m x 0.76 m enclosures with a 14:10 h light-dark cycle in animal facilities at Purdue University. No more than four individuals were permanently housed together at a time. We fed individuals a mix of white millet, game bird chow, and sunflower seeds *ad libitum*. All housing, handling and experimental procedures were approved by Purdue Animal Care and Use Committee (protocol # 1201000582).

Visual saliency

Understanding the visual contrast of an approaching object from a different species' sensory perspective is important, as birds have a much more complex visual system than humans. We first determined the visual saliency of colored lights (what color LED light stood out the most from the visual background from the perspective of cowbirds). We tested the visual saliency of LED lights by calculating chromatic contrast using Vorobyev and Osorio's physiological visual model (Vorobyev & Osorio 1998) in Avicol v5 (Gomez, 2006). We entered the following parameters into the visual model: 1) irradiance (spectral properties of ambient light), 2) reflectance of the visual background, 3) reflectance of the object of interest (LED lights), and 4) the sensitivity of the cowbird visual system (peak absorbance of visual pigments and oil droplets as well as the relative density of the photoreceptors, which were characterized in a previous study, Fernández-Juricic et al. 2013).

Irradiance and background reflectance measurements were taken at Purdue's Forestry and Natural Resources Farm. Irradiance and reflectance were measured using a

StellarNet EPP2000 portable spectroradiometer (StellarNet, Tampa, FL, U.S.A) under sunny, cloudy, and partly cloudy conditions in different days. Irradiance was measured at the height of the cowbird head and at a 90° angle parallel to the ground at the four cardinal directions and pointed 90° up towards the sky. We averaged the irradiance measurements (Watts m^{-2}) to obtain one measurement for each wavelength, which was converted from Watts m^{-2} to $\mu Molm^{-2}s^{-1}nm^{-1}$ for the visual contrast model.

With our experimental approach (animals in an enclosure with aircraft approaching them, see below), cowbirds would have different background elements. Therefore, we video recorded the approach of the RC aircraft in our study area from the cowbird's head height. Reflectance of the background included measurements from the sky, tree line, grass and the aircraft. We averaged the reflectance of these different components considering their relative proportions. For the sky, reflectance was taken at cowbird head height with the probe held at an upward 45° angle pointed towards the sky. Reflectance of the tree line was taken at the same height but with the probe held at a 90° angle towards the trees. Reflectance for the ground was taken with the reflectance probe pointed towards the ground. The aircraft was multi-colored (white, red, yellow and blue), and thus reflectance measurements were taken on all the colored sections and averaged together taking into account their relative proportions. We then calculated the proportion of the aircraft relative to the proportion of the sky when the RC aircraft was at two locations (a far distance, ~50-100 m, and a close distance, ~5-15 m) relative to the enclosure position. The reflectance measurement of the background included the weighted proportion of the aircraft at the two distances, as well as the weighted proportion of the sky, tree line and ground.

Methods used to obtain LED light reflectance measurements were slightly modified from Blackwell et al (2012). We were restricted by the viewing angle of commercially available lights. Since we were interested in having the birds see the lights from the ground (i.e., below the aircraft), we used lights with a wide viewing angle (70°) and high light intensity (greater than 3.5 cd per light). We obtained LED light spectra from CoolLED, Andover, UK (http://www.coolled.com/Life-Sciences-Analytical/Technical-Information/LED-Wavelengths/) and used five LED light wavelengths (470 nm, 525 nm, 585 nm, 595 nm and 635 nm) that are representative of different portions of the wavelength range of the spectrum that birds can perceive. We could not find a commercially available light in the UV range of the spectrum that would have the comparable luminance and visual angle. We fitted individual curves to match those from CoolLED and normalized the fitted curves to a reflectance value of 20,000 photon counts, the peak reflectance of the standard white light (Blackwell et al. 2012). We then estimated chromatic contrast of each light at the two distances from the enclosure to establish which light would have the highest saliency from the cowbird's visual perspective. Chromatic contrast is calculated in units of "just noticeable differences", or JNDs, where values > 1 suggest that the object can be discriminated from the background (Vorobyev & Osorio 1998). The LED light with the highest chromatic contrast was used in our behavioral experiments.

Behavioral experiments

We conducted two behavioral experiments. The first evaluated the ability of cowbirds to respond to the lights mounted to the static aircraft at two distances. The second assessed different behavioral responses to the RC aircraft moving towards the birds. Experiments were conducted in semi-natural conditions in a grass field in Tippecanoe County, Indiana, near Purdue University's Airport (latitude: 40.417, longitude: -86.942). Trials were performed between May and November 2012, from 0730 to 1200 hrs under calm weather conditions. During the trials, we held the birds in bottomless circular enclosures made of hardware cloth (mesh with 0.912 mm wire; 38.1 cm tall and 40 cm radius). The enclosure had a wooden base with 3 cm plastic tubing placed on a 1.5 cm grid and spray painted green to mimic the grassy substrate. Before each trial, we spread fresh sawdust and approximately 5.0 g of white millet on the base. Black landscape fabric was used as blinds towards the sides and back of the enclosure (Fig. 1) to obstruct view of the observer. Three cameras were used to monitor the enclosure, one from 1.5 m above and two from behind (1 m away; Fig. 1). We used a PelikanCam CRM-36DW B&W Weatherproof Infrared Cameras ("bulletcams") above the enclosure and two JVC Everio (GZ-MG330AU) camcorders behind the enclosures (Fig.1). To record video, we used a portable DVR system that consisted of a video splitter, Ganz DVR and a monitor that allowed all videos to be synced together.

We used an electric powered RC aircraft (General Trainer^{TM}) for both experiments. The aircraft had a wing span of 157.5 cm and fuselage length of 130.8 cm. We mounted high contrasting LED lights (7.4 mm; 3.5 cd per LED light) to the underside of each wing separated by 1.03 m facing towards the direction of movement. Four LED lights were clustered side by side (two on top and two on the bottom) on each side of the wing. For the lights steady treatment, the lights on the aircraft were continuously on; for the lights pulsing treatment, the lights were alternatively pulsing at a rate of 2 Hz (lights were on under one wing while the lights under the other wing were off). A lithium polymer 4-cell battery pack powered the RC aircraft, both sets of lights, as well as the motor. Two individuals (C. Wall and T. Snyder) custom-built a circuit into the fuselage of the aircraft that allowed the pilot to control the lights (lights off, lights on steady, lights on pulsing). The RC aircraft was flown by two experienced pilots (R. Needham or C. Meyers).

For each trial, temperature, humidity, and wind speed were recorded using a portable Kestrel hand-held weather station. Cloud cover was recorded by visual estimation. We measured ambient light intensity with a portable digital lux meter and ambient noise levels with a portable digital sound meter. All measurements were taken behind the experimental enclosure blinds before the stimulus, with the exception of ambient noise level that was recorded as the aircraft went over the enclosures.

