THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 117, 2015, pp. 165–177
DOI: 10.1650/CONDOR-14-157.1

RESEARCH ARTICLE

Cowbird responses to aircraft with lights tuned to their eyes: Implications for bird–aircraft collisions

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Submitted October 1, 2014; Accepted January 28, 2015; Published April 8, 2015

ABSTRACT

Collisions between birds and aircraft (bird strikes) are expensive, risk human lives, and increase bird mortality. Aircraft lighting has been proposed as a potential means of enhancing avian responses to aircraft. Determining the optimal changes to lighting to reduce bird strikes is a complicated problem because avian visual systems differ markedly from that of humans. Icteridae, including Brown-headed Cowbirds (*Molothrus ater*; hereafter "cowbirds"), are involved in bird strikes, have a well-described visual system, and respond to approaching vehicles and lights. Our goal was to assess cowbirds' responses to a remote-controlled (RC) aircraft fitted with lights tuned to the cowbird eye. On the basis of perceptual modeling (i.e. visual physiology, object and background reflectance, and ambient light conditions), we found that 470-nm lights ("blue" portion of the human spectrum) would be the most conspicuous wavelength for cowbirds. We used field experiments to examine cowbird response to 470-nm light treatments. Cowbirds exhibited alert behaviors to a stationary RC aircraft with lights on (both continuous and pulsing) in less than half the time they took to do so with lights off. In response to an approaching RC aircraft, cowbird alert responses were delayed at higher aircraft speeds with the lights off, and we noted a less pronounced speed effect with pulsing lights. However, this interaction effect of aircraft speed and lighting was eliminated with continuous lights. Additionally, higher ambient noise levels delayed cowbirds' avoidance responses to the RC aircraft, possibly influencing cowbird behavior as a sensory distractor. We suggest that some types of lighting may enhance the birds' detection and visual tracking of aircraft at high speeds and, thus, holds some potential as a means of reducing the frequency of bird strikes. This sensory-based approach also has implications for management of other bird–object collision problems.

Keywords: aircraft, airports, bird strikes, lighting and wildlife, wildlife–vehicle collisions

Respuestas de los tordos a las aeronaves iluminadas: implicancias para las colisiones entre aves y aeronaves

RESUMEN

Las colisiones entre aves y aeronaves (choques de aves) son costosas, ponen en riego vidas humanas y aumentan la mortalidad de aves. Se ha propuesto que la iluminación de las aeronaves podría aumentar la respuesta de las aves a las aeronaves. Determinar los cambios que deben hacerse en los sistemas de iluminación para reducir los choques con las aves es un problema complejo porque los sistemas visuales de las aves son diferentes del de los humanos. Los Icteridae, incluyendo a *Molothrus ater*, están involucrados en los choques con aeronaves, tienen sistemas visuales bien descritos y responden a vehículos y luces que se aproximan. Nuestro objetivo fue evaluar las respuestas de los tordos a una aeronave operada por control remoto equipada con luces sintonizadas con sus ojos. Encontramos que la luz de 470 nm (la parte "azul" del espectro humano) sería la longitud de onda más conspicua para los tordos, basados en un modelo perceptual (i.e., fisiología visual, reflectancia del objeto y del fondo, y propiedades espectrales de la luz). Mediante experimentos de campo examinamos la respuesta de los tordos a los tratamientos de luz de 470 nm. Los tordos mostraron comportamientos de alerta hacia las aeronaves operadas por control remoto con las luces encendidas (tanto continua como parpadeante) en la mitad del tiempo que les llevo para con las aeronaves con las luces apagadas. Las respuestas de alerta de los tordos fueron más lentas hacia aeronaves volando a mayores velocidades con las luces apagadas, pero notamos un efecto menos pronunciado de la velocidad hacia las aeronaves con las luces parpadeantes. Sin embargo, este efecto de la velocidad de la aeronave se eliminó con la aeronave con las luces continuas. Adicionalmente, mayores niveles de ruido ambiental demoraron las respuestas de escape hacia las aeronaves operadas por radio control, actuando como una distracción sensorial que posiblemente afecta el comportamiento de los tordos. Sugerimos que algunos tipos de iluminación pueden aumentar la detección por parte de las aves y el seguimiento visual de la aeronave a altas velocidades, y por ende tienen cierto potencial como un modo de reducir la frecuencia de choque entre aeronaves y aves. Esta aproximación basada en los sistemas sensoriales también tiene implicancias para el manejo otras colisiones entre aves y objetos.

Palabras clave: aeronave, aeropuertos, choques de aves, colisiones entre animales y vehículos, iluminación y vida silvestre

INTRODUCTION

Collisions between wildlife and moving vehicles (e.g., aircraft and cars) have been on the rise in recent years (Erritzoe et al. 2003, Dolbeer 2011, Kociolek et al. 2011). For instance, in the United States, >127,000 bird–aircraft collisions (hereafter "bird strikes") have been reported since 1990, but many more strikes have gone unreported (61–80%; Dolbeer et al. 2013). Bird strikes cause economic losses (e.g., $700 million annually in USA) and pose safety risks to passengers (e.g., 23 human deaths and 223 injuries from 1990 to 2011 in USA) (Dolbeer 2011, Dolbeer et al. 2013). In addition, bird strikes are a source of mortality for birds (Blackwell et al. 2009a), which becomes a conservation concern when threatened or vulnerable species are struck—for example, the endangered Hawaiian Duck (*Anas wyvilliana*; Linnell et al. 1999) and Tasmanian Wedge-tailed Eagle (*Aquila audax fleayi*; Bekessy et al. 2009). With increases in the number of routes and flights, this threat to birds is on the rise.

Airports have implemented multiple management strategies to reduce the density of species that can cause damaging strikes (Cleary and Dolbeer 2005, Blackwell et al. 2009a, DeVault et al. 2013). However, these strategies are limited because many strikes occur beyond airport jurisdiction (Blackwell et al. 2009a, Dolbeer 2011). This means that commercial aircraft themselves do not currently have any specific means of minimizing the chances of bird strikes. However, aircraft lights have been proposed to increase visibility to birds (Lustick 1973, Larkin et al. 1975). For instance, Brown-headed Cowbirds (*Molothrus ater*; hereafter "cowbirds") and Canada Geese (*Branta canadensis*) exhibited quicker responses (avoidance and alert behaviors, respectively) when presented with an approaching vehicle with pulsing "white" lights on than when the lights were off (Blackwell and Bernhardt 2004, Blackwell et al. 2012). Furthermore, the cowbird's response to vehicle approach and lighting depends on ambient light conditions. Blackwell et al. (2009a) found that under bright daylight, cowbirds alerted to an approaching truck more quickly with continuous than with pulsing lights, but the opposite trend was found under cloudy conditions.

