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Avian visual system configuration and behavioural response to object approach

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Antipredator behaviour theory provides a framework to understand the mechanisms behind human–wildlife interactions; however, little is known about the role of visual systems in the responses to humans. We quantified responses of brown-headed cowbirds, *Molothrus ater* (Boddaert), and mourning doves, *Zenaida macroura* (Linnaeus), to object approach (a ground-based vehicle) and vehicle lighting regimen, and we examined two visual properties (visual acuity and visual fields) that could influence antipredator behaviour. Brown-headed cowbird groups exposed to vehicle approach and constant illumination of the vehicle-mounted lamp showed alert behaviour earlier than did groups exposed to pulsating treatments or no lamp. Interestingly, light treatments interacted with ambient light; cowbird alert response occurred sooner under sunny conditions and constant illumination of the lamp. Mourning doves were not affected by light treatments. Between species, mourning dove groups had a quicker alert response (and slower flight response) than brown-headed cowbirds. Visual acuity was higher and the visual field was wider in mourning doves than in brown-headed cowbirds. We speculate that brown-headed cowbirds might flush sooner to reduce predation risk costs associated with a relatively lower ability to visually track a given object. Our findings have theoretical and applied implications, as our model species belong to families that show different antipredator responses, and provide insight as to how object lighting might be used to reduce bird–structure/vehicle collisions, an increasing source of mortality in birds.

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The interplay between animal behaviour and conservation biology has facilitated learning about basic behavioural mechanisms (e.g. mating systems, antipredator strategies, habitat requirements) that can have a direct application to the protection (e.g. species of conservation concern) and management (e.g. nuisance species) of wildlife (e.g. Sutherland 1998; Buchholz 2007). For instance, the framework of antipredator behaviour theory has been used to address not only basic (e.g. Lima 1998), but also applied questions (e.g. Frid & Dill 2002). In an applied context, antipredator behaviour allows us to understand the mechanisms behind the responses of wildlife to different types of human activities. Here, the assumption is that birds use strategies to respond to human disturbance that are similar to those used when reacting to a predator, which has been corroborated empirically (e.g. Frid & Dill 2002; Møller et al. 2008). This mechanistic approach can help predict reactions of different species based on variations in ecological conditions and life history traits (Blumstein 2006).

Two factors that can influence interspecific variations in antipredator responses are the size and shape of detection windows: areas around an animal where the probabilities of detecting objects are higher (Blumstein et al. 2005). Characterizing detection windows can help us understand between-species variations in detection and reaction times to different types of objects with which animals interact on a regular basis (e.g. conspecifics, predators, recreationists, vehicles, etc.). Different visual properties could affect the configuration of detection windows. For example, visual acuity (the ability to distinguish two objects as separate) can influence the distance at which a bird resolves an object (Kiltie 2000), and potentially the size of the detection window of a species. Furthermore, the configuration of the visual fields determines the volume of space around the head from which visual information can be obtained at any given moment (Martin & Katzir 2000). The width of the visual field can potentially affect the shape of the detection window, depending upon body posture and head orientation in relation to an object (Fernández-Juricic et al. 2004a).

Visual detection of an object also depends on ambient light conditions, the contrast between the object and the background,

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and the looming effect (see Dittrich & Lea 2001). A measure of temporal resolution that has been used with several avian species is the critical fusion frequency (CFF), the point at which a time-varying stimulus just appears to be steady instead of flickering (Powell & Smith 1968; Jarvis et al. 2003). Species-specific CFFs are intensity (contrast) dependent, with higher CFFs under brighter light intensities (Powell & Smith 1968). Furthermore, contrast sensitivity, the ability to discriminate between adjacent stimuli (e.g. an approaching object and the surrounding environment) is affected by ambient light conditions and distance to the object (Ghim & Hodos 2006). Finally, the symmetrical expansion of an object's image (looming) on the avian retina is a critical variable in determining whether an object is on a collision course (see Gibson 1966, 1979; Wang & Frost 1992; Sun & Frost 1998). Large, expanding flow-fields might precipitate manoeuvres such as turning or landing (Wang & Frost 1992).

Understanding the factors limiting (or enhancing) the responses of species with different visual systems can have implications for manipulating their behaviour in applied contexts (e.g. reducing the frequency of human–wildlife interactions). In this study, we questioned whether a lighting regimen might enhance detection of (and reaction to) the approach of a ground-based vehicle in two species with different visual sensory constraints. Our goal was two-fold. First, we assessed between-species differences in two visual properties related to detection windows: visual acuity and configuration of visual fields. Second, we quantified species-specific behavioural responses to the approach of a vehicle and lighting regimen. We conducted our experiments under semicontrolled conditions, and we used two model species, brown-headed cowbirds, *Molothrus ater* (Boddaert), and mourning doves, *Zenaida macroura* (Linnaeus).

We chose these model species for several reasons. First, they belong to families that have different antipredator behaviours (e.g. Lima 1993), which allowed us to explore whether there might be an association (not causation) between detection and response behaviours, and visual acuity and visual fields (Fernández-Juricic et al. 2004a). Second, both species are ground foragers and, consequently, the receptors involved in motion detection are likely to be distributed in similar areas of the retina (Hart 2001), which minimizes the biases associated with the detection of an approaching object. Third, both species belong to families (Icteridae and Columbidae) that are frequently involved in bird–aircraft collisions (e.g. bird strikes; Allan 2002; Dolbeer & Wright 2008). Furthermore, bird collisions with communication towers have resulted in as many as 2000 mortalities annually at some structures (Evans et al. 2007), and collisions with static structures and vehicles result in approximately 500 million bird mortalities annually in the U.S.A. (Erickson et al. 2005).

This study has implications for predator–prey interactions, as we quantified visual properties that could influence the costs of gathering personal and social information about a threat (e.g. Fernández-Juricic et al. 2004b). Our approach is novel in that we combined key factors in avian visual cognition (vision and behaviour; Lea & Dittrich 2000; Dittrich & Lea 2001) to better understand the mechanisms involved in avian responses to object approach and, particularly, the visual signals that could enhance avoidance responses. Consequently, although our study revolves around a basic question, it has realistic conservation applications, such as reducing bird collisions with aircraft (Dolbeer 2006; Dolbeer & Wright 2008), communication towers (Manville 2000; Evans et al. 2007), wind turbines (Drewitt & Langston 2006) and other vehicles (Erickson et al. 2005).

METHODS

Study Area

We conducted our study at California State University, Long Beach, and the National Aeronautic and Space Administration's (NASA) Plum Brook Station (PB), Erie County, Ohio, U.S.A. (41°22′N, 82°41′W). The 2200 ha PB is enclosed by a 2.4 m high chain-link fence with barbed-wire outriggers. Habitat within PB differs from the surrounding mix of agricultural and suburban area, comprising canopy-dogwood (*Cornus* spp.; 39%), old field and grasslands (31%), open woodlands (15%) and mixed hardwood forests (11%) interspersed by abandoned and actively used structures relating to NASA and prior operations, and paved roads that circle and bisect the station. Plum Brook Station has restricted public access.

Bird Capture and Maintenance

We captured 336 male brown-headed cowbirds on PB (27 March–29 June 2006) by using decoy traps. We held the birds in $2.4 \times 2.4 \times 1.8$ m cages in an outdoor aviary on the station, where they received black oil sunflower, millet, grit and water ad libitum. We live-trapped 240 mourning doves by using walk-in traps on PB and Cleveland Hopkins International Airport, Cleveland, Ohio (03 July–08 September 2006). We transferred the birds to $2.4 \times 2.4 \times 1.8$ m cages in the outdoor aviary on the station. The birds were maintained on millet, cracked corn, safflower, black oil sunflower, grit and water ad libitum. Because of limited availability of mourning doves, our experimental groups of doves comprised adults and, probably, juvenile birds. However, we considered that possible variation in experience with ground-based vehicles had a negligible effect on our results because all individuals were captured from areas with active roads.