Static aircraft experiment

This experiment allowed us to determine if cowbirds changed their alert behavior to a static RC aircraft with lights off or on (pulsing or steady). We used 92 wild-caught cowbirds, which were randomly assigned to pairs, totaling 46 pairs. This experiment consisted of two independent factors: light treatment (lights off, lights steady and lights pulsing) and distance to static aircraft (25 m and 100 m).

A pair of birds, in a single enclosure, was exposed to the aircraft throughout each trial (Fig. 1a). In addition to the camcorders recording the enclosure, one JVC Everio

(GZ-MG330AU) camcorder was placed approximately 10 m away from the experimental area to focus on the static aircraft to record when the lights were presented to the individuals (Fig. 1a). Individuals were placed into the experimental enclosure and allowed to forage for 3 min before the stimulus was presented remotely from a controller. Three minutes after the birds were exposed to the stimulus, the trial was ended. Temperature, humidity and wind speed ranges were 0.2 to 19.9 °C, 53.0 to 97.2 % and 0.0 to 10.5 km hr^{-1}, respectively. Cloud cover, light and sound intensity ranges were 0 to 100%, 4,500 to 58,300 lux and 56.8 to 102.2 dB, respectively.

Moving aircraft experiment

This experiment aimed at assessing how cowbirds responded to an approaching RC aircraft with lights off, lights on steady, and lights on pulsing. For this experiment, we used 140 wild-caught cowbirds that were randomly placed into pairs, totaling 70 pairs. To increase the number of birds exposed to the aircraft per trial (due to logistic, weather, and regulatory restrictions to fly the RC aircraft close to an airport), we had two enclosures (with two birds in each) separated by a visual barrier (Fig. 1b). Therefore, two pairs of birds were exposed to each light treatment in each trial. We exposed 20 pairs of birds to the lights off treatment, 22 pairs to the light steady treatment, and 28 pairs to the light pulsing treatment. However, only 9, 10, and 11 pairs were used for analysis, respectively. The other trials were compromised because of mechanical problems with the aircraft, changes in its trajectory due high winds, aircraft crashing after take-off, either before, during or after the approach.

The aircraft took off from a take-off strip that was centered 207 m away in front of the two enclosures (Fig. 1b). The pilot was located on the take-off strip and a camcorder operator was located to the side of the approach pathway, approximately halfway between the enclosures and take-off strip (Fig. 1b). The approach path was oriented so that the aircraft flew in a southwest trajectory to reduce the effect of crosswinds (Fig. 1b). A camcorder was situated perpendicular to the flight path about 50 m from the enclosures to observe when the aircraft flew over them (Fig. 1b). A second camcorder was placed 102 m in front of the enclosures 50 m off perpendicular to the flight path (Fig. 1b). An operator (obstructed from the birds' view by a large bush) rotated the second camcorder to follow the aircraft from approach to landing. A third camcorder was placed at the end of the take-off strip, approximately 50 m perpendicular to the flight path to record when the aircraft took off and began the approach (Fig. 1b). All camcorders were synced as described above. Markers were placed every 9 m parallel to the flight path (Figure 1b). These markers and camcorders were used to calculate the speed of the aircraft for each trial (see below for details).

A trial was begun by simultaneously releasing a pair of birds into each of the enclosures. Each pair was allowed to acclimate to their enclosure for 5 min. After the acclimation period, the aircraft took off and flew above the approach path approximately 6 m above ground level until it reached the enclosures. The aircraft then ascended to approximately 40 m and circled back to the take-off strip to land. Five minutes after the aircraft landed, the trials ended. Temperature, humidity and wind speed ranges were 2.0 to 34.6 °C, 41.0 to 90.2 % and 0.0 to 13.1 km hr^{-1}, respectively. Cloud cover, light and sound intensity ranges were 0 to 100 %, 8,000 to 81,200 lux and 55.7 to 76.3 dB, respectively.

Behavioral coding

Virtual Dub (Avery Lee, Version 1.9.11) was used for frame by frame analysis with 29.9 frames per second (fps). The behavior of both individuals in the cage was analyzed separately. The focal individual was examined for 1,000 frames before the stimulus onset to establish its baseline behavior. The first change in behavior after stimulus onset associated with alert behavior was recorded (refer to Table A.1 for description of behaviors observed and Figure A.1 for their schematic representation). The most common behavior seen was stretched neck, followed by head up movements, and crouching.

In the static experiment, we first went through the videos to determine the frame for when the first individuals in the arena began to forage (first peck) and the frame of stimulus onset (i.e. when the aircraft lights turned on). In order to assign a frame of stimulus onset to the no light treatment, which was meant to establish the baseline alert behavior, we used the frame 3 minutes after the first peck, as the stimulus was presented 3 minutes after the first peck.

During the static aircraft experiment, we measured the amount of time it took each bird to alert to the light stimulus at the different distances (latency to alert) using frame by frame analysis. Only birds that were able to detect the stimulus within the trial time were included in the statistical analysis. There were 13 individuals from the 92 for which we could not determine their alert behavior from the videos (5 for lights off, 3 for steady lights, and 5 for pulsing lights). Latency to alert was measured from the onset of the stimuli, thus smaller values indicate a quicker response.

In the moving aircraft experiment, frame by frame analysis was used to determine the aircraft speed, as well as time to "collision" at alert and at avoidance. We used two camcorders along the flight path to determine the frame in which the aircraft began approach and reached the vertical plane of the arenas (expected collision frame), respectively. Using these two frames, and knowing the distance of the approach, we calculated the speed of the aircraft ($207\,m\,/\,[k * 1/fps] - [a * 1/fps]$; where fps is frames per second; 17.846 ± 2.659 m s^{-1}). During some trials, camcorder 9 malfunctioned during a trial and we were unable to get the exact frame for when the aircraft began the approach. In these cases, we used camcorder 8 to determine a known location with the markers and used that known distance, rather than 207 m, accordingly.

Two types of behavioral responses were measured for each individual to the approach of the RC aircraft: alert and avoidance response. We first recorded the frame at which these behaviors occurred and then calculated the time it would take the aircraft to reach the individual after alert and avoidance behavior, called time to "collision" at alert and time to "collision" at avoidance, respectively. We defined alert response as the first change in behavior of the individual after the aircraft began the approach. Avoidance response was when the individual changed its behavior to avoid the approaching aircraft (e.g., flush, body movement away from the aircraft; refer to Appendix 1 for description of coded behaviors and their schematic representation). To determine the alert and avoidance frames, the individual was watched frame-by-frame for 1,000 frames before the aircraft took off to determine baseline behavior. The frame at alert response was determined as the first alert behavior the bird showed toward the aircraft (generally head-up movement, stretched neck, crouch or body movement towards the aircraft; see Appendix 1 for details). The frame at avoidance response was the first avoidance behavior the bird showed in response to the aircraft (generally a crouch, body movement, jump or flush; e.g., Blackwell et al. 2009; see Appendix 1 for details).