Blackwell et al.'s (2009b) study underscores an important factor when assessing how birds respond to lights: The way birds perceive visual stimuli is markedly different from the way humans perceive them (Cuthill 2006). For instance, birds have 4 types of single-cone photoreceptors (Hart 2001a), providing them a wider color space than humans, who have only 3 types. Birds have oil droplets—carotenoid-filled, lipid-based organelles in their photoreceptors—that filter light as it enters the cone, enhancing color discrimination (Goldsmith et al. 1984, Partridge 1989, Hart 2001b). Additionally, the avian vitreous humor (i.e. gel between the lens and the retina) does not absorb in the ultraviolet portion of the spectrum as much as that of humans (Cuthill 2006). The overall implication is that lights that are visually conspicuous to humans may not necessarily be so to birds. These between-taxa differences in visual perception can actually be an opportunity for applied ecologists to develop new management strategies. For instance, lights tuned to the avian, rather than the human, eye could be used as beacons on objects in order to reduce bird mortality due to collisions, not just with aircraft but with wind turbines and buildings (Fernández-Juricic 2015), which are important sources of mortality for birds (Loss et al. 2013, 2014).

In the context of bird–aircraft collisions, all experimental studies to date have been conducted with "white" or broad-spectrum lights (e.g., Blackwell and Bernhardt 2004, Blackwell et al. 2012), which are heavily regulated by the Federal Aviation Administration. However, from the perspective of developing lights tuned to the avian eye that could lead to detection and avoidance behaviors, using white lights could actually complicate the interpretation of behavioral responses because it is not possible to establish which wavelength animals are responding to. This is because "white" lights have similar representation of multiple wavelengths. The goal of the present study was to determine the responses of cowbirds to an approaching remote-controlled (RC) aircraft with single-wavelength lights tuned to their visual system (i.e. maximizing the lights' conspicuousness) during daylight conditions. We focused on diurnal responses because >51,400 bird strikes have been recorded during the day, about twice as many as at night, over a 22-yr sample (Dolbeer et al. 2013). Cowbirds belong to the family Icteridae, whose species are involved in collisions with commercial aircraft (Dolbeer et al. 2013). Furthermore, cowbirds are an appropriate model species because their visual systems have been described (Blackwell et al. 2009b, Dolan and Fernández-Juricic 2010, Fernández-Juricic et al. 2013), allowing us to determine wavelengths targeted to this particular species. Finally, cowbirds show avoidance behavior when exposed to approaching objects (Blackwell et al. 2009b).

Our study had 3 main components: (1) determination of the wavelength with the highest conspicuousness to cowbirds, (2) evaluation of behavioral responses to static lights, and (3) evaluation of behavioral responses to approaching lights. To address the first component, we followed established methods in the visual ecology literature (i.e. perceptual modeling) that use species-specific visual physiology data to estimate the wavelengths that would be the most conspicuous to a nonhuman species (Vorobyev and Osorio 1998). Perceptual models take into account the visual characteristics of a species (i.e. sensitivity and density of cone photoreceptors), the reflectance spectrum of a specified object (i.e. LED lights) and visual background (i.e. open field), and the spectral properties of ambient light. Perceptual models estimate the distance between the object and the background in the color space of a given species (i.e. tetrahedral because cowbirds have 4 color-sensitive photoreceptors; Fernández-Juricic et al. 2013). The greater the difference between these 2 points in space (i.e. higher chromatic contrast), the more conspicuous the object is from the background. Behavioral tests have corroborated the physiologically based predictions of perceptual models in foraging (Cazetta et al. 2009, Behbahaninia et al. 2012) as well as brood-parasitism (Avilés et al. 2010) contexts.

Our first experiment tested whether cowbird behavior would change when presented with static lights on (continuous, pulsing), compared with lights off. This experiment was necessary to determine whether cowbirds would pay attention (based on changes in vigilance behavior) to the lights tuned to their visual system. In the second experiment, we established whether the use of lights on (continuous or pulsing) compared with lights off in an approaching aircraft would affect key behavioral responses (alert and avoidance) that could potentially reduce the chances of collisions between aircraft and birds. To that end, we measured the time from the moment a bird became alert or avoided the approaching RC aircraft to the moment it would potentially be struck (hereafter "time to collision at alert" [TTC_{alert}] and "time to collision at avoidance" [$TTC_{avoidance}$]) when lights were off, pulsing, or continuous. Using RC aircraft allowed us to simulate as much as possible, under semicontrolled conditions, the circumstances surrounding bird–aircraft interactions.

METHODS

The 77 female and 143 male adult cowbirds used in the study were captured in Erie County, Ohio, USA. We transferred individuals to West Lafayette, Indiana, USA, and color banded them. Cowbirds were housed in 0.61 × 0.61 × 0.76 m enclosures with a 14:10 hr light:dark cycle in animal facilities at Purdue University. No more than 4 individuals were permanently housed together at a time. We fed individuals a mix of white millet, game bird chow, and sunflower seeds ad libitum.

Perceptual Modeling of LED Lights

To predict which LED light wavelength(s) was the most conspicuous to cowbirds, we used perceptual modeling, which estimates the relative distance between the object of interest (in our case, LED lights) and the visual background in a tetrahedral color space established by the sensory physiology of cowbirds (Fernández-Juricic et al. 2013) and under specific ambient light conditions. The difference between the object and the background is called "chromatic contrast." LED lights with the highest chromatic contrast are expected to be the most conspicuous for cowbirds under the ambient light conditions modeled. We calculated the chromatic contrast of LED lights using Vorobyev and Osorio's perceptual model (see mathematical details in Vorobyev and Osorio 1998) in Avicol version 5 (Gomez 2006). We entered the following parameters into the 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; also see Appendix).

Irradiance and background reflectance measurements were taken at Purdue's Forestry and Natural Resources Farm. We measured irradiance and reflectance with a StellarNet EPP2000 portable spectroradiometer (StellarNet, Tampa, Florida, USA) under sunny, cloudy, and partly cloudy conditions on different days. Irradiance and background reflectance measurements were taken at the height of the cowbird head. Background reflectance included the sky, trees, ground, and aircraft. Given that the aircraft approached the birds, we took into account the proportional size of the aircraft at ~50 m and ~100 m away from the bird. Spectra were taken from 5 commercially available LED lights that were representative of the cowbird visual spectrum (470, 525, 585, 595, or 635 nm). Cowbirds can see into the ultraviolet. Unfortunately, we could not find a commercially available light in the ultraviolet range of the spectrum that would have luminance and visual angle comparable to that of the other 5 lights for the purposes of modeling.

The model predicted the chromatic contrast of each light at ~50 m and ~100 m to establish which light would have the highest conspicuousness from the cowbird's visual perspective. The LED light with the highest predicted chromatic contrast was used in our behavioral experiments.

