



A songbird can detect the eyes of conspecifics under daylight and artificial nighttime lighting[☆]

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ABSTRACT

Eyes convey important information about the external and internal worlds of animals. Individuals can follow the gaze of others to learn about the location of salient objects as well as assess eye qualities to evaluate the health, age or other internal states of conspecifics. Because of the increasing prevalence of artificial lighting at night (ALAN), urbanized individuals can potentially garner information from conspecific eyes under both daylight and ALAN. We tested this possibility using a visual modeling approach in which we estimated the maximum distance at which individuals could detect conspecific eyes under daylight and high levels of ALAN. We also estimated the minimum light level at which individuals could detect conspecific eyes. Great-tailed grackles (*Quiscalus mexicanus*) were used as our study species because they are highly social and are unusual among birds in that they regularly gather at nocturnal roosts in areas with high levels of ALAN. This visual modelling approach revealed that grackles can detect conspecific eyes under both daylight and ALAN, regardless of iris coloration. The grackles could detect conspecific eyes at farther distances in daylight compared to ALAN. Our results highlight the potential importance of lighting conditions in shaping social interactions.

1. Introduction

The eyes of many species provide a rich source of information. Individuals can follow the gaze of others to learn about the location of conspecifics, predators, and food (Emery, 2000). Furthermore, eyes can reveal information about emotional states. Individuals with large pupils may be fearful or sad (Yorzinski & Platt, 2014), while individuals with smaller pupils may be angry (Kret, 2017). The health status of individuals can be reflected in eyes, with sick individuals exhibiting eyes that are discolored or misshapen (Provine et al., 2013; Griggs, 2019). Eyes can also provide basic demographic information; for example, in some species, iris color predictably changes with age and differs between the sexes (Bortolotti et al., 2003).

The vision of diurnal birds is adapted to provide color vision under daylight conditions (Martin, 1993), so these birds likely utilize information from colorful conspecific eyes during daylight. However, the increasing prevalence of artificial light at night (ALAN) has allowed

some diurnal animals to remain active at night (Kurvers & Hölker, 2015) and potentially use visual information to guide their nocturnal behaviors. European blackbirds (*Turdus merula*) forage later into the evening under artificial light compared with no artificial light (Russ et al., 2015), possibly because they can see their prey better. Peahens perform more head scans under artificial nighttime lighting (Yorzinski et al., 2015) and potentially do so to visually detect predators that they otherwise would be unable to see at night. Similarly, individuals under ALAN might be able to engage in social behaviors throughout the night (Kurvers & Hölker, 2015). For example, Kurvers & Hölker (2015) predict that visual sexual signals will be more conspicuous under ALAN and this will result in increased mating interactions. Similarly, they predict that individuals will be more likely to detect foraging conspecifics under ALAN, which could lead to increased interference competition or increased food sharing, depending on the social system. Despite the increasing number of studies examining the effects of ALAN on animals (Sanders et al., 2021), we still know relatively little about how ALAN influences social

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interactions. Since many social interactions rely on information extracted from conspecific eyes, it is important to determine whether individuals can detect conspecific eyes under ALAN conditions.

Given their highly social nature and attraction to ALAN, great-tailed grackles (*Quiscalus mexicanus*; henceforth ‘grackles’) are an excellent model system to study social behavior under ALAN. Grackles are an avian species that are highly social and commonly roost in areas with artificial light at night. They are unusual in the degree to which they seek out locations with artificial lights: they commonly congregate in brightly-lit shopping areas at night and remain active long past sunset (c. f., [Debrot, 2014](#)). Grackles exhibit a range of iris colors, ranging from brown irises in younger birds to yellow irises in adult birds ([Selander, 1958](#)). Furthermore, grackles are sexually dimorphic, with adult males being larger and exhibiting black feathers surrounding their eyes, while adult females exhibit brown feathers surrounding their eyes.