Time to "collision" times were calculated by the following equation: (expected collision frame – frame at alert or avoidance) / 29.907 frames per s. Higher values of time to "collision" time (both alert and avoidance) indicate that the individual responded quicker to the aircraft after it began approach, as the aircraft was further away when the individual responded. We also measured the buffer time (i.e., difference in time between time to "collision" at alert and at avoidance), which is a proxy of how long it took the individual to avoid the aircraft after it became alert. Higher values of buffer time indicate that after becoming alert to the aircraft, the focal individual took longer to avoid the approaching aircraft.

Statistical analysis

We used a general linear mixed model to analyze the time to alert in the static aircraft experiment, in which we included light treatment (lights off, lights on pulsing, lights on steady), distance to the aircraft (25 and 100 m from the enclosure), and their interaction as categorical factors. We also included ambient light intensity and wind speed as continuous factors. Trial was considered a random factor. We also ran a generalized linear model to establish the effects of light treatment, distance to the aircraft, and their interaction on the probability of animals showing alert behavior over a 30 s period. In this model, we also included ambient light intensity and wind speed as covariates.

We used general linear mixed models to assess the factors influencing time to "collision" at alert, time to "collision" at avoidance, and buffer times (i.e., difference between time to "collision" at alert and at avoidance). We included in the models: light treatment (lights off, lights on pulsing, lights on steady), aircraft speed, ambient light intensity, ambient noise, and wind speed. We also included the interaction between ambient light intensity and light treatment as a similar effect was found to influence cowbird responses to vehicle approach in a previous study (Blackwell, Fernández-Juricic, et al. 2009). Additionally, we tested for an interaction between light treatments and aircraft speed as vehicle speed could potentially enhance or decrease the perceptual limitations to detect objects at different speeds. In these models, we included experimental arena as a random subgroup to control for the two arenas tested per trial. We used t-tests to assess differences.

RESULTS

Visual contrast of lights

Visual saliency, or chromatic contrast, was measured from five different LED light wavelengths (470 nm, 525 nm, 585 nm, 595 nm, and 635 nm), in three ambient light conditions (sunny, cloudy, partly cloudy), and when the aircraft was about 50 m and 5 m away from the birds. Higher values of chromatic contrast would indicate a higher visual saliency of the lights in relation to the background from the perspective of the brown-headed cowbird visual system. Across all ambient light conditions, chromatic contrast decreased as the aircraft became closer to the birds for the 525 nm, 585 nm, 595 nm, and 635 nm LED lights, but the 470 nm LED light showed the opposite pattern (Table 1). Overall, chromatic contrast values were highest for 470 nm lights across all ambient light conditions irrespective of distance (Table 1).

Static aircraft experiment

The time it took cowbirds to show alert behaviors to a static RC aircraft varied with the type of treatment (Table 2a; Fig. 2a). Cowbirds showed alert behaviors more quickly in response to the static RC aircraft with the light steady ($t_{34.7} = 4.82$, $P < 0.001$) and with the lights pulsing ($t_{33.9} = -5.81$, $P < 0.001$) compared to the baseline alert behavior recorded when the lights were off (Fig. 2a), irrespective of the distance between the birds and the aircraft. We did not find significant differences in time to show alert behaviors between lights steady and lights pulsing ($t_{35.2} = 1.27$, $P = 0.213$). All other factors were not significant (Table 2a).

Additionally, we found a significant light treatment effect on the probabilities of cowbirds showing alert behavior to the RC aircraft within 30 s (Table 2b), with >75% probability of reacting to the lights pulsing and steady compared to ~15% baseline reaction when the lights were off (Fig. 2b). All other factors were not significant (Table 2b).

Moving aircraft experiment

Time to "collision" at alert was significantly affected by light treatment and aircraft speed (Table 3). Time to "collision" at alert increased when the lights were off (9.85 ± 0.43 s) than when steady (7.82 ± 0.51 s; $t_{35.9} = 3.10$, $P = 0.004$). No significant differences were found in time to "collision" at alert between lights pulsing (9.09 ± 0.70 s) and the other two light treatments ($P > 0.150$). Additionally, cowbirds became alert more quickly in response to slower aircraft speeds than higher speeds (coefficient, -0.73 ± 0.22, $t_{35.7} = 3.30$, $P = 0.002$).

However, these independent effects on time to "collision" at alert cannot be interpreted separately as both light treatment and aircraft speed interacted significantly (Table 3). When the lights were off, we found a strong and significant speed effect (slope, -0.92 ± 0.15, $R^2 = 0.70$; $t_{40.3} = 5.94$, $P < 0.001$), by which cowbirds took significantly longer to become alert when the RC aircraft approached at higher speeds (Fig. 3a). When the lights were pulsing, the negative speed effect on alert time was still significant ($t_{41} = 4.19$, $P < 0.001$), but its strength decreased (slope, -0.88 ± 0.21; $R^2 = 0.53$; Fig. 3b). However, when the lights were steady, there was no significant relationship between alert time and speed (slope, 0.17 ± 0.16, $R^2 = 0.03$; $t_{40.4} = 1.10$, $P = 0.280$; Fig. 3c). No other factors significantly influenced the time it took cowbirds to become alert to the approaching aircraft (Table 3).

Time to "collision" at avoidance was significantly influenced by ambient noise levels when the aircraft flew over the enclosures (Table 3). Higher ambient noise levels significantly delayed cowbird avoidance responses to the RC aircraft approach, although this was a weak relationship (slope, -0.05, $R^2 = 0.09$). No other factor significantly affected time to "collision" at avoidance (Table 3). Given the significant noise effect, we ran a similar model but including the interaction between light treatment and noise, which did not turn out to be significant ($F_{2, 40} = 0.31$, $P = 0.736$). Additionally, aircraft speed was not significantly correlated with ambient noise levels ($r = 0.36$, $P = 0.063$).

Finally, the time difference between time to “collision” at avoidance and time to “collision” at alert (buffer time) was affected significantly by light treatment as well as aircraft speed (Table 3). It took significantly longer for cowbirds to avoid the aircraft after becoming alert when the lights were off (7.29 ± 0.39 s) compared to when the lights were steady (5.70 ± 0.48 s; $t_{35.2} = 2.61$, $P = 0.013$). We did not find significant differences in buffer times between lights pulsing (6.36 ± 0.61 s) and the other two light treatments ($P > 0.200$). Furthermore, cowbirds took longer to avoid the aircraft after becoming alert at slower aircraft speeds than higher speeds (coefficient, -0.88 ± 0.20, $t_{34.9} = 4.32$, $P < 0.001$).

We also found a significant interaction effect between light treatment and aircraft speed affecting buffer times (Table 3, Fig. 4). When the lights were off, buffer times decreased significantly with aircraft speed (slope, -0.95± 0.15, $R^2 = 0.73$; $t_{39.4} = 6.40$, $P <0.001$; Fig. 4a). However, this speed effect decreased slightly with lights pulsing (slope, -0.56 ± 0.20; $R^2 = 0.56$; $t_{40.1} = 2.81$, $P = 0.008$; Fig. 4b), and became non-significant with lights steady (slope, 0.15 ± 0.16; $R^2 = 0.03$; $t_{39.5} = 0.92$, $P = 0365$; Fig. 4c). No other factor influenced buffer times significantly (Table 3).