Behavioral Experiments

We conducted 2 experiments, one involving a stationary RC aircraft and another with the same aircraft flying toward the birds. Both experiments were conducted in

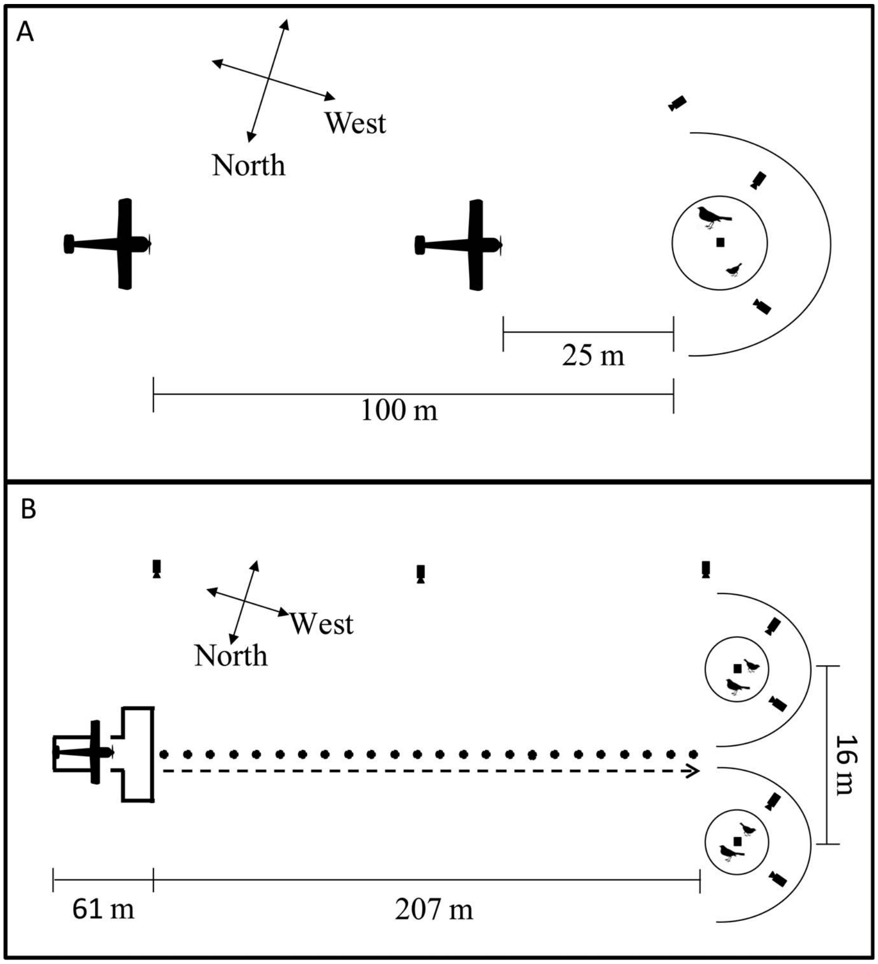

FIGURE 1. (**A**) Experimental setup for the stationary-aircraft experiment. The aircraft silhouettes represent the 2 distances (25 m or 100 m from the enclosure) where the RC aircraft was located. The circle represents the enclosure housing 2 individuals. Also shown are the locations of the cameras. (**B**) Experimental setup for the moving-aircraft experiment. The T-shape represents the takeoff–landing strip, and the dashed arrow line represents the approach path. The filled circles are the distance markers used to locate the aircraft during approach (separated by 9 m). The larger open circles represent the enclosures (each housing 2 birds). Also shown are the locations of the cameras.

seminatural conditions in a grass field in Tippecanoe County, Indiana, near Purdue University Airport (latitude: 40°24′N, longitude: 86°56′W). Trials were performed between May and November 2012, from 0730 to 1200 hr under calm weather conditions (i.e. wind speeds under 16 km hr^{-1}, no precipitation, and no fog). During the trials, we held the birds in 2 circular enclosures made of hardware cloth (mesh with 0.912-mm wire; height = 38.1 cm, radius = 40 cm). Before each trial, we spread fresh sawdust and ~5.0 g of white millet on the base of the enclosure. Black landscape fabric was used to screen out the sides and back of the enclosure (Figure 1A, 1B). Three cameras were used to monitor the enclosure, 1 from 1.5 m above and 2 from behind (1 m away; Figure 1A, 1B). 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 synchronized.

We used an electrically powered RC aircraft (Tower Trainer 40 wing on a fuselage similar to that of the Tower Trainer 40; Tower Hobbies, Champaign, Illinois, USA) for both experiments. The aircraft had a wingspan of 157.5 cm and fuselage length of 130.8 cm. We mounted high-contrast LED lights (7.4 mm; 3.5 cd per LED light) on the underside of each wing. For the continuous treatment, the lights on the aircraft were continuously on; for the pulsing treatment, the lights were alternatively pulsing at a rate of 2 Hz. This pulse frequency falls within the range of frequencies deemed safe for civilian aircraft pilots (Rash 2004).

We considered other factors that could affect the responses to the aircraft: aircraft speed, ambient light conditions, and ambient noise. In humans, approach speed affects the perception of a looming stimulus, with an increase in speed decreasing the ability to track a looming object (Wann et al. 2011). This may also hold true for birds, because they are more likely to be struck on roads with higher speed limits (Farmer and Brooks 2012, Legagneux and Ducatez 2013). This suggests a perceptual constraint on the ability of birds to determine the time to contact with a fast-approaching object (DeVault et al. 2014). Additionally, ambient light conditions can influence the probability of detecting an approaching object (Blackwell et al. 2009b).

Stationary-Aircraft Experiment Setup

This experiment allowed us to determine whether cowbirds changed their behavior in response to a stationary RC aircraft with pulsing or continuous lights, compared with the same RC aircraft with the lights off. The occurrence of a behavioral change in response to the lights when the aircraft was not moving allowed us to establish indirectly whether the animals would pay attention to these lights. We used 92 cowbirds, which were randomly assigned to 46 pairs (male–male or female–male). This experiment consisted of 2 independent factors, light treatment (lights off, continuous lights, and pulsing lights at 2 Hz) and distance to stationary aircraft (25 m and 100 m), resulting in 6 treatment combinations.

Pairs of birds were exposed to the aircraft in each trial (Figure 1A). We exposed 16 pairs of birds to the lights-off treatment, 15 pairs to the continuous-lights treatment, and 14 pairs to the lights-pulsing treatment. Twelve individuals, evenly distributed across all treatments, did not exhibit any response to the aircraft and, thus, were not included in the analysis. In addition to the camcorders recording the enclosure, a camcorder was placed ~10 m away from the experimental area to focus on the stationary RC aircraft (Figure 1A). Individuals were placed in the enclosure and allowed to acclimate and forage for 3 min before we started recording their behavior in each of the 3 treatments for 3 min. We measured wind speed (0.0–10.5 km hr^{-1}) and ambient light intensity (4,500–58,300 lux) immediately prior to stimulus presentation.