The aim of our study was to determine the visual conditions under which grackles can detect conspecific eyes. We hypothesized that they should be able to discriminate conspecific eyes under daylight and comparatively intense ALAN conditions (regardless of iris color) and would be able to do so at greater distances under daylight compared to ALAN conditions. We expected the grackles to perform worse under ALAN conditions because the spectrum of artificial light is more limited (no ultraviolet wavelengths), has a different shape, and is dimmer compared to daylight. We adopted a visual modelling approach that allowed us to estimate the maximum distances at which grackles could discriminate conspecific eyes under daylight and bright ALAN. This visual modelling approach has previously been used to examine gaze discriminability in nonhuman primates ([Whitham et al., 2022a; b](#)) as well as discriminability in a wide range of other contexts and species (e. g., [Nokelainen et al., 2021](#); [Rodríguez-Morales et al., 2021](#); [Feldmann et al., 2021](#)). We then used low-light visual modelling to estimate the minimum artificial light level at which grackles could discriminate conspecific eyes, using techniques inspired by recent work modelling color discrimination by nocturnal hawkmoths under ALAN ([Briolat et al., 2021](#)). Lastly, we examined whether the age and sex of the grackles impacted eye detection. Because iris color likely varies with age in grackles ([Selander, 1958](#)), we examined whether body size (a proxy for age) impacted gaze discriminations.

2. Methods

2.1. Study animals

We examined eye discriminability in 30 great-tailed grackles (22 females; 8 males) between August and November 2021. The birds were captured from the wild in Brazos (30.66° N, 96.30° W) and Bastrop (30.10° N, 97.31° W) counties in Texas. The birds were housed in outdoor aviaries (2.1 m × 2.1 m × 1.9 m; 30.56° N, 96.41° W). We measured their wing length upon capture. The study was approved by Texas A&M University’s Animal Care and Use Committee (#2019–0219).

The grackles measured in this study often roost very close (as close as 2.9 m at our study site) to artificial light sources at night, where the luminance levels exceed 800 lux, meaning eye color would likely be assessed under photopic (daytime equivalent) light intensities ([Olsson et al., 2015](#); [Renoult et al., 2017](#)). However, the grackles also sometimes roost farther away from artificial light sources, or they roost within trees that block some of the artificial light; in these cases, at our study site, the luminance levels were as low as 2 lux and are best modeled with low-light visual models. We have anecdotally observed grackles under ALAN engaging in aggressive (e.g., fighting for food) and other types of interactions (e.g., begging for food) after sunset ([Video S1](#)).

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.envpol.2022.120000>.

2.2. Photography collection

We photographed each bird using methods for measuring animal coloration from digital photography ([Stevens et al., 2007](#); [Troschianko & Stevens, 2015](#)). For each photograph, the birds were temporarily restrained with velcro straps in a foam cradle and placed atop a wooden board ([Fig. 1A](#)). The wooden board was covered in black ethylene-vinyl acetate (EVA) foam to minimize UV background reflectance ([Dell’Aglio et al., 2018](#)). The birds’ beaks were held stationary by securing them to a wooden beak holder with tape. A 20% gray standard (Spectralon Lab-sphere) and a ruler were directly beside the beak holder. The camera was positioned perpendicular to the birds’ left eye (0.06 m away). In order to take UV photographs, the camera (Sony a7 II Mirrorless) underwent a full spectrum conversion (Kolari Vision). The camera was then outfitted with a M42-M42 lens adjustable focusing helicoid (25–55