We also captured 16 brown-headed cowbirds and 15 mourning doves to characterize visual acuity and visual fields. These birds were captured in decoy traps from populations in Los Angeles and Orange Counties, California, U.S.A. Different numbers of individuals were used for the different visual physiology procedures (see below). Animals were housed on the California State University Long Beach Animal Research Facilities with two to four birds per cage (0.80×0.55 m $\times$ 0.60 m). The birds were kept on a 12:12 h light:dark cycle at approximately 25°C. Food and water was provided ad libitum. Brown-headed cowbirds were fed mixed birdseed (Royal Feeds Leech, Feed, and Milling Co., Downey, CA), whereas mourning doves were fed dove mix (Black Smith's Corner Feed Store, Bellflower, CA).

Visual Acuity

We estimated visual acuity based on the density of retinal ganglion cells (see formula below). Pettigrew et al. (1988) concluded that the use of retinal ganglion cell density as a proxy of visual acuity is appropriate under certain conditions (e.g. species with a defined area of high concentration of ganglion cells, etc.). We met these conditions (see below). Furthermore, Reymond (1985) noted a close correspondence between behavioural (via a two-choice discrimination task) and anatomical measures (photoreceptor distribution) of visual acuity, and linked the spatial resolving power of the retina to the distribution of ganglion cells involved in spatial processing (see also Martin 1986a). Similarly, avian use of frontal or lateral viewing areas in response to static, slow moving or rapidly moving objects is related to foveal densities of photoreceptors and retinal ganglion cells (Maldonado et al. 1988; Wathey & Pettigrew 1989; Hodos et al. 2002; Gaffney & Hodos 2003).

We used five brown-headed cowbirds and four mourning doves. From each individual, we extracted one retina, except for one mourning dove from which both the left and right retinas were extracted. We attempted to extract both retinas from each individual; however, sometimes the retinal tissue ruptured making it unusable to characterize cell density in specific parts of the retina. Overall, we studied three left and two right retinas for brown-headed cowbirds and four right and one left retinas for mourning doves. Animals were euthanized with CO_2, eyes were immediately extracted, and eye axial length was measured using digital calipers. We multiplied the eye axial length by 0.6 to estimate the average posterior nodal distance (PND, distance between the back of the lens and the anterior reflective surface of the retina; Reymond 1985), following Hughes (1977), Martin (1993) and Boire et al. (2001).

We hemisected eyes and placed the posterior portion in 2.5% gluteraldehyde in 0.1 M solution of Sorensen's Phosphate Buffer at a pH of 7.2 for 5 min. After rinsing the posterior portion of the eye (pH 7.2), we dissected the retina out and placed it in 4% paraformaldehyde for at least 24 h, then rinsed it in Phosphate Buffered Saline (PBS). We made radial cuts to allow the retina to lay flat on a gelatinized slide with a coverslip on top, then placed the slide in a vessel containing a few drops of formalin and placed the vessel on a hot plate at 50°C for 2 h to ensure that the retina adhered to the slide. The retina dried in the vessel for another 24 h (following Stone 1981; Hart 2002).

We cleared the retina for 20 min with Histo-Clear® (National Diagnostics, Atlanta, GA, U.S.A.), and rinsed it twice in 100% ethanol (2 min each). We then placed the retina in the following sequence of solutions for 2 min each: 95% ethanol with a few drops of glacial acetic acid, 80% alcohol, 70% alcohol, and distilled water with a few drops of glacial acetic acid. The retina was then immersed in 0.25% cresyl violet for approximately 6 min depending on the quality of the staining achieved, as cresyl violet strength changes over time (D. Lee, personal communication). After staining, we rinsed the retina in distilled water with drops of glacial acetic acid, dehydrated it in 70% ethanol and 80% ethanol (30 s each) and placed it in 95% ethanol with drops of acetic acid (60 s), then rinsed it twice in 100% ethanol (60 s each), differentiated the tissue in 95% ethanol with drops of acetic acid (1 min) and performed two quick rinses in 100% ethanol, and placed it back in Histo-Clear for two 10 min rinses (Stone 1981; Boire et al. 2001; Hart 2002). We coverslipped the retina out of Histo-Clear and allowed it to dry for at least 3 days. The excess mounting media was cleaned off the slide using Histo-Clear on a cotton swab.

Adherence of the retina onto the gelatinized slide was meant to reduce shrinkage (Hughes 1977; Stone 1981). However, measurements of retinal area were made before and after processing to determine the correction factor to account for tissue shrinkage using ImageJ area function (http://rsb.info.nih.gov/ij). When tissue shrinkage occurred, we adjusted the area of each picture to reflect the original retina size by estimating a percentage change in tissue size. The area captured in the photographs was 0.022 mm^2, so the correction was $0.022 + (0.022 \times \%$ shrinkage). The density of cells was then calculated by dividing the number of cells in each photograph by the corrected tissue area in each picture.

Stained ganglion cells were then examined under the microscope at 400× power. A 1×2 mm grid was drawn on the coverslip to divide the retina into quadrats. We photographed the ganglion cell layer with a Moticam 2000 microscope camera (Motic Instruments, Richmond, BC, Canada) using the shareware Motic Image Plus 2.0. Each quadrat was approximately seven images wide and three images high. We photographed the cell layers following a specific order to avoid overlap and to track the location of each image. We counted the number of retinal ganglion cells per image with ImageJ to later estimate density. We used retinal ganglion cell density and eye size to estimate the upper levels of visual acuity (Collin & Pettigrew 1989). The retinal ganglion cell layer also includes cells other than retinal ganglion cells, such as, amacrine and glial cells. We established standard criteria for identifying ganglion cells based on the large soma size, Nissl accumulation in the cytoplasm and staining of the nucleus (Hughes 1977; Freeman & Tancred 1978; Stone 1981; Rahman et al. 2006, 2007). To estimate cell density (and visual acuity), we only used areas of the retina with a high concentration of retinal ganglion cells. Cell types different from retinal ganglion cells (e.g. amacrine cells, glial cells) are less abundant in areas of high cell density (Hayes & Holden 1983), thereby reducing the bias associated with cell misidentification.

Previous studies have estimated the fovea (area with the highest concentration of photoreceptors) as having the highest 50 percentile of cell density (e.g. Franco et al. 2000). We were not able to establish in the retina of either species the presence of a pitted area (e.g. fovea); thus, we calculated two estimates of areas of high concentration of retinal ganglion cells (HRGC). We estimated cell density from areas in the retina with the highest 50 ($HRGC_{50}$) and 25 ($HRGC_{25}$) percentile cell density. These areas were located in the central and dorsal parts of the retina (T. Dolan & E. Fernández-Juricic, unpublished data).

To estimate visual acuity from ganglion cell density, we first estimated the retinal magnification factor (RMF), which is the linear distance on the retina that subtends 1° (Pettigrew et al. 1988), as:

$$\mathrm{RMF} = \frac{2\pi \mathrm{PND}}{360},$$

where PND is the posterior nodal distance, as defined above. We estimated visual acuity by estimating F_n, the highest spatial frequency that can be detected, measured in cycles per degree, as:

$$F_n = \frac{\mathrm{RMF}}{2}\sqrt{\frac{2D}{\sqrt{3}}},$$

where D represents retinal ganglion cell density, cells/mm^2 (Williams & Coletta 1987).