Moving-Aircraft Experiment Setup

This experiment was designed to assess how cowbirds responded to an approaching RC aircraft with different light treatments. For this experiment, we used 140 cowbirds that were assigned randomly to 70 pairs. To increase the number of birds exposed to the aircraft per trial, we had 2 enclosures (with 2 birds in each) separated by a visual barrier (Figure 1B). Each pair of naive birds was exposed to 1 of the following 3 treatments: (1) lights off, (2) continuous lights, or (3) pulsing lights (2 Hz). We exposed 20 pairs of birds to the lights-off treatment, 22 pairs to the continuous-lights treatment, and 28 pairs to the lights-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, deviations in its trajectory due to strong crosswinds, and aircraft crashes.

A trial began by simultaneously releasing a pair of birds into each of the enclosures. Each pair was allowed to acclimate for 5 min. Then the aircraft took off and flew above the approach path ~6 m above ground level until it reached the enclosures (see details in Appendix). The aircraft then ascended to ~40 m and circled back to the takeoff strip to land. The trials ended 5 min after the aircraft landed. Wind speed (0.0–13.1 km hr^{-1}), light intensity (8,000–81,200 lux), and sound intensity (55.7–76.3 dB as the aircraft flew over the enclosure) were measured during the trials.

Behavioral Coding

Virtual Dub version 1.9.11 (http://www.virtualdub.org/) was used for frame-by-frame analysis. The behavior of each individual in the enclosure was measured separately in both experiments. Each individual was examined for 1,000 frames before onset of the stimulus to establish its routine behavior. The first alert-related change in behavior after stimulus onset was recorded. The most common alert behavior observed was stretched neck, followed by head-up movements and crouching. Stretched neck occurred when birds elevated their head and neck while in a head-up body posture (beak held parallel to the ground). Head-up movements occurred when birds moved their heads sideways in head-up body postures. Crouching occurred when birds lowered their whole bodies close to the ground. We also observed and recorded body movement toward the aircraft (i.e. the bird moved its body in the enclosure toward the approaching aircraft), body movement away from the aircraft (i.e. the bird moved its body in the enclosure away from the approaching aircraft), and flushing behavior (i.e. the bird moved its body off the ground to begin a flight). The Appendix provides further descriptions and schematics of the observed behaviors.

In the stationary-aircraft experiment, we examined the videos to determine the frame when the first individuals in the enclosures began to forage (i.e. first peck) and the frame of stimulus onset (i.e. when the aircraft lights were turned on). For the stimulus onset in the lights-off treatment, which was meant to establish the routine alert behavior, we used the frame of 3 min after the first peck, because the stimulus was presented 3 min after the first peck in the pulsing-lights and continuous-lights treatments. We measured the amount of time it took each bird to become alert after the stimulus onset at the different distances (latency to alert). Latency to alert was measured from the onset of the stimulus; thus, smaller values indicate a quicker response. There were 13 of the 92 individuals for which we could not determine their alert behavior (Appendix) from the videos (5 for lights off, 3 for continuous lights, and 5 for pulsing lights). These 13 individuals were not included in the analysis.

In the approaching-aircraft experiment, we measured alert and avoidance responses. We defined "alert" as the first change in behavior indicative of an alert response. These alert-behavior changes included head-up movement, stretched neck, crouch, or body movement toward the aircraft. We defined "avoidance" as the first change in behavior indicative of an avoidance or escape response. To determine the alert and avoidance frames, the individual was watched frame-by-frame for 1,000 frames to establish routine behavior before the aircraft took off. We then measured the first frames when alert and avoidance responses were observed. Our study focused on alert and avoidance behaviors, so our analyses did not include individuals that did not show those behaviors.

In the moving-aircraft experiment, we used frame-by-frame analysis to determine the aircraft speed. Using 2 camcorders along the flight path, we measured the frames in which the aircraft began the approach and reached the enclosures (i.e. expected collision frame). Using these 2 frames and knowing the distance between the take-off strip and the enclosures (207 m), we calculated the speed of the aircraft using the equation

$$\frac{207\ \mathrm{m}}{\left(k^{*}\frac{1}{\mathrm{fps}}\right)-\left(a^{*}\frac{1}{\mathrm{fps}}\right)}$$

where k is the frame in which the aircraft reached the position of the enclosures, fps is frames per second, and a is the frame in which the aircraft began the approach (see Figure 1). Average speed (± SE) was 17.84 ± 2.66 m s^{-1}. During 4 trials, the camcorder near takeoff malfunctioned and we were unable to determine the exact frame when the aircraft began the approach. In these cases, we used a camcorder in the middle of the flight path to determine a known location and used that known distance, rather than the 207 m mentioned above.

We then calculated the time it would take the RC aircraft to reach the individual after showing the first alert and avoidance responses. This time to "collision" (TTC) was calculated using the equation

$$\frac{k-f}{\mathrm{fps}}$$

where f is either the frame at alert or the frame at avoidance, depending on which "collision" time was calculated (k and fps are as defined above). We established 2 variables: TTC_{alert} and $TTC_{avoidance}$ (defined above). Higher values of time to collision at alert and at avoidance indicate that the individual responded earlier during the aircraft's approach.

Statistical Analysis

We used a generalized linear mixed model (GLMM) to analyze the latency to alert (continuous response variable) in the stationary-aircraft experiment, in which we included light treatment (lights off, pulsing lights, continuous lights), distance to the aircraft (25 m 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 an individual showing alert behavior over a 30-s period (binary response variable). To that end, we scored whether individuals showed any kind of alert response (1) or not (0). In this model, we also included ambient light intensity and wind speed as covariates.

We used GLMMs to assess the factors affecting TTC_{alert} and $TTC_{avoidance}$. We included in the models light treatment, aircraft speed, ambient light intensity, ambient noise, and wind speed. We also included the interaction between ambient light intensity and light treatment, because a similar effect influenced cowbirds' responses to vehicle approach in a previous study (Blackwell et al. 2009b). Additionally, we tested for an interaction between light treatments and aircraft speed, because different vehicle speeds could potentially enhance or decrease the perceptual limitations to detect objects (DeVault et al. 2014). In these models, we included the average response from each individual used in the trials, but we added enclosure as a random subgroup to control for the 2 enclosures tested per trial. We used t-tests to assess pairwise differences between treatments.

In the GLMMs, we used backward stepwise selection procedures, and backward elimination for factor selection based on F statistics. When interactions were significant, we kept in the models the individual factors that were interacting. Results are reported as means ± SE.

RESULTS

Visual Contrast of Lights

Across all ambient light conditions, chromatic contrast was lower when the aircraft was close than when it was far for the 525-nm, 585-nm, 595-nm, and 635-nm LED lights; however, 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). Because the 470 nm light was the most conspicuous one for the cowbird visual system, we used this wavelength for our behavioral experiments.