DISCUSSION

In the context of detection and response to a static and approaching aircraft by brown-headed cowbirds, we found: the cowbird visual system would perceive 470 nm aircraft mounted LED lights with greater saliency than other commercially available lights, cowbird alert behavior changed when exposed to a static RC aircraft with visually salient lights compared to one with lights off, and cowbird responses to an approaching aircraft were affected by light treatment, aircraft speed and ambient noise.

Using published data on the physiology of the cowbird visual system (i.e., sensitivity of the visual pigments and oil droplets, relative density of cone photoreceptors; Fernández-Juricic et al. 2013) we used perceptual models to estimate the degree of visibility of different lights. This step has rarely been implemented in studies aimed at developing wildlife attractants and repellents. This allowed us to use a visual stimulus that was more likely to be tuned to the cowbird visual system, which is particularly relevant with birds due to their substantially different visual system compared to humans (Bowmaker et al. 1997). An implicit assumption we made was that greater visual saliency would enhance alert and flight responses of cowbird. Cowbirds did show alert and avoidance responses to the approaching aircraft, but with our design we cannot tease apart whether the response was the result of the salient light or the looming stimulus. Future studies should test the relationship between visual saliency of colors of various wavelengths and type of response (avoidance, attraction).

Previous studies have shown that lights affect avian behavior (Jones & Francis 2003; Blackwell, Fernández-Juricic, et al. 2009; Blackwell & Bernhardt 2004; Blackwell et al. 2012), suggesting that birds pay attention to lights, although this explicit assumption had not been tested. The results of our static aircraft experiment provided some corroboration in cowbirds by showing that they changed their behavior to the aircraft with lights on compared to their baseline alert behaviors (i.e., aircraft with lights off). Previously, cowbirds and geese have been shown to respond more quickly to an approaching object with pulsing white lights compared to steady white lights (Blackwell et al., 2004; Blackwell et al., 2012). Furthermore, European starlings increase their activity (i.e., movements within the experimental arena) when presented with a pulsing laser lights compared to steady ones (Lustick 1973). Overall, birds appear to allocate visual attention to the sudden appearance of lights, including the ones that show higher saliency to their visual systems, which supports the contention that their detection behavior could be manipulated (e.g., enhanced) with this kind of artificial stimuli.

When the aircraft approached the animals, we found an effect of aircraft speed that depended upon the type of light condition. When the lights were off, cowbird alert responses were delayed at high aircraft speeds. In an anti-predator context, predator speed actually enhances prey alert behaviors (reviewed in Stankowich & Blumstein 2005). However, the range of speeds of our RC aircraft was relatively higher than the approach speeds of some aerial predators (e.g., red-tailed hawks, ~ 8 to 17 m/s; Broun & Goodwin 1943). It is possible that the aircraft is approaching faster than what cowbirds are capable of detecting. The ability of organisms to detect the looming stimuli may decrease at higher speeds (Wann et al. 2011). There are some neurons that are sensitive to looming objects in the optic tectum of birds, of which one type is sensitive to object speed (Sun & Frost 1998). Slow approach speeds elicit quicker responses from these neurons (Sun & Frost 1998). Perhaps, at our high aircraft speeds, the firing rate of these neurons reached a plateau, reducing the ability to track the movement of the aircraft. As it happens, higher vehicle speeds have been found to increase mortality (European birds, Legagneux & Ducatez 2013; amphibians, birds, mammals, frogs, lizards, toads, snakes, Farmer & Brooks 2012).

In the pulsing lights treatment, the speed effect was still significant but decreased in strength. One potential explanation is that the bird’s visual attention may have been mostly focused on the aircraft as it was the most constant cue from the approaching object, resulting in the same overall pattern seen with lights off. The reduced effect of speed may have come from additional information provided by the pulsing lights, as large luminance differences increases the probability of visual attention to an appearing object (Rauschenberger 2003). If so, cowbirds may have used each light pulse to better establish the relative position of the aircraft during the approach. The aircraft traveled shorter distances in between pulses of light at slower speeds compared to higher speeds, so that there would be more information present during the slow approaches than fast approaches. This would facilitate looming neurons to track the object and determine time to contact (Wang & Frost 1992; Sun & Frost 1998) and thus enhance alert response behaviors.

Interestingly, the steady light treatment essentially eliminated the negative effects of aircraft speed on alert time. The bird's visual attention may have been focused on the lights rather than the aircraft itself. The aircraft with steady lights had higher luminance per unit time because its luminance came from all eight LED bulbs on at the same time compared with the aircraft with the lights pulsing where only four LED bulbs were on at a time. The increase in visual attention on the lights would allow the birds to track the aircraft across all speeds.

Time to "collision" at avoidance was significantly negatively influenced by noise level: birds delayed showing avoidance behaviors to the aircraft at higher noise levels (35% higher) than lower levels. However, this was a very weak relationship. No other factors influenced time to "collision"; it may be the case that regardless of other factors, cowbirds avoided the aircraft at the same point in time. Studies show that avoidance behavior is influenced by the approaching object's start distance (Blumstein 2003; Cooper et al. 2009; Rodríguez-Prieto et al. 2009), where greater starting distances lead to greater avoidance times. Furthermore, faster objects tend to have a stronger influence on avoidance time at different starting distances (Cooper et al. 2009). We found no light treatment differences nor speed effect; implying that these factors to not alter the appearance on starting distance. If these factors were to increase or decrease the perceived starting distance, we would see either an increase or decrease in avoidance times, respectively. Buffer times, the difference between time to "collision" at alert and avoidance initiation time, were influenced by light treatment and speed. With lights off, buffer times were lower at higher speeds, but this effect was less pronounced with the pulsing lights. With the steady lights, speed no longer influenced buffer times. Changes in buffer time could be the result of at least three scenarios: 1) variation in time to "collision" at alert with time to "collision" at avoidance remaining constant, 2) time to "collision" at alert remaining constant with time to "collision" at avoidance changing, 3) changes in both alert and time to "collision" at avoidance but at different rates. Because time to "collision" at alert was similarly influenced by light treatment and speed, and time to "collision" at avoidance was not significantly affected by either, our data supports scenario 1. Therefore, to increase the time the animal has available to make a decision to avoid the approaching vehicle (i.e., increasing buffer times), our results suggest that enhancing alert behavior is key for cowbirds.

Applied implications

We found that avian alert responses may potentially be associated with constraints in the visual system of birds. We found that the lights could ameliorate the speed effects. Because commercial aircraft move at different speeds depending on the flight phase, we suggest that light stimuli should also vary with flight phase to maximize potential detectability. One possibility is having two sets of lights, tuned to the visual system of birds, which could be used to alter bird behavior: a set of static lights near the runway and a set of onboard lights. Birds' alert time is quicker for static objects when lights (steady or pulsing) are present; thus, static lights along runways could be coordinated just prior to taxiing to bring the attention of the birds to the runway. The second set of lights onboard could be off or on and pulsing to enhance alert behaviors at different speeds, as aircraft begin to move for take-off (taxiing at 3.1-10.3 $m\ s^{-1}$). During aircraft take-off (approximately 27.7 $m\ s^{-1}$), steady lights could be used because they significantly reduce the effects of aircraft speed on alert behavior. The use of continuous onboard, steady lights beyond airport property could potentially enhance alert behavior of in-flight birds to a fast approaching aircraft.