Visual Fields

We established the retinal visual field using an ophthalmoscopic reflex technique (Martin 1984), which estimates whether the retina can capture visual stimuli at different directions around the head. This technique has been widely used to characterize interspecific variations in the configuration of visual fields and foraging behaviour (e.g. Martin 2007). Bischof (1988) reported close correspondence between an estimate of the visual field in the zebra finch, *Taeniopygia guttata*, and visually guided behaviours that included movement detection, pecking and courtship singing. However, unlike our technique, Bischof used a dissecting microscope, a coordinate system and an optokinetic approach to estimate the visual fields.

An individual was secured with Velcro straps on a foam cradle at the centre of the visual field apparatus (Martin et al. 2007). The animal was restrained 15–30 min. The beak was fixed at the position adopted in the wild by taping it to a specially designed metal beak holder. We used a coordinate system in which 0° was directly above the bird's head, and 90° was at the horizontal plane. We were not able to record the projections of the retinal margins from 160° to 240° (and 120° in the brown-headed cowbird) below the bill tip because of feather, body and tripod obstructions.

We recorded the position of the projection of the retinal margin of each eye with a Keeler Professional ophthalmoscope (Keeler Instruments, Broomall, PA, U.S.A.) to an accuracy of $\pm 0.5^\circ$ at each elevation, which varied in 10°-increments in the median sagittal plane of the bird. We measured the maximum and minimum limits of the visual fields produced by eye movements. We took into account eye movement variations in the estimation of visual fields because they differ between passerine and nonpasserine birds (Martin 1986b; Martin & Katzir 1999; Appendix 1 in Martin & Coetzee 2004) and, therefore, are necessary for between-species comparisons.

In four brown-headed cowbirds and three mourning doves, we elicited eye movements by producing slight sounds and flashes of a small light source presented to the side of the bird's head. We recorded the extreme positions of the retinal field margins produced by the movement of the eyes, and calculated the difference between these values as the maximum amplitude of eye movement at different elevations. We calculated the extent of the binocular and lateral visual fields, and the extent of the blind areas behind the head in the horizontal plane, under the following assumptions: (1) the maximum binocular overlap is produced when eyes are converged (i.e. rotated maximally forward) and (2) the minimum binocular overlap is produced when eyes are diverged (i.e. rotated maximally backwards). To calculate the extent of the lateral field (monocular field–binocular field) for each eye, we used the following formula: (360 − (mean blind field + mean binocular field)/2), and represented graphically the configuration of all areas in the approximately horizontal plane (following Martin & Katzir 1999). We also determined the average eye movement amplitude at all elevations. In another group of 12 individuals of each species, we measured the vertical extent of the binocular field to establish the ability of each species to detect stimuli around their sagittal plane. We calculated the vertical extent for each bird as the number of consecutive 10° elevations that had binocular overlap.

Our experimental protocol (no. 220) was approved by the Institutional Animal Care and Use Committee of California State University Long Beach.

Behavioural Experiments

We conducted our behavioural experiments under seminatural conditions. Our experimental protocol comprised the exposure of wild-caught brown-headed cowbirds and mourning doves to the approach of a ground-based vehicle (i.e. a 2002 Ford Ranger pickup truck) and four vehicle-mounted lighting treatments. We used a flight cage placed on pavement to remove visibility barriers between an experimental group and the approaching vehicle, reduce their foraging opportunities and increase the time that the birds would spend vigilant (see Elgar 1989).

To create the specific lighting treatments we used an Altman Steel Par 46 lighting can (Altman Lighting, Inc., Yonkers, NY, U.S.A.) housing a 13 V Philips Sealed Beam 4049 Automotive Lamp (Philips Lighting Company, Somerset, NJ, U.S.A.). The lamp is comparable in voltage and wattage to other PAR 46 Sealed Beam lighting designed specifically for small aircraft. We wired the lamp to the pulse-control device, a Pulselite™ (Precise Flight, Inc., Bend, Oregon, U.S.A.), from which leads were connected to the battery of the truck. On the front of the lighting can, we mounted a flat, 0.5 cm thick, clear glass plate. The plate served to reduce insect and dust accumulation on the lamp and within the lighting can. The lighting can was mounted atop the cab of the truck, approximately 1.7 m above ground level and centred. We used a Fluke 110 True RMS Multimeter (Fluke Corp., Everett, WA, U.S.A.) connected to the Pulselite to monitor pulse rate.

We randomly assigned groups (six birds per group per species) to four treatments: (1) vehicle approach without the lamp illuminated, thus controlling for movement effect; (2) vehicle approach with a 2 Hz pulse of the lamp; (3) vehicle approach with a 16 Hz pulse; and (4) vehicle approach with constant lamp illumination. In all treatments, the vehicle approach speed was approximately 6.7 m/s. We based our selection of pulse rates not on avian CFF estimates (noted above), but on the Pulselite™ product application range, the approximate human CFF threshold (Sokol & Riggs 1971; Seitz et al. 2005), and ranges that would meet pilot safety requirements (Rash 2004).

We held each experimental group within a $2.4 \times 2.4 \times 1.8$ m outdoor flight cage during the vehicle approach. The cage dimensions and group size allowed us to minimize distance-to-neighbour effects and the effects of individual variance in vigilance (e.g. Fernández-Juricic et al. 2007). For brown-headed cowbirds, we positioned a 2.4 m long perch approximately 15.2 cm high and 20.3 cm from the cage front. However, because of the ground-dwelling habits of the mourning dove, we did not include a perch for this species. For all groups, the flight cage was 122 m from the approach vehicle (Fig. 1).

For each day of the experiment, we randomly selected treatment order. We exposed groups to treatments one group at a time; each group of six birds represented an experimental unit within species and treatment. Furthermore, we exposed each species group within a treatment to one approach only. Therefore, each bird (and group) was used only once throughout the experiment to avoid habituation or sensitization effects. We used an equal number of groups within each treatment and within the same period of the day (0830–1230 h or 1300–1600 h). Transition between groups generally required less than 30 min, and we

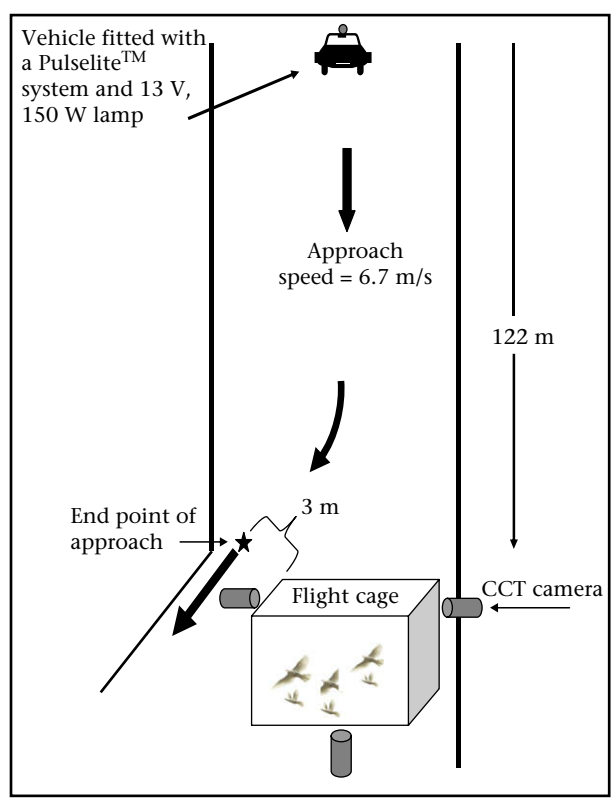

Figure 1. Schematic representation of the experimental site showing the relative trajectory of the vehicle in relation to the position of the cage. Experiments were conducted in Erie County, Ohio, U.S.A., from 12 June through 26 September 2006.

completed four groups (one group/treatment) within 90 min. Also, because of forest cover surrounding our experiment site, wind speed variability was minimized relative to prevailing winds. Nevertheless, we conducted vehicle approaches only when the true wind was blowing towards the approaching vehicle and away from the flight cage. We used the Beaufort scale for wind conditions in decisions to hold (wind speed > Beaufort III or 19 km/h) or proceed with a vehicle approach.