TABLE 1. Chromatic contrast values of LED lights of different wavelengths from the visual perspective of Brown-headed Cowbirds. Chromatic contrast was calculated when the aircraft was at 2 locations on the approach path (25 m and 100 m) and under 3 different ambient light treatments (sunny days, cloudy days, and partly cloudy days). Values are given in just noticeable distances (JND). The higher the visual contrast value, the greater the conspicuousness of the object in relation to the visual background. Numbers in bold indicate the wavelength with the highest conspicuousness in each ambient-light scenario.

	470 nm	525 nm	585 nm	595 nm	635 nm
Sunny					
Far aircraft	187.6	144.2	64.4	152.0	148.3
Close aircraft	**199.1**	137.7	50.5	135.8	136.1
Cloudy					
Far aircraft	179.5	150.4	76.0	164.6	157.3
Close aircraft	**196.8**	139.3	52.6	139.1	137.9
Partly cloudy					
Far aircraft	186.4	143.8	67.2	153.7	151.8
Close aircraft	**200.3**	138.5	51.3	135.6	137.3

Stationary-Aircraft Experiment

The time that it took cowbirds to show alert behaviors in response to a stationary RC aircraft varied significantly with the type of treatment ($F_{2,\ 39.6} = 20.5$, $P < 0.001$; Figure 2A). Cowbirds showed alert behaviors more quickly in response to the stationary RC aircraft with the continuous lights ($t_{39.4} = 4.9$, $P < 0.001$) and with the pulsing lights ($t_{39.8} = 5.9$, $P < 0.001$), compared with the baseline alert behavior recorded when the lights were off (Figure 2A). We did not find significant differences in the latency to alert between continuous lights and pulsing lights ($t_{39.4} = 1.2$, $P = 0.23$). All other factors were not included in the model after the backward elimination procedure.

Additionally, we found a significant light-treatment effect on the probabilities of cowbirds showing alert behavior in response to the RC aircraft ($\chi^2_2 = 39.21$, $P <$ 0.001), with >75% probability of birds reacting to the pulsing lights and the continuous lights, compared with ~15% probability when the lights were off (Figure 2B). All other factors were not included in the final model.

Moving-Aircraft Experiment

Time to collision at alert (TTC_{alert}) was significantly affected by light treatment ($F_{2,\ 40.7} = 15.2$, $P < 0.001$) and aircraft speed ($F_{1,\ 41.2} = 18.4$, $P < 0.001$). However, these independent effects on TTC_{alert} cannot be interpreted separately given that both light treatment and aircraft speed interacted significantly ($F_{2,\ 40.9} = 12.4$, $P < 0.001$). When the lights were off, we found a strong and significant speed effect (slope = –1.02 ± 0.19, $R^2 = 0.67$; $t_{38.8} = 5.3$, $P < 0.001$), whereby cowbirds took significantly longer to alert when the RC aircraft approached at higher speeds (Figure 3A). When the lights were pulsing, the negative speed effect on TTC_{alert} was still significant, but its strength decreased (slope = –0.74 ± 0.22, $R^2 = 0.37$; $t_{44.8}$ = 3.3, $P = 0.002$; Figure 3B). However, when the lights were continuously on, there was no significant relationship between TTC_{alert} and speed (slope = 0.26 ± 0.19, $R^2 =$ 0.07; $t_{39} = 1.4$, $P = 0.17$; Figure 3C), which suggests that the aircraft-speed effect vanished. No other factors were included in the model.

Time to collision at avoidance ($TTC_{avoidance}$) was affected significantly only by ambient noise levels when the aircraft flew over the enclosures ($F_{1,\ 45.3} = 5.0$, $P =$ 0.03). Higher ambient noise levels significantly delayed cowbird avoidance responses to the RC aircraft approach (slope = –0.07, $R^2 = 0.10$; $P = 0.02$). No other factors were included in the model. Ambient noise levels and aircraft speed were marginally correlated ($r = 0.36$, $P = 0.06$).

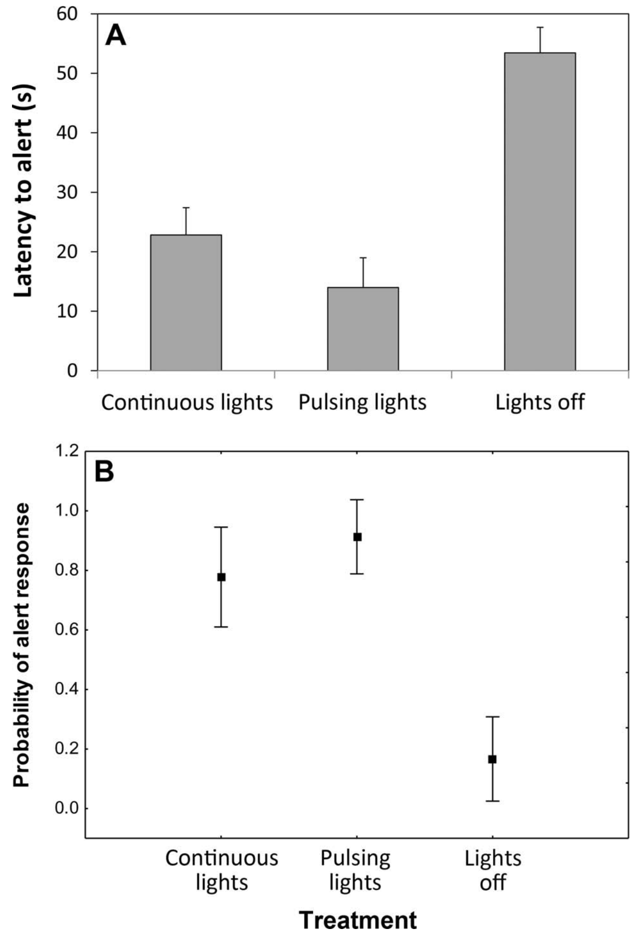

FIGURE 2. Cowbird (**A**) latency to alert (higher values indicate more delayed responses) and (**B**) probability of showing alert behavior within 30 s in response to a stationary RC aircraft under different treatments: aircraft with continuous lights, pulsing lights, and lights off.