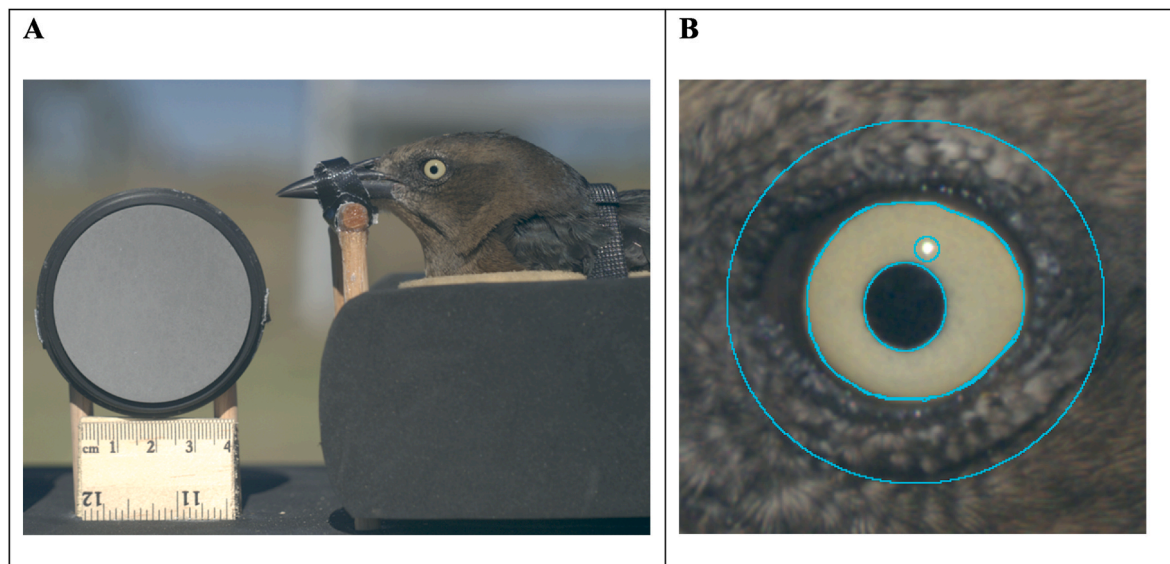


Fig. 1. (A) Experimental set-up. (B) ROIs demarcating the pupil, iris (excluding the corneal reflection from the sun), and feathers surrounding the iris.

mm) and a Nikon EI-Nikkor 80 mm (1:5.6) lens. A custom filter adapter was attached to the Nikkor lens so that a UV/IR blocking filter (Baader UV/IR-Cut filter; 400 nm–680 nm) or a UV pass filter (Baader U-filter; 320 nm–380 nm) could be added. We took sequential photographs using a wired remote (Revo VRS-Multi) in the human-visible spectrum (UV/IR Cut filter) and UV spectrum (U filter). We used the same settings for all photographs: RAW format, 400 ISO, f/5.6 aperture, and exposure set to aperture priority.

We photographed each bird under two conditions: daylight and ALAN. The daylight photographs were taken outside on clear days between 11:00 and 17:00 (at least 3 h after sunrise and 2 h before sunset) in an open field. The ALAN photographs were taken at night between 20:00 and 23:00 (between one and 5 h after sunset) in the parking lot of a local shopping complex at a spot beside lampposts (using LED lighting) where grackles often roost at night. We avoided taking photographs when vehicles were directly driving by our setup. Because the artificial light did not contain ultraviolet light, we only took photographs in the human-visible spectrum for the ALAN photographs. We recorded the irradiance at the time each photograph was taken (JETI specbos 1211UV; 230–900 nm; Fig. 2). It was not always possible to photograph

a bird during daylight and ALAN conditions within 24 h of when it was captured (because the weather was poor or logistical reasons prevented us from doing so). In these cases, we photographed these birds ($n = 20$) in an indoor light box (1 m × 1 m × 1 m) within 24 h of capture as well as within 24 h of the daylight or ALAN photograph (whichever was last). The final photograph in the light box was usually completed within seven days of capture (mean ± SE: 7 days ± 1.4; range: 4–32 days). These photographs were taken inside a light box with the only light source being an Iwasaki eye-Color MT70D G12 6500K lightbulb; we removed the UV filter on the lightbulb with a steel brush so that it would emit light in the UV–visible range (300–700 nm). By photographing birds in the lightbox (using a consistent lighting source), we could assess whether the birds' coloration or luminance changed while in captivity. We did not photograph birds in the lightbox when we were able to photograph them during daylight and ALAN conditions within 24 h of when they were captured. We did not collect lightbox photographs of these birds ($n = 10$) to minimize stress associated with restraining them additional times within a short period; furthermore, our results (see below) indicated that their eye coloration and luminance remained the same even after they were in captivity for a week or more.