All species groups were provided ample feed and water before and after, but not during, a given trial. Each group was allowed at least 15 min to acclimate prior to the vehicle approach. At the beginning of this acclimation period, the driver positioned the truck in an area obstructed from the animals' view, and then checked the function of the lighting system. Next, the driver positioned the vehicle at the starting point and with the engine running. An observer was stationed in another vehicle within an area of scrub vegetation approximately 28 m from the side of the experimental cage. This second vehicle housed a video monitor and recorder. We filmed each trial using three American Dynamics Color Camera PrePack 470 TVL High-Resolution with Night Saver video cameras (Tyco International, Inc., Princeton, NJ, U.S.A.), and we stored the digital data on a Pelco DX8000 16-channel, 250 gb digital video recorder (Pelco, Clovis, CA, U.S.A.). We monitored trials remotely via a quad split-screen Pelco 17-inch LCD Panel SXGA Flat Panel Display. Three cameras were oriented towards the animals in the enclosure (one elevated behind the enclosure, and the other two from opposing sides).

A trial began with the driver accelerating to 6.7 m/s and holding the vehicle direction on the centre of the cage (Fig. 1). Approximately 12.8 m from the cage, the driver veered the vehicle to the right along a marked route that crossed a point 3 m from the front corner of the cage (i.e. the end point for the approach). Each vehicle approach required approximately 20–23 s to reach this end point. At the completion of each approach to a group, we recorded an index of lamp intensity (μmol/s/m^2) over 15 s with a Li-Cor LI-250 Light Meter and LI-190SA Quantum Sensor (LI-COR Biosciences, Lincoln, NE, U.S.A.). We obtained the reading by placing the sensor in the end of a tube (2 cm inside diameter, 11 cm long), thereby limiting outside light intrusion, and placing the opposite end of the tube on the centre of the glass plate covering the lamp. We also recorded an index of ambient light intensity at the flight cage, again using the Li-Cor LI-250 Light Meter and LI-190SA Quantum Sensor. We held the sensor at approximately 1 m above ground level, face up, and recorded the average intensity over 15 s.

Our experimental protocol (no. 1152) was approved by the Institutional Animal Care and Use Committee of the United States Department of Agriculture, National Wildlife Research Center.

Response metrics

We examined each group video at approximately 0.1 s intervals, a period that allowed for slight variation in time per camera for storage of the digital data to the hard drive. We recorded the time (seconds into an approach) that each individual within a group showed an alert response and a flight response, relative to the marked end point (noted above) for the vehicle approach. Alert and flight response times were correlated with alert and flight response distances; specifically, high values of these variables indicated quick alert and flushing reactions.

We measured alert and flight responses at the individual (e.g. the first individual in the group that reacted) and group (e.g. the overall reaction of the individuals in the group) levels, as birds may react to threats using different combinations of behaviours (Lind & Cresswell 2005). Alert behaviour is defined as the increase in vigilance-related behaviours (rate and proportion of time head-up scanning) in response to a threat. We considered an alert response as a marked transition in an individual's behaviour (e.g. pecking, preening or loafing), in response to the initiation of a treatment, to behaviours that might include head-up with neck extended, sudden and increased scanning behaviour, or sudden crouching (Fernández-Juricic et al. 2001). In addition, we required that the individual alert behaviours be maintained throughout the vehicle approach or that a bird transitioned from alert behaviour to a flight response. In this manner, we controlled for inclusion of alert responses to factors other than the vehicle approach.

We defined flight response as a marked transition in behaviour (e.g. from perching, pecking or alert scanning) in response to vehicle approach, to a behaviour that could propel the bird away from the vehicle or road. However, we recognized that flight response would differ between species (Lima 1993). For example, the typical escape response by brown-headed cowbirds within a cage is flight to the highest point (Blackwell & Bernhardt 2004). Also, Blackwell & Bernhardt (2004) noted that mourning doves within a cage walk or run from an approaching vehicle, showing flight as a secondary response (possibly an initial attempt to seek cover before flushing). Furthermore, we recognized that the boundaries of the cage probably affected the initiation of the flight response of some individuals; thus, by our definition of flight response, we considered only those individuals within a group that were on the pavement (or the low perch for brown-headed cowbirds) at the initiation of the vehicle approach. We considered birds perched high within the cage prior to the initiation of an approach as showing alert behaviour in response to other factors, limited on escape routes and, therefore, 'outside' the framework of our definition of alert or flight response. Importantly, seminatural conditions (including use of enclosures) have been used successfully in research examining avian social foraging and vigilance (Fernández-Juricic & Kacelnik 2004; Fernández-Juricic et al. 2004b, 2007), as well as predator detection and response (Van Der Veen & Lindström 2000; Cresswell et al. 2003; Fernández-Juricic & Tran 2007). Because we were interested in comparing between-species responses to vehicle approaches, it was essential to provide similar experimental conditions to minimize the bias associated with characterizing these responses in free-ranging birds (e.g. distance to protective cover, grass height, flock size, etc.).

Analyses

Differences in retinal ganglion cell densities and visual acuities between species were calculated with two-sample t tests. We compared the average widths of the binocular field, blind areas and eye movement amplitude between species with general linear models, and added elevation to the model to control for its effects. For this analysis, we averaged the binocular and blind widths when the eyes were converged and diverged, and among individuals at each elevation. The average vertical extent of the binocular area was compared between species with a two-sample t test. We conducted each general linear model (GLM) with type III sums of squares because of the unbalanced number of observations per combination of factors (e.g. elevation and species).

For the behavioural experiments, each group within a treatment represented an experimental unit. We calculated individual alert response and flight response times for each member of a treatment group, and relative to the vehicle position in the approach. Specifically, our behavioural measurements reflect the time between response and the vehicle reaching the end point (see above) of the approach. For each group, we then calculated means for alert and flight response metrics (i.e. our group response variables reflected the group mean). We used the following response factors for each species: first alert response and group alert

response. However, given potential cage effects on flight response (noted above) we used group flight response only in a comparison between species. We used a mixed linear model (MLM), type III sums of squares (SAS ver. 8.2, SAS Institute, Cary, NC, U.S.A.) and, because of lack of normality, log-transformed our data. Treatment served as the fixed effect, ambient lighting and the interaction of treatment and ambient lighting as random effects. For purposes of between-species comparisons, we compared ambient light intensity and lamp intensity within treatment, respectively, using a GLM and type III sums of squares (SAS ver. 8.2, SAS Institute).

RESULTS

Visual Acuity

Mean ± SD cell densities within the $HRGC_{50}$ areas of brown-headed cowbirds (16 359.59 ± 3242.95 cells/mm^2) and mourning doves (15 783.93 ± 787.47 cells/mm^2) did not differ (two-sample *t* test: $t_8 = 0.39$, $P = 0.709$). However, mean ± SD visual acuity based on $HRGC_{50}$ areas was higher in the mourning dove (6.53 ± 0.01 cycles/degree) than in the brown-headed cowbird (4.81 ± 0.53 cycles/degree; two-sample *t* test: $t_8 = 7.03$, $P < 0.001$).