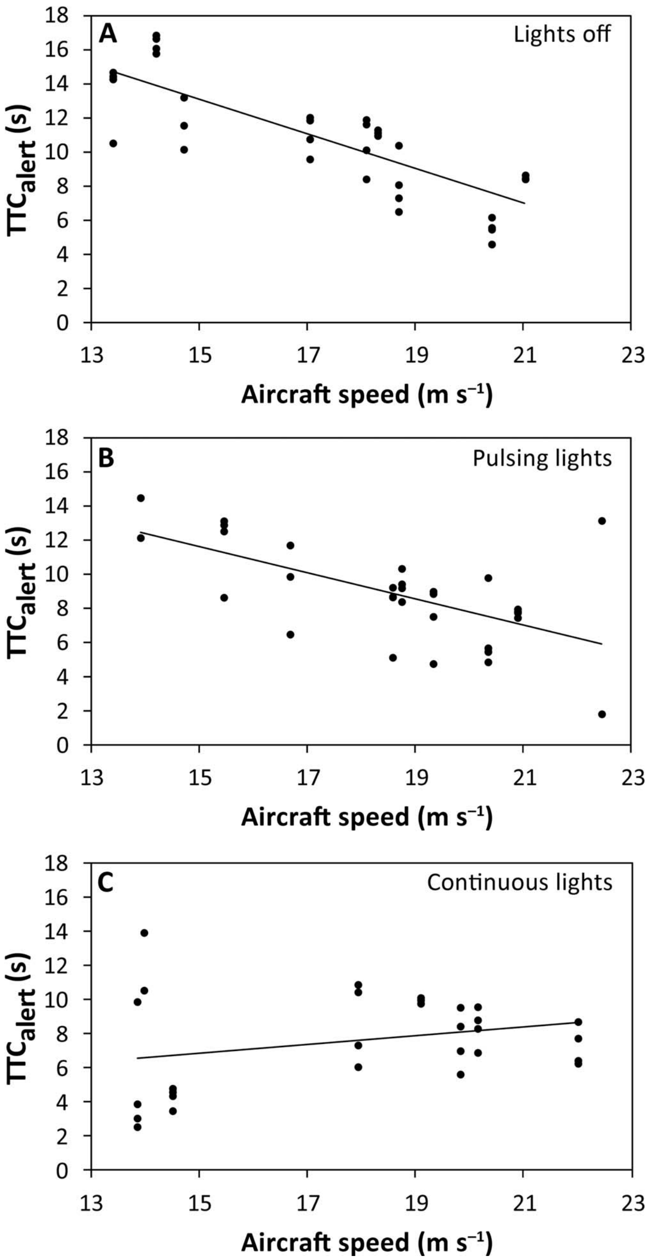

FIGURE 3. Time to collision (TTC) when Brown-headed Cowbirds became alert to an approaching aircraft with varying speeds. Lights mounted on the aircraft were (**A**) off, (**B**) pulsing, or (**C**) continuous. Higher values indicate a quicker response.

DISCUSSION

The use of perceptual models is common in visual and behavioral ecology (Maia et al. 2013), particularly in the context of mate choice and predator–prey interactions (Stevens 2013). By using species-specific visual physiology information (i.e. sensitivity of the visual pigments and oil droplets, and relative density of cone photoreceptors; Fernández-Juricic et al. 2013), we reverse engineered these perceptual models to get an estimate of the most visually conspicuous wavelength for cowbirds and investigated their behavioral responses to this stimulus (Blackwell and Fernández-Juricic 2013). This step has rarely been implemented in studies aimed at developing wildlife attractants and repellents (Blackwell and Fernández-Juricic 2013). This allowed us to choose a visual stimulus that was more likely to be tuned and salient to the target species' visual system, which is particularly relevant with birds because their visual systems are different from that of humans (Cuthill 2006). For cowbirds, the commercially available LED light most conspicuous from their visual perspective was determined to be 470-nm (the "blue" portion of the human spectrum).

Cowbirds exhibited alert behaviors more quickly in response to a stationary aircraft with these lights on (both continuous and pulsing) than to the aircraft with the lights off. Additionally, with the aircraft approaching, the speed effect (i.e. delayed alert responses at higher speeds) was minimized with pulsing lights. Finally, higher ambient noise levels delayed cowbird avoidance responses to the aircraft.

Previous studies have shown that lights can affect avian behavior in daylight (Jones and Francis 2003, Blackwell and Bernhardt 2004, Blackwell et al. 2009b, 2012) and nighttime light conditions (Gehring et al. 2009, Kerlinger et al. 2010). The results of our stationary-aircraft experiment showed that cowbirds were more responsive to the RC aircraft with lights on, supporting the contention that cowbird detection behavior could be enhanced with the 470-nm lights used in the present study.

When the aircraft approached the birds, we found an effect of aircraft speed that depended on the type of light treatment. When the lights were off, cowbirds' alert responses were delayed at high aircraft speeds. In an antipredator context, predator speed enhances prey alert behaviors (reviewed in Stankowich and Blumstein 2005). However, the range of speeds of our RC aircraft was higher than the approach speeds of some aerial predators—for example, Red-tailed Hawks (*Buteo jamaicensis*; approximately 8–17 m s^{-1}; Broun and Goodwin 1943). In humans, the speed of an approaching object is a key factor in the estimation of time to collision (Kerzel et al. 1999). The responses of cowbirds to the aircraft with the lights off are not surprising, because the aircraft may have approached individuals at faster speeds than what they were capable of processing, as found in humans (Wann et al. 2011). Higher vehicle speeds increase mortality in a wide variety of vertebrates (e.g., amphibians, birds, mammals, frogs, lizards, toads, snakes; Farmer and Brooks 2012). Furthermore, DeVault et al. (2014) reported that Turkey Vultures (*Cathartes aura*) experienced more near collisions (i.e. initiating avoidance behaviors when the vehicle was $<$1.7 s away) as vehicle speed increased from 30 to 90 km hr^{-1}.

In the pulsing-lights treatment, the speed effect on alert behavior was still significant but decreased in strength. The reduced effect of speed may have come from additional information provided by the pulsing lights, because large luminance differences increase the probability of visual attention to an object (Rauschenberger 2003). If so, cowbirds may have used the light pulses to better establish the relative position of the aircraft during the approach. This is particularly likely for the slow rather than the fast aircraft approaches, because the aircraft traveled shorter distances between pulses of light at slower speeds. However, the continuous-lights treatment essentially eliminated the negative effects of aircraft speed on time to collision at alert. The aircraft with continuous lights had higher luminance per unit time because all 8 LED bulbs were on at the same time, compared with the aircraft with the pulsing lights, on which only 4 LED bulbs were on at a time. If cowbirds increased their visual attention to continuous lights rather than to the aircraft itself, this may have facilitated tracking the aircraft across the range of speeds used, potentially reducing the problem of estimating the aircraft position.

Avoidance behavior was influenced only by ambient noise: Birds had delayed avoidance behaviors to the aircraft at higher noise levels. A recent study suggested that noise can be a sensory distractor for different taxa (Chan and Blumstein 2011). Noise has been shown to negatively affect avoidance behaviors in some species (Chan et al. 2010, Wale et al. 2013). For example, shore crabs (*Carcinus maenas*) took longer to retreat when presented with noise that was 36% more intense than the background noise (Wale et al. 2013). In our experiment, it is possible that loud ambient noise may have acted as an "informational mask" (Bee and Swanson 2007, Herrera-Montes and Aide 2011) by concealing the auditory cues from the approaching aircraft. Light treatment and aircraft speed did not significantly influence avoidance behavior. One potential reason could be that the RC aircraft maintained a leveled flight (6 m above ground) throughout the approach. From the bird's perspective within the enclosure, the aircraft may have been perceived as riskier far away, but as it approached, the risk (and thus the need to take evasive action) may have decreased as it veered away from a collision course. In pigeons, for instance, time-to-collision neurons fire only when an approaching object is on a direct collision course (Wang and Frost 1992). Previous studies actually simulated a more direct approach of predators toward birds (e.g., Cresswell et al. 2003, 2009). However, our RC pilots were unable to reliably simulate a direct collision course while avoiding the risk of crashing the aircraft.