Overall, our results provide a new window to understanding the responses of birds to aircraft. As air travel increases, the rate of bird strikes will increase, escalating human and wildlife mortality, as well as the cost of damage. The design of aircraft lights can be used to minimize bird strikes. Our results show that more future studies should look into the effects of other light wavelengths on the behavioral response of birds commonly involved in bird-strikes to provide additional insight into more effective lighting systems.

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TABLES

Table 1

Chromatic contrast values of LED lights from the visual perspective of brown-headed cowbirds. Chromatic contrast was calculated when the aircraft was at two locations on the approach path (aircraft at a far distance and at a close distance, relative to the bird's position), as well as three different ambient light treatments (sunny days, cloudy days and partly cloudy days). Numbers in bold reflect the LED light with the highest saliency in each ambient light scenario.

	LED lights from CoolLED[1]				
	470 nm	**525 nm**	**585 nm**	**595 nm**	**635 nm**
Sunny					
Far Aircraft	187.62	144.23	64.38	152.03	148.34
Close Aircraft	**199.06**	137.73	50.49	135.76	136.10
Cloudy					
Far Aircraft	179.47	150.44	75.97	164.56	157.29
Close Aircraft	**196.77**	139.28	52.56	139.11	137.89
Partly Cloudy					
Far Aircraft	186.42	143.75	67.22	153.73	151.79
Close Aircraft	**200.27**	138.49	51.25	135.61	137.33

[1] Values in table given in Just Noticeable Distance (JNDs). The higher the visual contrast value, the, the greater the saliency of the object in relation to the visual background.

Table 2

(a) Latency to alert, and (b) probability of reaction within 30 s to a static RC aircraft under three treatment treatments: aircraft with lights off (NL), lights on steady (BS), lights on pulsing (BP). Significant values are marked in bold.

(a)

	F	d.f.	P
Light treatment	21.41	2, 34.6	**<0.001**
Distance	1.05	1, 34.3	0.3133
Light treatment X Distance	3.23	2, 33.6	0.0522
Ambient light intensity	0.01	1, 39.7	0.9304
Wind speed	0.02	1, 31.9	0.8894

(b)

	χ^2	d.f.	P
Light treatment	42.70	2	**<0.001**
Distance	3.66	1	0.056
Light treatment X Distance	5.90	2	0.052
Ambient light intensity	0.34	1	0.562
Wind speed	0.31	1	0.580

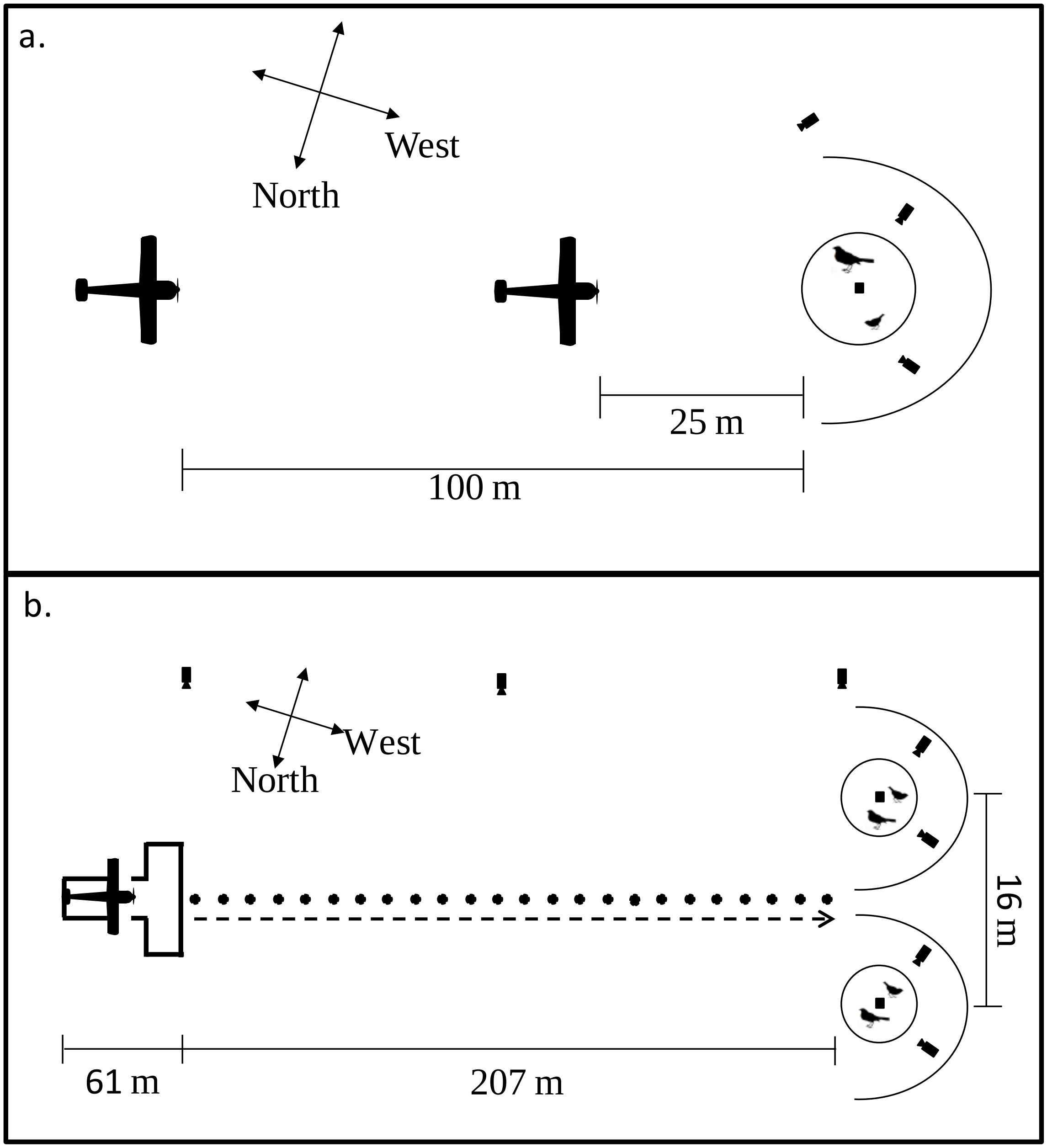
Table 3

General linear mixed model showing the factors affecting the time it took BHCO to become alert and avoid, as well as the difference between alert and avoidance, in response to an approaching RC aircraft under three treatment treatments: aircraft with lights off, lights on steady, lights on pulsing. Significant values are marked in bold.