Similarly, cell densities within the $HRGC_{25}$ areas for brown-headed cowbirds (18 286.16 ± 3587.70 cells/mm^2) and mourning doves (17 501.82 ± 1141.56 cells/mm^2) were not different (two-sample *t* test: $t_8 = 0.46$, $P = 0.654$). Visual acuity based on $HRGC_{25}$ areas was again higher in the mourning dove (6.89 ± 0.21 cycles/degree) than in the brown-headed cowbird (5.10 ± 0.55 cycles/degree; two-sample *t* test: $t_8 = 6.77$, $P = 0.001$). Given the lack of difference in cell density between species, the differences in visual acuity were probably caused by differences in eye size (see Kiltie 2000).

Visual Fields

In the approximately horizontal plane, the binocular field width differed between species when the eyes were converged maximally, being 364% higher in the brown-headed cowbird than in the mourning dove (Fig. 2a, c). However, the binocular field width when the eyes were diverged maximally was 400% higher in the mourning dove than in the brown-headed cowbird (Fig. 2b, d).

The blind area width was 215% and 105% higher in the brown-headed cowbird than in the mourning dove, when the eyes were converged and diverged maximally, respectively (Fig. 2). Eye movements changed the width of the blind area by 29% in the mourning dove and by 98% in the brown-headed cowbird. The cyclopean areas (the area around the head with visual coverage, including both binocular and lateral fields) were 21% and 7% wider in the mourning dove (converged eyes, 333°; diverged eyes, 339°) than in the brown-headed cowbird (converged eyes, 275°; diverged eyes, 317°) when the eyes were converged and diverged, respectively.

Averaging values between converged and diverged eyes and considering all elevations, we found that the maximum width of the binocular field occurred above the projection of the bill at an elevation of 40° in the mourning dove, and at an elevation of 60° in the brown-headed cowbird. Controlling for elevation (GLM: $F_{1,24} = 0.01$, $P = 0.973$), the average ± SD width of the binocular field was larger in the brown-headed cowbird (15.70 ± 2.22°) than in the mourning dove (7.99 ± 2.13°; $F_{1,22} = 6.25$, $P = 0.019$). The averaged maximum width of the blind area occurred behind the head at the approximate horizontal plane at an elevation of 260° for the mourning dove and 270° for the brown-headed cowbird. Controlling for elevation (GLM: $F_{1,22} = 0.66$, $P = 0.426$), the average ± SD width of the blind area was larger in the brown-headed cowbird (42.73 ± 4.76°) than in the mourning dove (13.47 ± 4.57°; $F_{1,22} = 19.66$, $P < 0.001$).

The average ± SD maximum eye movement amplitude for mourning doves was recorded at 20° above the horizontal, whereas that for brown-headed cowbirds was recorded at 20° below the horizontal. Eye movements in brown-headed cowbirds (19.17 ± 0.65°) were on average larger than those in mourning doves (3.11 ± 0.62°; GLM: $F_{1,49} = 319.04$, $P < 0.001$), controlling for elevation ($F_{1,49} = 2.02$, $P = 0.162$). The average vertical extent of the binocular field did not differ between species (mourning dove, 170.83 ± 7.12°; brown-headed cowbird, 169.17 ± 7.23°; two-sample *t* test: $t_{22} = 0.16$, $P = 0.871$).

Behavioural Experiments

We completed our experiment with brown-headed cowbirds using 14 groups per treatment, but removed some groups from the analysis because of erratic flight behaviour that prevented the measurement of alert and flight responses under the criteria outlined above. We completed our analysis with the following sample sizes: control, 14 groups; 2 Hz, 11 groups; 16 Hz, 13 groups; constant illumination, 13 groups. We obtained data from at least two birds per treatment group ($\overline{X} \pm SE = 5.3 \pm 0.5$ birds per group). Ambient light conditions among treatments in the brown-headed cowbird experiment were similar (GLM: $F_{3,55} = 0.21$, $P = 0.887$).

In our experiment with mourning doves, we used 10 groups per treatment and recorded observations of six birds per group, with the exception of a single group in the constant illumination treatment that comprised seven birds. The group with seven birds included one bird (unidentified) that was mistakenly not removed from the cage after the previous 16 Hz treatment group; however, we found no extremes in behavioural response metrics for this group that would indicate bias. Ambient light conditions among treatments in the mourning dove experiment were similar (GLM: $F_{3,39} = 0.10$, $P = 0.958$).

Brown-headed cowbird experiment

The general reaction of brown-headed cowbirds to vehicle approach was a marked transition from loafing and active ground searching to alert status and, subsequently, flight. Across treatments, the mean ± SE first alert response of brown-headed cowbird groups occurred 11.5 ± 1.5 s before the vehicle reached the end point. Groups exposed to constant illumination had a mean first alert response that occurred 2.7–3.1 s before that of other groups (MLM: $F_{3,43} = 2.26$, $P = 0.095$; Table 1), with responses by constant illumination and 2 Hz groups differing ($F_{1,43} = 6.31$, $P = 0.016$; Table 1). In addition, we found a significant interaction effect of ambient light and constant illumination on first alert response (Table 1, Fig. 3a, b); brown-headed cowbirds became alert sooner as ambient light intensity increased. The interaction effect of ambient light and the 2 Hz treatment on first alert response was marginally nonsignificant (Table 1, Fig. 3a, b); here, brown-headed cowbirds showed alert behaviour generally sooner as ambient light intensity decreased.

Groups exposed to constant illumination had a mean group alert response that was 1.2–1.3 s faster than that of other treatment groups (MLM: $F_{3,43} = 1.81$, $P = 0.159$; Table 1), and responses by constant illumination and 2 Hz groups also differed ($F_{1,43} = 4.82$, $P = 0.034$). Furthermore, the interaction effect of ambient light and constant illumination on mean group alert response was significant (Table 1): brown-headed cowbirds reacted 0.16–0.34 s (0.24 ± 0.54 s) sooner for every 50 μmol/s/m^2 increase in light intensity (Fig. 3a, b).

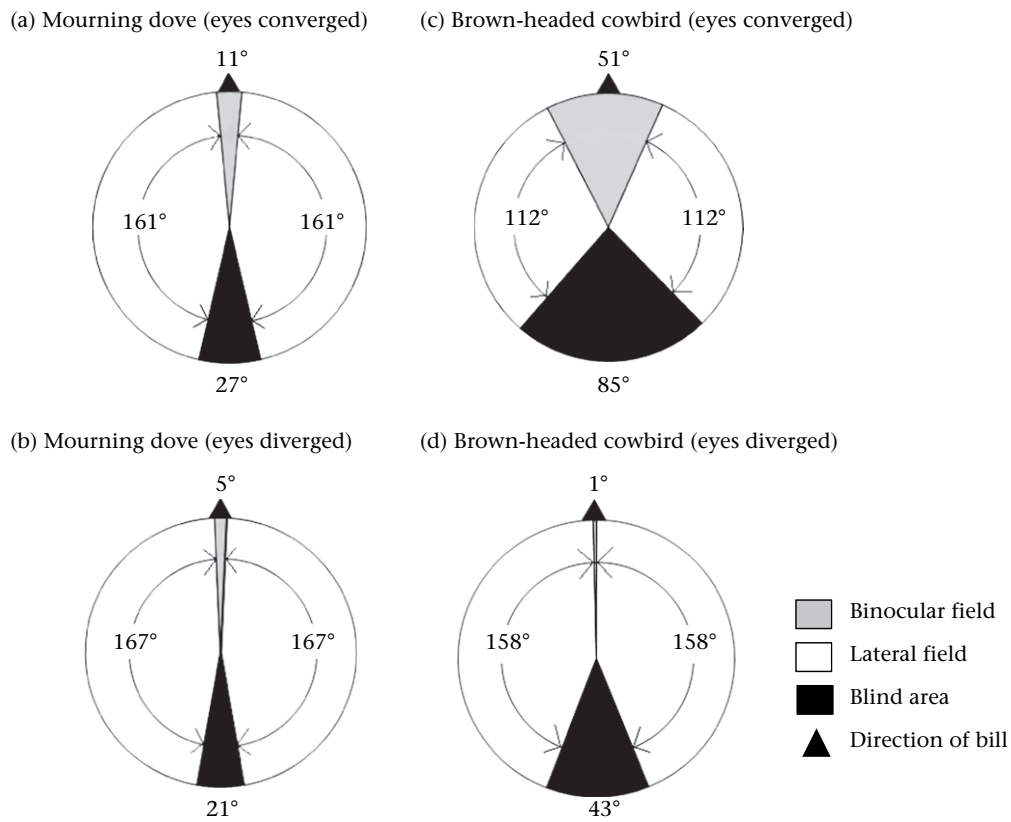

Figure 2. Horizontal sections through the retinal visual fields of the mourning dove (a, b) and brown-headed cowbird (c, d) at the approximately horizontal plane. For each species, we present the average retinal field when the eyes were fully converged (eyes rotated fully forward: a, c) and fully diverged (eye rotated fully backward: b, d).