2.3. Visual modelling

We processed the photographs using the micaToolbox plugin (v.2.2.2) for Image J (v.1.53a; Rasband, 1997; Stevens et al., 2007; Troscianko and Stevens, 2015). We extracted linear images from the RAW files, then used the known color values of the gray standard to normalize light levels across the images. Next, a model was used to transform the pixel values of the images from a form representative of the spectral sensitivities of the camera to a form representative of the visual sensitivity of the blue tit (*Cyanistes caeruleus*; Hart et al., 2000), a commonly-used model species representing ultraviolet-sensitive avian vision. While the exact visual sensitivities of grackles are unknown, they and their close relatives fall within the ultraviolet-sensitive category of avian visual systems (Ödeen & Hästad, 2003, 2010), within which there is very little difference in color vision capabilities between species (Hart & Hunt, 2007; Kelber, 2019). We used the spectral sensitivity of a camera system that was included within micaToolbox (daylight: Sony A7 Nikkor EI 800 300–700; ALAN: Sony A7 Nikkor EI 800 400–700). For modeling purposes, we set the photography and model illuminant to the irradiance measurements that we recorded when we took each photograph. These steps produced short wave (SW), medium wave (MW), long wave (LW), ultraviolet (UV; daylight photographs only), and double cone (D; double cone, luminance) mapped images. We created regions-of-interest (ROIs; Fig. 1B) within these images and measured the cone catch values for the SW, MW, LW, UV (daylight photographs only), and D receptors of each ROI; the cone catch values indicate how much each cone type is stimulated.

We also calculated the hue and chroma of each ROI from the cone catch values. Hue is the type of color, while chroma (or saturation) is the perceived intensity of a color. We calculated hue based on a principal component analysis approach (Komdeur et al., 2005; Winters et al., 2014). We first calculated the relative cone catch values for the SW, MW, LW, and UV receptors, and then performed a principal component analysis on the covariance matrix with these four variables. The first principal component explained 93.8% of the variation, with the cone catch values for LW and MW receptors loading positively and the SW and UV receptors loading negatively. Based on these loadings, we calculated hue as the ratio of LW + MW cone catches to SW + UV cone catches. This calculation of hue is only one possible hue dimension, but similar ratios have been used previously to characterize hue in passerines (Spottiswoode & Stevens, 2011). Chroma was calculated based on the Euclidean distance in tetrahedral color space from the achromatic origin. We created three ROIs: pupil (oval outlining the pupil), iris (ring outlining the iris) and feathers (ring outlining the feathers immediately surrounding the iris; the outer diameter of the ring was two mm); we