	F	**d.f.**	**P**
Time to "collision" at alert			
Light treatment	7.10	2, 35.8	**0.003**
Ambient light intensity	0.18	1, 35.9	0.671
Light treatment X Ambient light intensity	0.12	2, 36.2	0.887
Wind speed	0.13	1, 36.9	0.721
Aircraft speed	7.34	1, 35.9	**0.010**
Noise level	1.81	1, 36.3	0.186
Light treatment X Aircraft speed	7.22	2, 35.6	**0.002**
Time to "collision" at avoidance			
Treatment	3.14	2, 41.4	0.054
Ambient light intensity	2.20	1, 41.8	0.146
Light treatment X Ambient light intensity	2.55	2, 41.9	0.091
Wind speed	0.80	1, 41.9	0.376
Aircraft speed	0.00	1, 42.9	0.971
Noise level	5.64	1, 43.2	**0.022**
Light treatment X Aircraft speed	2.41	2, 41.4	0.102
Difference between time to "collision" at alert and avoidance			
Light treatment	8.65	2, 35	**0.001**
Ambient light intensity	3.02	1, 35.1	0.091
Light treatment X Ambient light intensity	1.32	2, 35.4	0.280
Wind speed	0.29	1, 36	0.593
Aircraft speed	10.93	1, 35.1	**0.002**
Noise level	0.31	1, 35.8	0.578
Light treatment X Aircraft speed	7.36	2, 34.8	**0.002**

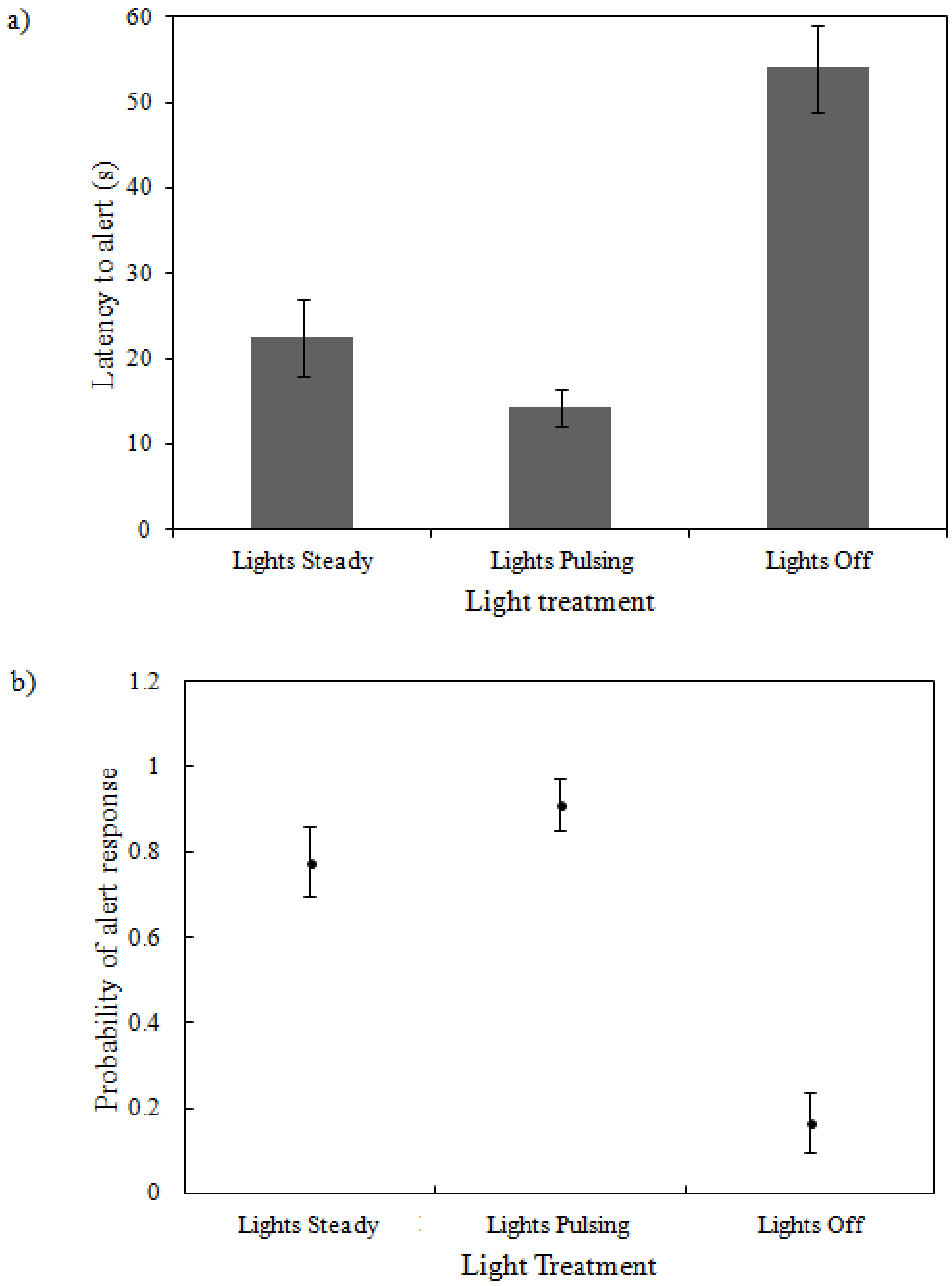
FIGURES

Figure 1



(a) Experimental set-up for Static Aircraft Experiment. Aircraft silhouette: the two distances in which the RC aircraft was located (either 100 m or 25 m from the experimental enclosures); open large circles: the enclosures – each housing two individuals; dark circle with numbers: the locations of all the cameras used; numbers refer to the camera input and channel when analyzed. (b) Experimental set-up for Moving Aircraft Experiment. T-Shape: the take-off/landing strip – aircraft pilot stands here; aircraft silhouette: where the RC aircraft begins the approach; dashed arrow line: the approach path of the flying aircraft; small dark circles: the distance markers used to locate the aircraft during approach (separated by 9 m); open large circles: the enclosures – each housing two birds; numbered dark circle: the locations of all the cameras used; numbers refer to the camera number.

Figure 2



Cowbird a) latency to alert (higher values indicate more delayed responses) and b) probability of showing alert behavior within 30 s to an static RC aircraft under different treatment treatments: aircraft with lights steady, pulsing, and off.