Mourning dove experiment

During the vehicle approach, mourning doves generally remained in close proximity to other group members, loafing and pecking. However, upon initiation of the flight response, we often observed a mixed response by group members ($\overline{X} \pm$ SE birds per group showing a specific flight response behaviour: run only $= 4.0 \pm 0.8$ birds; run, then fly $= 1.8 \pm 0.7$ birds; fly $= 0.2 \pm 0.1$ birds; seek cover against cage wall $= 0.1 \pm 0.1$ birds). Again, we attribute these varied flight response behaviours to the lack of cover within the flight cage and the confines of the cage.

Mean $\pm$ SE first alert response of mourning dove groups occurred 14.8 ± 0.6 s before the vehicle reached the end point, with negligible differences between treatments (range 0.5–1.3 s; MLM: $F_{3,32} = 1.02$, $P = 0.3963$; Table 1). Mean group alert response differed between treatments by only 0.5–1.1 s, and without significant differences (MLM: $F_{3,32} = 0.71$, $P = 0.5516$; Table 1).

Between-species comparison

Between experiments (i.e. between species), ambient light conditions within treatment were similar, with the exception of constant illumination groups (GLM 16 Hz: $F_{1,22} = 2.82$, $P = 0.108$; 2 Hz: $F_{1,20} = 1.11$, $P = 0.306$; constant illumination: $F_{1,21} = 4.29$, $P = 0.051$; no lamp: $F_{1,22} = 0.47$, $P = 0.501$; Table 2). Also, lamp intensity within treatment was similar (GLM 16 Hz: $F_{1,22} = 3.66$, $P = 0.069$; 2 Hz: $F_{1,20} = 2.62$, $P = 0.122$; constant illumination: $F_{1,22} < 0.00$, $P = 0.992$; Table 2). Mourning doves showed first alert response, on average, 3.3 s before brown-headed cowbirds (MLM: $F_{1,89} = 11.56$, $P = 0.001$; Table 1), and showed group alert response, on average, 2.1 s before brown-headed cowbirds ($F_{1,89} = 6.18$, $P = 0.015$; Table 1). However, brown-headed cowbirds showed group flight response, on average, 1.0 s before mourning doves (brown-headed cowbirds: 5.4 ± 0.02 s; mourning doves: 4.4 ± 0.50 s; $F_{1,89} = 14.81$, $P < 0.001$).

DISCUSSION

Within species, we found that brown-headed cowbirds, but not mourning doves, were sensitive to the light treatments. However, these results were influenced by ambient light intensity. Between species, we found that the species with the higher acuity and the wider visual fields (mourning dove) detected the approaching vehicle sooner, but flushed later, than the species with the relatively lower acuity and narrower visual fields. We first discuss between-species differences in visual properties and behavioural responses and then focus on the light treatments.

The density of retinal ganglion cells is a good estimate of the upper levels of acuity (e.g. Collin & Pettigrew 1989); however, visual acuity could vary under different light conditions (e.g. variations in weather). This caveat applies to both species; therefore, our results should be used as proxies of between-species differences in visual resolution. The higher visual acuity of the mourning dove suggests that this species would have a greater ability to resolve objects in its visual field, and thus, may be able to detect objects from further away than do brown-headed cowbirds (e.g. increase the depth of the detection windows; Kiltie 2000).

The degree of eye movement of brown-headed cowbirds was much higher than that of mourning doves, which agrees with previous results found in other passerine and nonpasserine species (Martin & Katzir 1999). For instance, brown-headed cowbirds can converge their eyes to attain a higher degree of binocular overlap, or diverge their eyes and almost abolish the binocular area. The functional implications of this high variability in visual field

Table 1
Alert responses* and model estimates of fixed and random treatment effects for species treatment groups exposed to an approaching 2002 Ford Ranger pickup truck displaying one of four light treatments during experiments in Erie County, Ohio, U.S.A., 12 June–26 September 2006

Experiment phase	Behavioural metric	Lamp effect	Time (s)*	Model†			
				Estimate	SE	*t*	*P*
Brown-headed cowbird	First alert	Intercept	•	1.07950	0.10440	10.34	<0.001
		16 Hz	10.8 (3.7)	−0.12230	0.17930	−0.68	0.499
		2 Hz	11.0 (3.5)	0.13520	0.14690	0.92	0.362
		Constant	13.7 (5.3)	−0.28270	0.16710	−1.69	0.098
		No lamp	10.6 (3.6)	•	•	•	•
		Ambient light	•	•	•	•	•
		Ambient×16 Hz	•	0.00003	0.00009	0.37	0.714
		Ambient×2 Hz	•	−0.00012	0.00006	−1.98	0.054
		Ambient×Constant	•	0.00019	0.00008	2.47	0.018
		Ambient×No lamp	•	−0.00005	0.00007	−0.76	0.453
Brown-headed cowbird	Group alert	Intercept		0.92930	0.08608	10.80	<0.001
		16 Hz	8.1 (2.5)	−0.04048	0.14680	−0.28	0.784
		2 Hz	8.0 (1.7)	0.03150	0.12130	0.26	0.796
		Constant	9.3 (3.2)	−0.26910	0.13740	−1.96	0.057
		No lamp	8.0 (1.6)	•	•	•	•
		Ambient light	•	•	•	•	•
		Ambient×16 Hz	•	<0.00001	0.00007	0.01	0.992
		Ambient×2 Hz	•	−0.00004	0.00005	−0.81	0.425
		Ambient×Constant	•	0.00017	0.00006	2.76	0.008
		Ambient×No lamp	•	−0.00002	0.00006	−0.42	0.674
Mourning dove	First alert	Intercept	•	1.2066	0.09336	12.92	<0.001
		16 Hz	15.1 (5.1)	0.04642	0.12760	0.36	0.718
		2 Hz	14.3 (4.4)	−0.07725	0.13180	−0.59	0.562
		Constant	14.4 (5.1)	−0.14870	0.12400	−1.20	0.240
		No lamp	15.6 (4.9)	•	•	•	•
		Ambient light	•	•	•	•	•
		Ambient×16 Hz	•	−0.00008	0.00006	−1.39	0.175
		Ambient×2 Hz	•	<0.00001	0.00006	0.03	0.973
		Ambient×Constant	•	0.00006	0.00006	1.08	0.288
		Ambient×No lamp	•	−0.00003	0.00006	−0.50	0.620
Mourning dove	Group alert	Intercept	•	1.0649	0.10950	9.73	<0.001
		16 Hz	10.6 (5.2)	0.04954	0.14910	0.33	0.742
		2 Hz	10.4 (3.7)	−0.05491	0.15420	−0.36	0.724
		Constant	10.0 (3.7)	−0.14490	0.14500	−1.00	0.325
		No lamp	11.1 (4.8)	•	•	•	•
		Ambient light	•	<−0.00001	0.00001	−0.16	0.875
		Ambient×16 Hz	•	−0.00010	0.00007	−1.59	0.122
		Ambient×2 Hz	•	−0.00001	0.00007	−0.17	0.865
		Ambient×Constant	•	0.00004	0.00006	0.63	0.534
		Ambient×No lamp	•	−0.00004	0.00007	−0.62	0.539