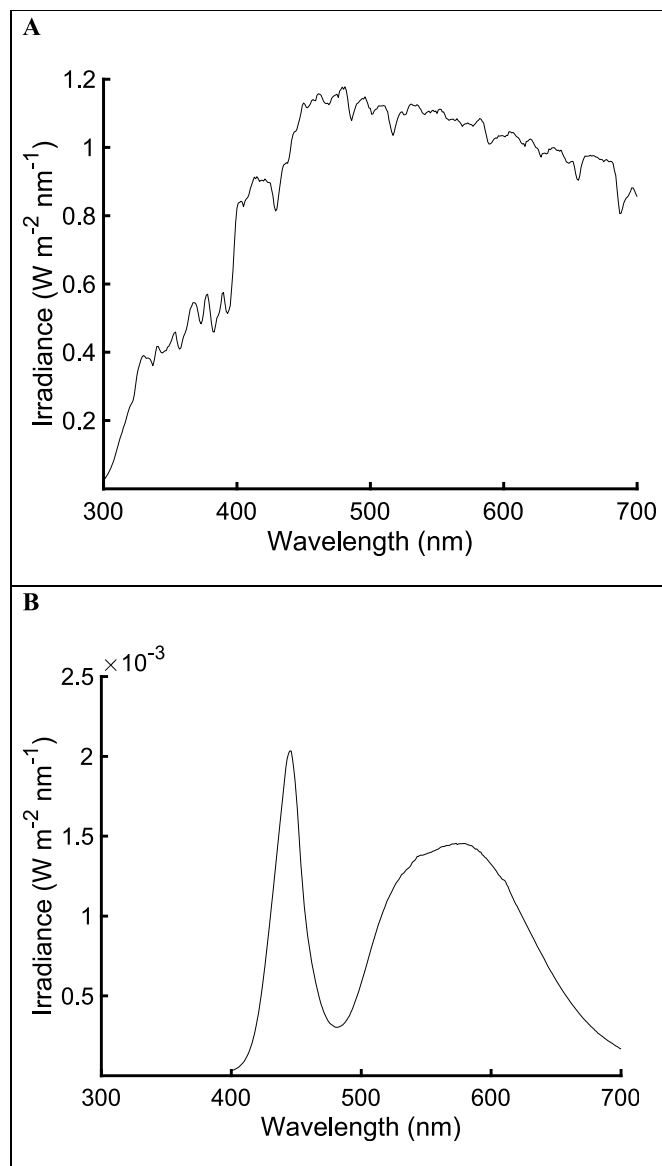


Fig. 2. Irradiance of (A) daylight and (B) ALAN conditions averaged across all birds.

excluded corneal reflections from the ROIs. Lastly, the above steps were repeated on images generated by AcuityView (Caves & Johnsen, 2018; van den Berg et al., 2020a), which created images that were representative of the birds' vision at varying distances (0–12 m in increments of 0.25 m). While the visual acuity of grackles is not known, acuity scales closely with eye size (Kiltie, 2000; Martin, 2017), so acuity of the closely related and similarly sized blackbird (*Turdus merula*; 22.5 cycles per degree; Donner, 1951) provides a reasonable estimate.

We modeled eye discriminability in grackles using both photopic and low-light visual models because grackles are active during the daytime (photopic conditions) but roost in areas with a range of artificial light intensities at night (photopic and low-light conditions). Low light levels are associated with gradually poorer chromatic discrimination through the mesopic range associated with dusk and dawn, and eventually a switch from cone-based to rod-based scotopic (achromatic) vision at night.

Our photopic visual models used the chromatic receptor noise limited (RNL) model (Vorobyev & Osorio, 1998) and the achromatic RNL model (Siddiqi et al., 2004) to estimate the discriminability of ROIs using the processed images. In RNL modeling, a Weber fraction is used to describe an animal's capacity to make discriminations based on chromatic or achromatic information, with lower numbers suggesting the animal is capable of finer discriminations. We set the Weber fractions in the chromatic model such that the grackles' Weber fraction was 0.05 for their most numerous cone receptor type, and values for other cone types were a function of their frequency relative to the most numerous cone type; this parameterization, and the 0.05 fraction value for the most numerous receptor type, was preset in micaToolbox and is commonly used in avian studies (Vorobyev and Osorio, 1998). We set the Weber fraction in the achromatic model to 0.34, which is the value for another passerine species (*Sturnus vulgaris*; Olsson et al., 2017). These fraction values suggest that for equivalent chromatic and achromatic signals, grackles will be much more capable of making discriminations on a chromatic rather than achromatic basis. This modeling produced values (ΔS) among ROIs that predict whether ROIs are likely discriminable from each other or not at specific distances. A ΔS of three or greater typically indicates that ROIs are discriminable under natural settings (Siddiqi et al., 2004; Langmore et al., 2011).