Figure 3

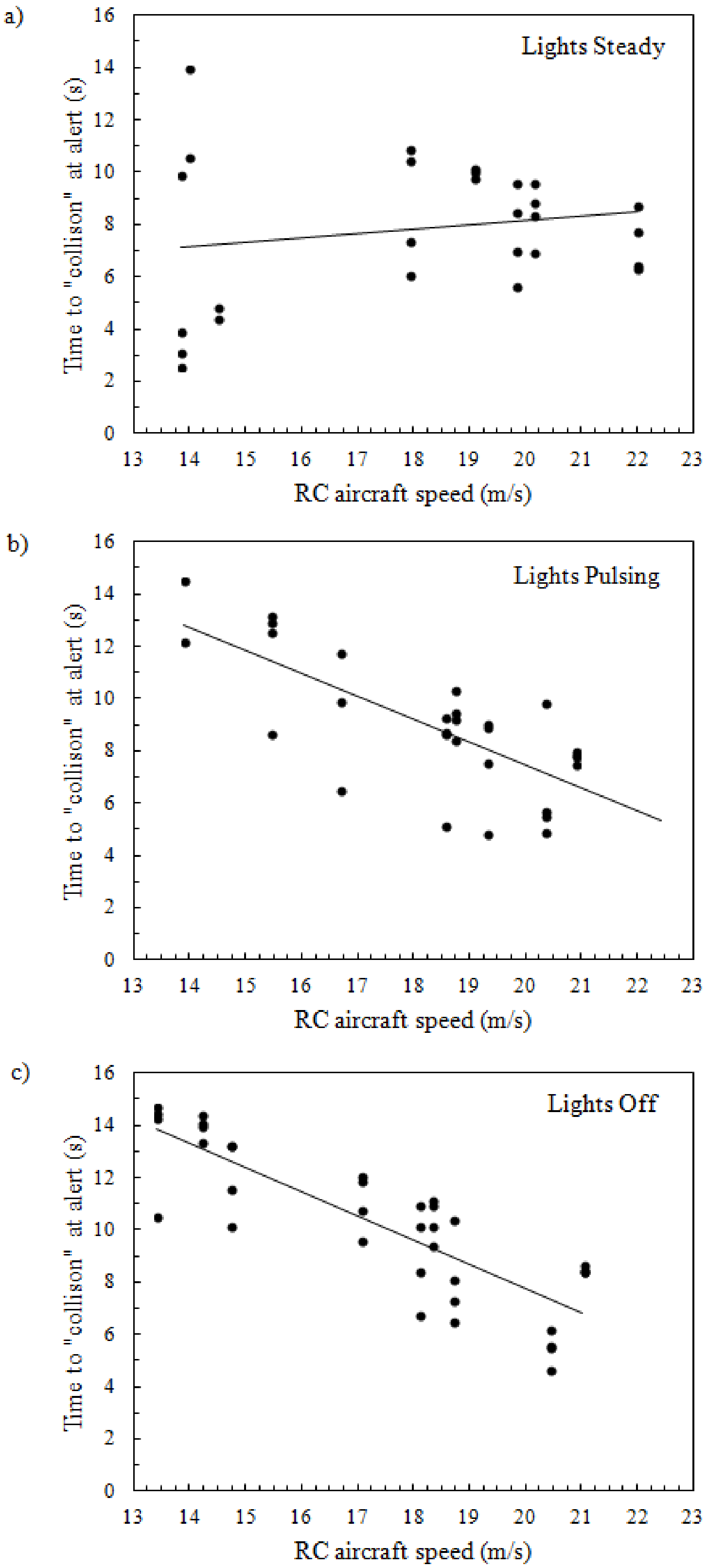

a)
Lights Steady
Time to "collison" at alert (s)
0
2
4
6
8
10
12
14
16
13
14
15
16
17
18
19
20
21
22
23
RC aircraft speed (m/s)
b)
Lights Pulsing
Time to "collison" at alert (s)
0
2
4
6
8
10
12
14
16
13
14
15
16
17
18
19
20
21
22
23
RC aircraft speed (m/s)
c)
Lights Off
Time to "collison" at alert (s)
0
2
4
6
8
10
12
14
16
13
14
15
16
17
18
19
20
21
22
23
RC aircraft speed (m/s)

Figure 3.

Time to “collision” when brown-headed cowbirds alert to an approaching aircraft with varying speeds. Lights mounted on the aircraft were a) off, b) pulsing and c) steady. Higher values indicate a quicker response.

Figure 4

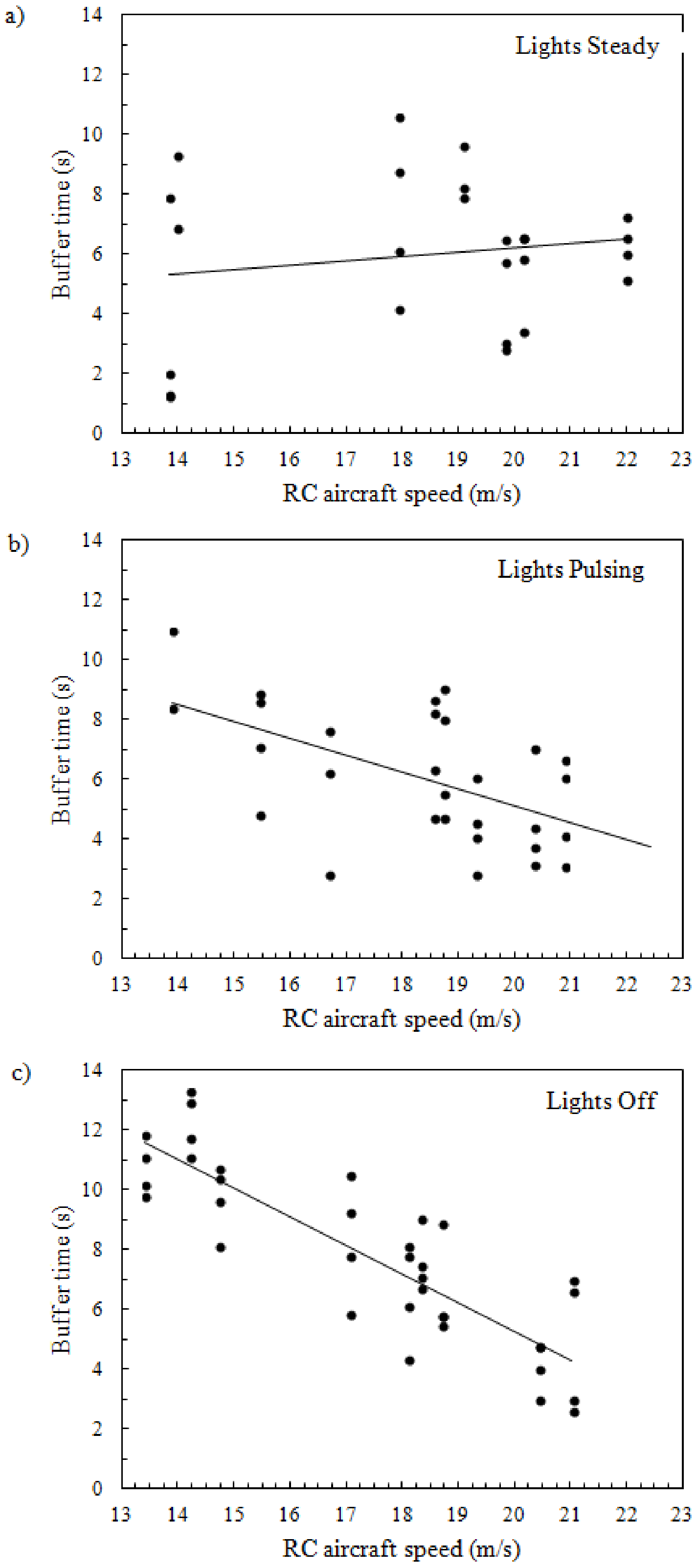

a)
Lights Steady
Buffer time (s)
0
2
4
6
8
10
12
14
13
14
15
16
17
18
19
20
21
22
23
RC aircraft speed (m/s)
b)
Lights Pulsing
Buffer time (s)
RC aircraft speed (m/s)
c)
Lights Off
Buffer time (s)
RC aircraft speed (m/s)

Figure 4.