* Mean (±SE) time from initiation of the behavioural response to the vehicle reaching the end point of the approach for each treatment (see Fig. 1).
† Analysis based on log of the observed behavioural response. Parameters that were not estimable are shown as '•'.

configuration have not been explored, but it can be argued that eye convergence could be used while foraging and divergence could be used while scanning for predators (Martin 2007). Therefore, changes in eye position in the brown-headed cowbird could enhance focus on certain visual targets, but simultaneously decrease the ability to gather visual information from as many points around the head as possible. We suggest, therefore, that the brown-headed cowbird might have a low probability of detecting objects approaching from the rear while in head-up and head-down positions. The high clyclopean (combination of the lateral and binocular visual fields) area of the mourning dove, on the contrary, can allow them to increase visual coverage at any given body posture (e.g. increasing the area of the detection window).

Although we cannot establish causal relationships between the visual properties measured and the behavioural responses, our findings indicate that visual acuity and visual fields might play a role in how these species respond to and assess risk. For example, Frid & Dill (2002) suggested that animal response to disturbance stimuli (e.g. recreationists, vehicles, etc.) is thought to follow similar economic principles as when prey respond to predators (see also Fernández-Juricic & Schroeder 2003; Fernández-Juricic et al. 2004b). Given its visual configuration (relatively higher acuity and wider visual fields), one would expect that the mourning dove would be able to track the movement of a vehicle more continuously. The mourning dove should then rely on stillness and crypsis (e.g. Endler 1978, 2006) when under threat, thereby conserving energy for sudden escape bursts. Such a delayed response to predator approach is typical of species that use 'tall' vegetation as protective cover (e.g. see Whittingham & Evans 2004; Butler et al. 2005; Whittingham et al. 2006), such as the mourning dove. In contrast, given the visual configuration of the brown-headed cowbird (relatively lower acuity and narrower visual fields), one would expect that the amount of visual information available about an approaching object at any given point in time might be more restricted, thus increasing the uncertainty about an attack. Therefore, the brown-headed cowbird should flush earlier than the mourning dove to reduce predation risk costs. Indeed, mourning doves showed alert behaviour significantly sooner than brown-headed cowbirds, but brown-headed cowbirds showed flight response earlier than mourning doves. A correspondence between the visual field (particularly the size of the blind area) and vigilance behaviour has also been found in dabbling ducks (Guillemain et al.

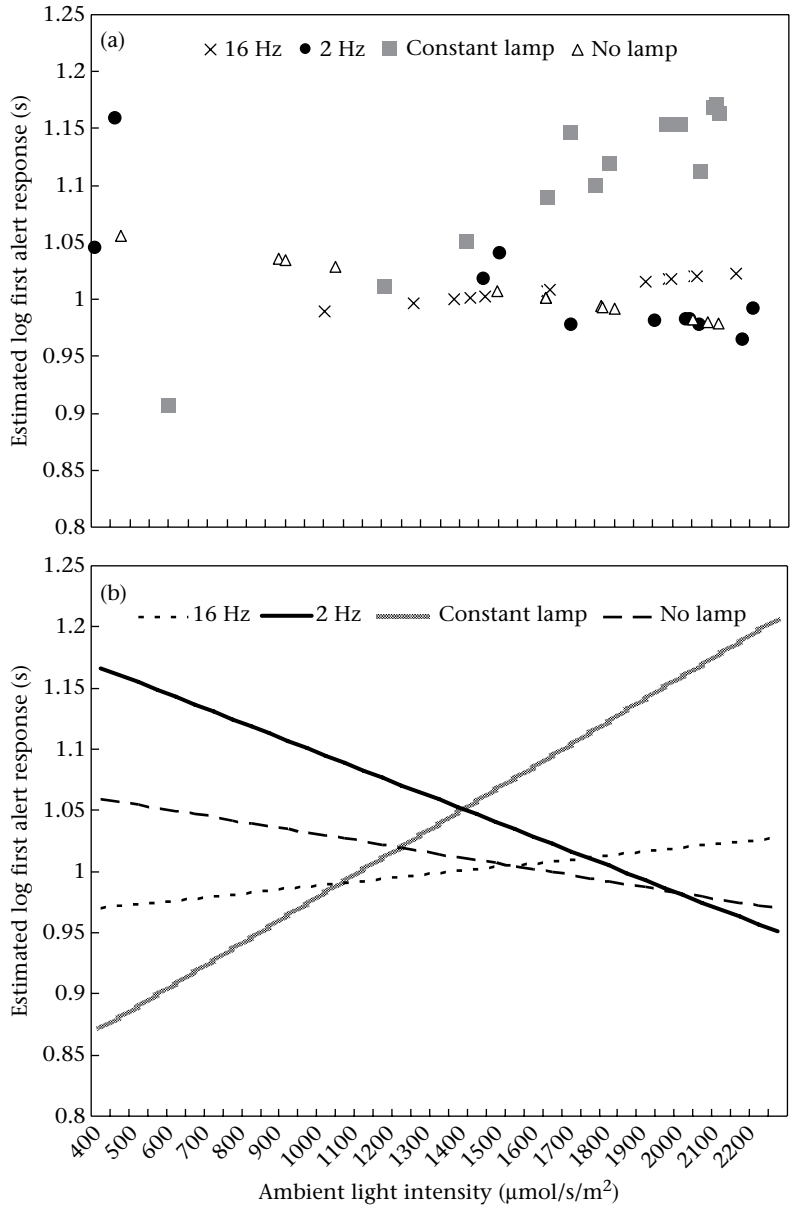

Figure 3. (a) Log of first alert responses by brown-headed cowbird groups ($N = 6$ birds/group) exposed to an approaching 2002 Ford Ranger pickup truck displaying one of four lighting treatments, via vehicle-mounted lamp, during experiments in Erie County, Ohio, U.S.A., from 12 June through 26 September 2006. First alert response represented the time (s) from initiation of the first behavioural response until the vehicle reached the end point of the approach (e.g. higher values indicate quicker detection). (b) Model (see Table 1) estimates of the log first alert response by brown-headed cowbird groups by lighting treatment (see Table 2). Here, the coefficient for the interaction of ambient light intensity and treatment was varied by units of 50 μmol/s/m^2 while other parameters were held constant. Slopes of the response were as follows: 16 Hz $= 3_{10}^{-5}$; 2 Hz $= -1.2_{10}^{-4}$; constant illumination $= 1.9_{10}^{-4}$; no lamp $= -5_{10}^{-5}$.

2002). Wigeons, *Anas penelope*, have a wider blind area and allocate a greater proportion of their time to scanning than shovelers, which have a narrower blind area, probably to compensate for the lack of information.