To estimate chromatic contrasts under lower levels of artificial light, we modified our calculations to account for photon-shot noise, caused by randomness in the arrival of low numbers of photons reaching photoreceptors in low light, following methods for estimating color discrimination by birds (Olsson et al., 2015) and nocturnal hawkmoths (Briolat et al., 2021). Modelling color differences in low light requires absolute quantum catches for the different photoreceptor types, calculated with spectral measurements of stimulus reflectance and a number of parameters relating to the visual system of the receiver. Here, we estimated quantum cone catches under various levels of ALAN by scaling the relative cone catch measurements obtained above under ALAN conditions to reasonable values, based on quantum catches for domestic chickens, as recorded in Olsson, Lind & Kelber (2015). This allows us to preserve the relative stimulation of different photoreceptor types, providing a best estimate of overall quantum catches at realistic orders of magnitude for different light levels. Receptor-specific photon-shot noise terms were calculated following equations in Briolat et al. (2021), modified from Olsson, Lind & Kelber (2015), and using relative cone ratios based on the visual system of *C. caeruleus* (Hart et al., 2000). These were then applied as noise terms when calculating coordinates in the tetrachromatic RNL space, with our estimated quantum catches, following equations in Renoult et al. (2017). Finally, chromatic contrast in low light conditions was calculated as the Euclidean distance between points in the RNL space. This method does not enable us to model the effects of distance between conspecifics on the attenuation of chromatic signals; however, it provides an estimate of the light levels under which grackles may no longer perceive color signals from conspecific eyes, even of birds close to them. Achromatic contrasts were not modeled

under low light conditions, as the RNL model has been shown to rather poorly capture behavioral responses to achromatic contrasts, and more context-specific information is required for better modelling of how achromatic information is processed (van den Berg et al., 2020b), problems which would only be accentuated under low light levels.

2.4. Statistical analysis

We analyzed the data using logistic regressions and mixed linear models (SAS; version 9.4; SAS Institute Inc., Cary, NC, USA). First, we assessed whether iris color and luminance were related to wing size (a proxy for overall body size, which likely correlates with age; Baldwin et al., 1933; Selander, 1958). We ran mixed linear models with hue, chroma, or luminance as the dependent variable; wing length (normalized), sex, and their interaction were the independent variables. For wing length, we calculated a normalized wing length value for each sex because males always had longer wing lengths than females (and it was otherwise not possible to run this model because of complete separation of datapoints). For testing this wing-size correlation, we only analyzed the daylight images because iris color and luminance in the daylight and ALAN were highly correlated (SW: $F_{1,28} = 93.06$, $p < 0.001$, $R^2 = 76.9\%$; MW: $F_{1,28} = 142.01$, $p < 0.001$, $R^2 = 83.5\%$; LW: $F_{1,28} = 144.15$, $p < 0.001$, $R^2 = 83.4\%$; D: $F_{1,28} = 141.87$, $p < 0.001$, $R^2 = 83.5\%$).

Second, using the photopic visual models, we determined whether the grackles' ability to discriminate between ROIs was influenced by lighting condition (daylight or ALAN), sex, or wing length. We calculated the maximum distance at which grackles could discriminate between the iris versus pupil as well as the iris versus feathers based on chromatic and achromatic information. Because we do not know which features the grackles may use to evaluate the eyes, we conservatively considered both the contrast between the iris and pupil as well as the contrast between the iris and surrounding feathers. The maximum distance was calculated by determining the farthest distance at which the ROIs were discriminable (i.e., ΔS was equal to three). In all cases, this maximum distance did not occur exactly at one of the distances that we simulated. We therefore performed a linear interpolation to determine the distance at which ΔS was exactly 3.0. For example, if ΔS was 3.4 at 3 m and ΔS was 2.7 at 3.25 m, we then estimated the maximum distance to be 3.1 m. Because some ROIs could not be discriminated at any distance, we ran this analysis in two steps. In the first step, we performed logistic regressions with a Firth correction with the dependent variable being whether the grackles could discriminate between the ROIs or not at any distance; in the second step, we performed mixed linear models with the dependent variable being the maximum distance at which the grackles could discriminate between ROIs (excluding any ROI comparisons that were not discriminable at any distance). The independent variables were lighting condition (daylight or ALAN), sex, wing length (normalized), and their two-way interactions (the three-way interaction was not significant in any model so was dropped from all analyses). Bird identity was included as a repeated measure. To directly compare the photopic visual models and low-light visual models for the ALAN condition, we also compared the ΔS values from the photopic visual models of the chromatic iris versus pupil contrasts and the iris versus feathers contrasts without the acuity correction (i.e., distance = 0).