Conservation Implications

In both experiments, 470-nm lights enhanced cowbirds' behavioral responses. However, before we can make specific recommendations, future studies should test other species that are frequently involved in collisions (particularly those with body masses and visual capacities different from those of our model species). Nevertheless, the fact that cowbirds tend to have lower acuity than other, larger species (waterfowl, gulls, raptors, etc.; Kiltie 2000) involved in bird strikes suggests that lights have the potential to be detected at farther distances by these species.

Our results may have different implications for illuminating aircraft (i.e. moving lights) as well as airports (i.e. stationary lights) to potentially minimize the chances of bird strikes. One possibility is having 2 sets of lights to alter bird behavior: a set of stationary lights near the runway and a set of onboard lights. Birds became alert more quickly to stationary objects with lights on (continuous or pulsing); thus, stationary lights along runways could be synced to capture the bird's attention to aircraft taxiing. However, we caution that the perception of lights in daylight may be different from that in nighttime light conditions. For example, night migrants are more "attracted" to steady or slowly pulsing red lights than to white lights (Gauthreaux and Belser 2006), which could lead to an increase in avian mortality around structures with these light types (Gehring et al. 2009).

Because commercial aircraft move at different speeds depending on the flight phase, we suggest that onboard lights could also change with flight phase to maximize potential detectability. For instance, onboard lights could be off or pulsing as aircraft taxi (3.1–10.3 m s^{-1}). During aircraft takeoff ($\sim$27.7 m s^{-1}), continuous lights could be used because they may reduce the effects of aircraft speed on alert behavior. The use of continuous lights beyond airport property could potentially enhance avian alert behavior in response to a fast-approaching aircraft, but future research simulating the cruising speeds of commercial aircraft would be necessary to validate this suggestion.

Our approach could also be applied to other contexts to enhance the detectability of wind turbines, towers, and other large stationary structures that are involved in collisions with birds (Gehring et al. 2009, Loss et al. 2013, 2014). Although the general application is similar (i.e. lights to warn birds of a danger), the problem is slightly different because rapidly moving birds approach a stationary object and, hence, the visual demands to enhance detection may be different. For instance, Hodos (2003) found that the wind turbines move at a speed that makes them "transparent" for the retina of some bird species. Future research should consider these sensory illusions when investigating the effects of lights on stationary objects as well as explore specific parts of the spectrum that are hidden to the human eye (e.g., ultraviolet) and thus less subject to regulation.

ACKNOWLEDGMENTS

We thank R. Needham and C. Meyer for flying the RC aircraft during the behavioral experiments, and T. Snyder and C. Wall for custom-building the light-control system in the aircraft fuselage.
Funding statement: Our research was supported by the Charles A. and Anne Morrow Lindbergh Foundation, Purdue University, and the USDA.
Ethics statement: All bird housing, handling, and experimental procedures were approved by the Purdue Animal Care and Use Committee (protocol 1201000582).

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APPENDIX

Perceptual Modeling of LED Lights

Irradiance and reflectance were measured using a StellarNet EPP2000 portable spectroradiometer (StellarNet, Tampa, Florida, USA). Irradiance was measured at the height of the cowbird head and at a 90° angle parallel to the ground in the 4 cardinal directions and pointed 90° up toward the sky. We averaged the irradiance measurements (Watts m^{-2}) to obtain 1 measurement for each wavelength, which was converted from Watts m^{-2} to $\mu Mol m^{-2}$ s^{-1} nm^{-1} for the visual contrast model.

With our experimental approach (aircraft approaching animals in an enclosure), cowbirds experienced different background elements that potentially affected aircraft contrast. Therefore, we video-recorded the approach of the RC aircraft in our study area from the cowbird's point of view to define these elements. Our background reflectance measurements included the sky, a tree line, grass, and the aircraft. We averaged the reflectance of these different components considering their relative proportions, based on the video. Reflectance of the sky was taken at cowbird head height with the probe angled upward at a 45° angle. Reflectance of the tree line was taken at the same height but with the probe held at a 90° angle toward the trees. Reflectance of the ground was taken with the reflectance probe pointed toward the ground. The aircraft was multicolored, so we decided to take reflectance measurements for all the colored sections to account for the visual complexity of the stimulus. We averaged these reflectance measurements, taking into account their relative proportions (approximately 68% white, 14% red, 7% blue, 4% exposed wood, 4% black, 1% gray, 1% silver, and 2% yellow). We then calculated the proportional size of the aircraft in relation to the sky when the RC aircraft was

TABLE 2. Observed alert responses of Brown-headed Cowbirds when presented with a static and an approaching aircraft, and avoidance reactions when presented with an approaching aircraft.

Behavior	Description
Alert	
Head-up movement	Move head while in a head-up body posture (beak held parallel to the ground) (Figure 4A).
Stretched neck	Elevate head with neck while in a head-up body posture. The head position does not move (Figure 4B).
Body movement toward aircraft	Move body from one location to another in the enclosure by walking or hopping toward the front of the enclosure (Figure 4C).
Crouch	Lower whole body close to the ground (Figure 4D).
Avoidance	
Body movement away from aircraft	Move body from one location to another in the enclosure by walking or hopping toward the back of the enclosure (Figure 4C).
Flush	Move body off the ground to begin flight (Figure 4E).

at 2 locations (a far distance, about 50–100 m, and a close distance, about 5–15 m) from the birds' position. The final background reflectance measurement included the weighted proportion of the aircraft at the 2 distances as well as the weighted proportion of the sky, tree line, and ground.

To choose the candidate light spectra for the behavioral experiments, we were restricted by the viewing angle of the commercially available ones. Because we were interested in having the birds see the lights from the ground (i.e. below the aircraft), we chose lights with a wide viewing angle (70°) and high light intensity (>3.5 cd per light). We found LEDs that met these criteria and obtained matching light spectra for these wavelengths from CoolLED, Andover, UK (http://www.coolled.com/). We used 5 LED light wavelengths (470, 525, 585, 595 and 635 nm) that are representative of different portions of the wavelength range of the spectrum that birds can perceive and that were commercially available for use.