However, there are alternative explanations for the between-species differences in antipredator behaviour that do not necessarily involve the visual properties studied. First, differences might stem from variations in scanning behaviour: brown-headed cowbirds with lower head-up scanning rates might experience delayed detection (e.g. Cresswell et al. 2003). However, we did not provide any foraging substrate or food for birds to trade-off vigilance with foraging time; so, both species remained vigilant during the trials. Second, brown-headed cowbirds are smaller (length: 17–22 cm, wing span: 28–36 cm; body weight: 38–50 g) than mourning doves (length: 23–34 cm, wing span: 37–45 cm; body weight: 86–170 g; http://www.birds.cornell.edu), thus their eyes are closer to the ground, probably changing the angle of elevation between the birds and the approaching vehicle. But, given the height of the vehicle (1.7 m wide × 1.7 m high), we believe the effect of the proximity of the bird's eyes to the ground might have been minimal. Third, even if both species have similar distributions of photoreceptors associated with motion detection because they are ground foragers (Hart 2001), there could be differences between species in the density of motion detectors (e.g. higher in mourning doves) that might have influenced alert distances. Notably, no study on photoreceptor density has been published on these species. Fourth, power required for flight is affected, in part, by drag components related to wing span, body frontal area, and

Table 2
Ambient light and lamp intensity (μmol/s/m^2) measurements (±SE) obtained during experiments in Erie County, Ohio, U.S.A., during 12 June–26 September 2006

Experimental phase and light metric	Lighting treatment			
	16 Hz	2 Hz	Constant illumination	No lamp
Brown-headed cowbird				
Ambient intensity	1625.5 (333.9)	1570.4 (606.4)	1659.6 (414.9)	1471.8 (471.2)
Lamp intensity	481.3 (133.3)	504.5 (141.0)	1466.8 (378.9)	•
Mourning dove				
Ambient intensity	1278.3 (644.9)	1305.9 (538.5)	1187.7 (674.5)	1327.9 (555.9)
Lamp intensity	602.6 (171.2)	619.6 (184.1)	1465.0 (466.9)	•

The lamp, a 13 V Philips Sealed Beam 4049 Automotive Lamp (Philips Lighting Company, Somerset, NJ, U.S.A.), was wired to a pulse-control device, a Pulselite™ (Precise Flight, Inc., Bend, OR, U.S.A.). Leads from the Pulselite were connected to battery of a 2002 Ford Ranger pickup truck. A Li-Cor LI-250 Light Meter and LI-190SA Quantum Sensor were used to obtain intensity readings.

wing lift (Pennycuick 1975; Hedenström 2002). Power requirements for initial climb and speed might, thus, contribute to the different flushing behaviours between these species.

Considering each species' visual configuration and taking into account the histological estimates of visual acuity, we can predict the distance at which each species would be able to resolve an object of 2 m in height (following Gaffney & Hodos 2003): mourning dove, 1363 m; brown-headed cowbird 1012 m. Although these are estimates of the upper levels of visual acuity with perfect light conditions, they indicate that both species have the ability to detect objects within their visual fields before they show any behavioural alert response (e.g. increase in scanning rate) towards the object. We suggest, therefore, that the lack of a light treatment effect on the mourning dove alert response was partly due to the size of the species' detection window relative to our approach distance (122 m) and partly due to the absence of cover in our experimental design. These conditions were intended to enhance alert behaviour in both species, but perception of risk is context specific and can affect vigilance (Lima & Bednekoff 1999a). Whereas brown-headed cowbirds used the entire enclosure to investigate potential threats, mourning doves were essentially restricted to the pavement. Therefore, a consistent alert response in the mourning dove might not be discernible when the approach distance of the vehicle is less than 1 km and experimental groups have no access to cover.

Also, counter to our hypothesis concerning specific effects of pulsating lighting on avoidance behaviour, our 2 Hz and 16 Hz pulse treatments had no statistical effect on alert response. Instead, brown-headed cowbird groups exposed to constant illumination had a quicker alert response in relation to only 2 Hz pulsed-light groups. However, we found an interaction effect between ambient light and light treatment, such that under constant illumination, alert response was observed sooner into an approach as ambient light increased (e.g. sunny conditions). In contrast, the interaction of ambient light and the 2 Hz treatment, although marginally nonsignificant, indicated a pattern such that brown-headed cowbirds became alert sooner when ambient light decreased (e.g. cloudy conditions). These interaction effects might have different nonmutually exclusive explanations.

The perceived brightness or intensity of a light source to a bird is a function not solely of species-specific photoreception in the eye and associated neural processes, but also the environmental conditions (e.g. humidity, dust, etc.) affecting light transmission and refraction (Endler 1990). For example, environmental conditions that increase ambient light intensity can result in increased species-specific critical fusion frequencies (Powell 1967; Powell & Smith 1968; Emmerton 1983; Jarvis et al. 2003). Also, spectral composition of the stimulus, which is important in avian mate choice (Bennett & Cuthill 1994; Bennett et al. 1994; Endler & Théry 1996), is probably important in threat detection as well. Here, the relative contrast (Ghim & Hodos 2006) of an approaching threat (e.g. a vehicle, tower, or turbine blade) to background conditions will vary with the ambient light spectrum and angle of incidence (see Endler 1993). Furthermore, as noted above, critical fusion frequency is contrast dependent (Powell & Smith 1968). Species also might not be able to physiologically compensate for extremes in ambient light conditions: in house finches, *Carpodacus mexicanus*, increased illumination of foraging patches could interfere with visual perception, decrease scan bout duration and increase latency in predator detection (Fernández-Juricic & Tran 2007; Fernández-Juricic et al. 2008).

We suggest, therefore, that our constant illumination treatment presented brown-headed cowbird groups with a consistent visual cue (i.e. a contrast) against increasing glare and incident radiation from the vehicle and surroundings as ambient light intensity increased, thus enhancing detection. Similarly, the 2 Hz treatment might have been more effective as a visual cue to vehicle approach under relatively low-intensity light conditions and, probably, had less interference from glare. In the 16 Hz treatment, the relative contrast of vehicle and light treatment to background conditions was probably negligible.

Importantly, our findings have theoretical and applied implications. First, many theoretical models in behavioural ecology assume that predators are detected as soon as they break cover (e.g. Fernández-Juricic et al. 2004b). However, we found that an approaching object may be detected at different distances depending upon the visual constraints of a species. Relaxing the fixed-predator detection assumption in theoretical models could have interesting implications for the development of antipredator strategies. Second, the quantification of species visual system and behavioural response to object approach (static or moving) can enhance investigations of factors affecting information flow between individuals within groups (e.g. orientation, density, spacing, structure; Lima & Bednekoff 1999b; Fernández-Juricic et al. 2004b; Ballerini et al. 2008). For example, certain intentional movements are thought to contribute to social cohesion within a group in response to an approaching threat (Davis 1975; Lima 1995); individual spacing, cover characteristics and visual configuration of the species are each important to understanding the behaviours used to convey threat information between detectors and nondetectors. Similarly, these same factors can figure prominently in how external individuals respond to groups (e.g. the distance at which seabirds recruit to foraging flocks; Haney et al. 1992) or how individuals respond to conspecifics (e.g. recognition of transient or permanent markings in pelagic fishes; Nakamura 1968). Furthermore, between-species comparisons of response to predation risk might yield more complete information when visual configuration is considered in combination with social and vigilance behaviours and morphology (see Van Der Veen & Lindström 2000). Third, our study provides a basic understanding of the factors that can be used to manipulate the behaviour of these species to reduce human–wildlife interactions, an important

component of the application of animal behaviour to conservation biology (Sutherland 1998; Angeloni et al. 2008).

Lighting treatments, particularly, hold promise as means of developing methods to directly or indirectly manipulate the behaviour of birds and, eventually, reduce bird–structure collision mortality in urban and suburban landscapes (see Van Tets et al. 1969; Larkin et al. 1975; Wiltschko et al. 1993; Blackwell et al. 2002; Blackwell & Bernhardt 2004). Our results suggest that vehicle-mounted lighting can influence avian alert behaviour depending (among other factors) upon the sensory system of the target species and ambient light conditions. We suggest that future experiments quantify species-specific response to a greater range of pulse rates of light under preselected ambient light conditions, taking into account measures of chromatic contrast and brightness.

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