Cowbird buffer time (amount of time it took bird to avoid the aircraft after becoming alert to it) to the approaching RC aircraft with varying speeds when the (a) lights were off, (b) pulsing, and (c) steady.

APPENDIX

Static aircraft Experiment

We coded when the individual became alert to the stimuli. Common behaviors were stretched neck, head-up movement, and crouch. We did not code flight behaviors, as the individuals did not avoid the static stimuli.

To determine head-movement rate before and after the presentation of the stimuli, we recorded the following behaviors: crouch, stretched neck, body maintenance, body movement, head-up, head-down, head-up movement, and peck (refer to Table A.1 for description of behaviors observed and Figure A.1their schematic representation). For these instances, body movement included: walk, hop, jump, and flush.

Moving Aircraft Experiment

We coded when the individual became alert (frame at alert response) to the stimulus and when the individual avoided (frame at flight response) the stimulus. Frame at alert response was determined as the first alert behavior the bird showed toward the aircraft (generally head-up movement, stretched neck, crouch and body movement). Frame at flight response was when the individual changed its behavior to avoid the approaching aircraft. The avoidance was the first flight behavior the bird showed in response to the aircraft (generally a crouch, body movement, jump and flush; e.g., Blackwell et al. 2009; see Table A.1 for details).

Figure A.1

A visual representation of alert and flight behaviors seen during the videos. HUM: Head-Up Movement; SN: Stretched Neck; BM: Body Movement; C-Crouch; BU; Body Up; J: Jump; F; Flush. Alert behaviors consisted of: HUM, SN, BM and C. Flight behaviors consisted of all the behaviors. Refer for Table A.1 for a description of these behaviors.

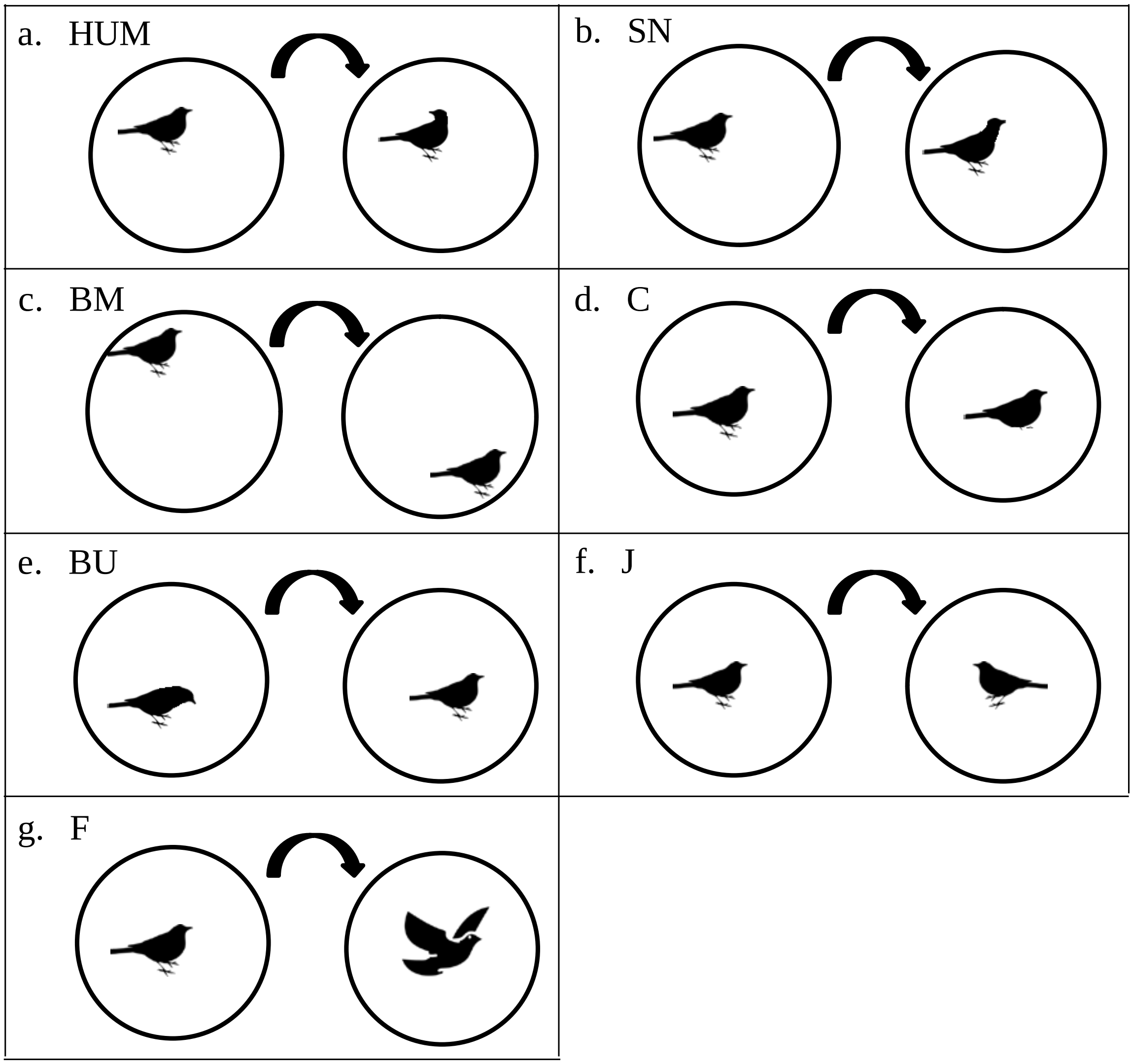


Table A.1

Observed behaviors of brown-headed cowbird reactions when presented with an approaching aircraft

Behavior	Description
Alert Behaviors	
Head-Up Movement	Move head while in a head-up body posture (beak held parallel to ground) (**A.1a**)
Stretched Neck	Elevate head with neck while in a head-up body posture. The head position does not move (**A.1b**)
Body Movement towards aircraft	Move body form one location to another in the enclosure by walking or hopping towards the front of the enclosure(**A.1c**)
Crouch	Lower whole body close to the ground (**A.1d**)
Flight Behaviors	
Head-Up Movement	Move head while in a head-up body posture (beak held parallel to ground) (**A.1a**)
Stretched Neck	Elevate head with neck while in a head-up body posture. The head position does not move (**A.1b**)
Body Movement away from aircraft	Move body form one location to another in the enclosure by walking or hopping towards the back of the enclosure (**A.1c**)
Crouch	Lower whole body close to the ground (**A.1d**)
Body Up	Move body from a head-down posture to a head-up posture (**A.1e**)
Jump	Move body from one position to another while remaining in the same location (**A.1f**)
Flush	Move body off the ground to begin flight (**A.1g**)