We fitted individual curves to match those from the available light spectra 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 the chromatic contrast of each light at the 2 distances from a bird's position to establish which light would have the greatest conspicuousness from the cowbird's perspective. Chromatic contrast is calculated in units of "just noticeable differences" (JND), where values >1 suggest that the object can be discriminated from the background (Vorobyev and Osorio 1998). In our behavioral experiments, we used the LED light with the highest chromatic contrast.

Behavioral Experiments

Details of the design. The enclosure had a wooden base with a grid of 3-cm-high plastic tubes, separated by 8 cm from one another, which were spray painted green to mimic a grassy substrate (following Cresswell et al. 2003). We used a PelikanCam CRM-36DW B&W weatherproof infrared camera ("bulletcam") above the enclosure and 2 JVC Everio (GZ-MG330AU) camcorders behind the enclosures. LED lights (7.4 mm; 3.5 cd per LED light) on the wing were separated by 1.03 m facing toward the front of the aircraft. Four LED lights were clustered side-by-side (2 on the top and 2 on the bottom) on each side of the wing. A lithium polymer 4-cell battery pack powered the RC aircraft, both sets of lights, and the engine. We installed a custom-built circuit in the fuselage of the aircraft that allowed the pilot to control the lights (lights off, continuous lights, pulsing lights). The RC aircraft was operated by 2 experienced pilots.

Moving-aircraft setup. The aircraft took off from a grass strip that was centered 207 m away in front of the 2 enclosures. The pilot was located on the takeoff strip, and a camcorder operator was located to the side of the approach pathway, halfway between the enclosures and the takeoff strip. The approach path was oriented so that the aircraft flew in a southwest trajectory to reduce the effect of crosswinds. A camcorder was situated perpendicular to the flight path ~50 m from the enclosures to observe when the aircraft flew over them. A second camcorder was placed 102 m in front of the enclosures 50 m off perpendicular to the flight path. 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 takeoff strip, ~50 m perpendicular to the flight path to record when the aircraft took off and began the approach. All camcorders were synchronized as described above. Markers were placed every 9 m, parallel to the flight path. These markers were used to calculate the speed of the aircraft for each trial. The pilots intended to keep similar aircraft speeds across trials, but this was challenging because of variations in environmental conditions (e.g., wind speed) that forced pilots to adjust thrust to avoid crashing. However, aircraft speed did not vary significantly between light treatments ($F_{2,\,22} = 0.9$, $P = 0.41$).

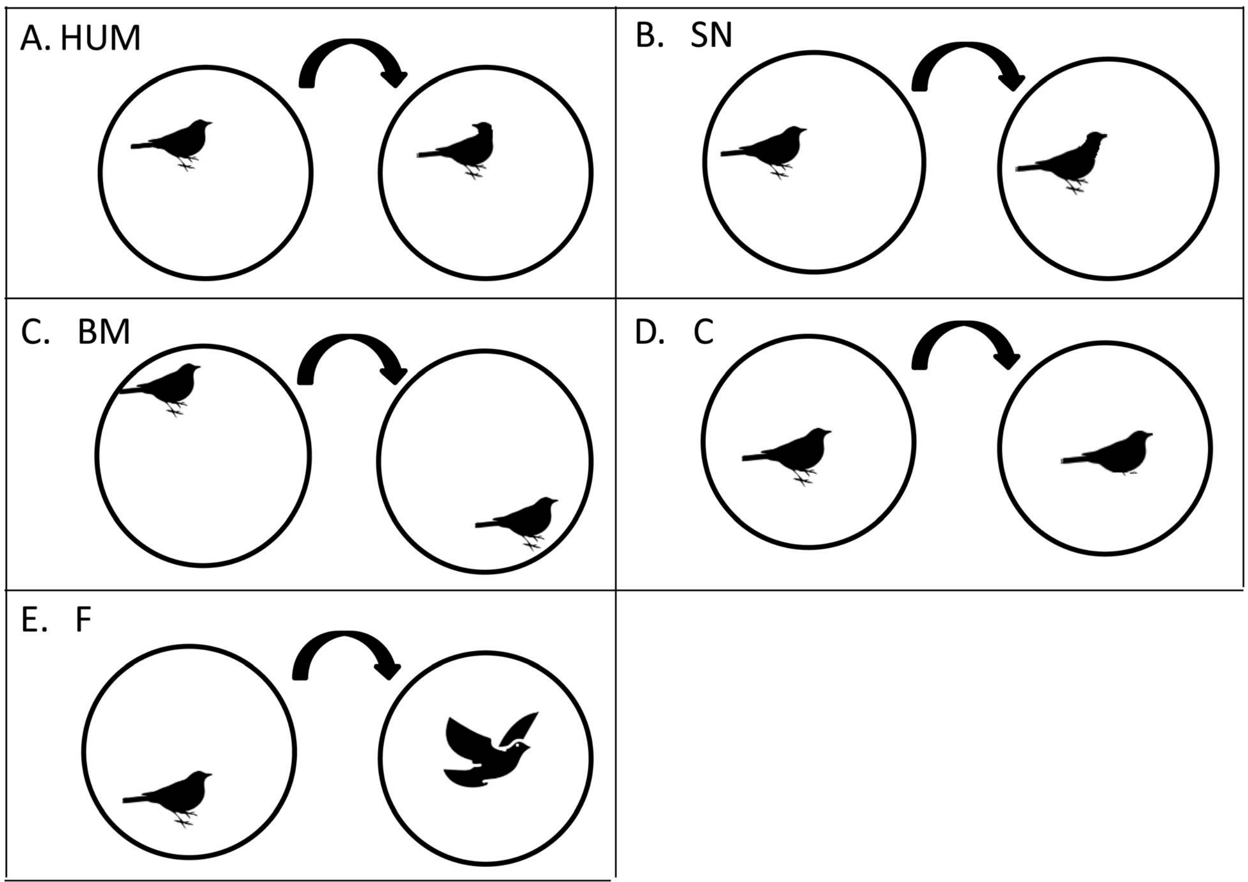

FIGURE 4. A visual representation of alert and avoidance behaviors seen during the moving-aircraft experiment: head-up movement (HUM), stretched neck (SN), body movement (BM), crouch (C), and flush (F). These behaviors are described in Table 2.

Behavioral Analysis

Static-aircraft experiment. We coded when the individual became alert to the stimuli using frame-by-frame analysis. Common behaviors were stretched neck, head-up movement, and crouch (for descriptions of the behaviors observed, see Appendix Table 2; for their schematic representation, see Appendix Figure 4). We did not code avoidance behaviors, because the individuals did not avoid the static stimuli.

Moving-aircraft experiment. We coded when the individual became alert (frame at alert response) to the stimulus and when the individual avoided (frame at avoidance 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, body movement toward the aircraft, and crouch). Frame at avoidance response was recorded when the individual changed its behavior to avoid the approaching aircraft (either body movement away from the aircraft or flush; e.g., Blackwell et al. 2009b; see Appendix Table 2 for details). Individuals that did not exhibit an alert or avoidance response were not included in the analyses.