We ran a mixed linear model to test whether grackle eye coloration changed while the birds were in captivity. The dependent variables were the maximum distance at which grackles could discriminate between the iris versus pupil as well as the iris versus feathers based on chromatic and achromatic information (excluding any ROI comparisons that were not discriminable at any distance); the independent variable was when the measurements were taken (within 24 h of the bird being captured or at a later date). Bird identity was included as a repeated measure. If an ROI comparison was not discriminable at any distance in the initial photograph (within 24 h of the bird being captured), it was also not discriminable in the photograph taken at the later date (except in the case of one bird for the pupil versus iris achromatic contrast and one bird

for the iris versus feather achromatic contrast).

Lastly, using the low-light visual models, we determined whether the grackles' ability to discriminate between ROIs in low light conditions was influenced by sex or wing length. We determined the minimum light level at which grackles could discriminate between the iris versus pupil as well as the iris versus feathers based on chromatic information. The minimum light level was calculated by determining the lowest light level (in increments of one lux) at which the ROIs were discriminable (i. e., ΔS was above three). The dependent variable was the minimum light level at which the grackles could discriminate between ROIs (excluding any ROI comparisons that were not discriminable at any distance); the independent variables were sex, wing length (normalized), and their interactions (the three-way interaction was not significant in any model so was dropped from all analyses).

3. Results

The iris color of grackles varied along a continuum from dull brown to bright yellow (Fig. 3; Fig. 4). Grackles with shorter wings had irises with greater hue (brownier), lower chroma (less saturated) and lower luminance (less bright) than grackles with longer wings (Table 1; Fig. 5). There were no differences between the sexes in iris color or luminance (Table 1).

3.1. Photopic visual models

Based on the photopic visual models, the grackles could discriminate between the iris versus pupil as well as the iris versus feathers at some distance for the majority of conspecifics in both daylight and ALAN (Table 2). The ability of grackles to discriminate or not at some distance between the iris versus pupil as well as the iris versus feathers using chromatic or achromatic information was unaffected by the lighting condition, sex, or wing length ($p > 0.05$ for all variables). However, the grackles were able to discriminate between the iris versus pupil as well as the iris versus feathers using chromatic or achromatic information at farther distances during daylight compared to ALAN (Table 3; Fig. 6; Fig. 7). On average, based on chromatic information during daylight conditions, the iris was discriminable from the pupil and feathers from as far away as 2.3 m and 5.0 m, respectively; on average, based on chromatic information during ALAN conditions, the iris was discriminable from the pupil and feathers from as far away as 2.0 m and 2.1 m, respectively (Fig. 7). Overall, these distances were shorter when using achromatic information. Based on achromatic information during daylight, the iris was discriminable from the pupil and feathers from as far away as 1.3 m and 2.1 m, respectively; on average, based on achromatic information during ALAN conditions, the iris was discriminable from the pupil and feathers from as far away as 1.0 m and 1.6 m, respectively (Fig. 7). At close-up distances (distance = 0) under ALAN, the chromatic contrast between the iris and pupil (ΔS : male mean \pm SE: 12.2 ± 1.0 , female mean \pm SE: 11.3 ± 0.6) is greater than the contrast between the iris and feathers (ΔS : male mean \pm SE: 8.5 ± 1.4 , female mean \pm SE: 5.2 ± 0.6 ; $F_{1,28} = 250.15$, $p < 0.0001$).

Furthermore, grackles could discriminate the iris versus feathers using chromatic information of male conspecifics at farther distances than female conspecifics (Table 3; Fig. 7). During daylight, they could discriminate the iris versus feathers of males at 8.0 m (on average) but could make this same discrimination of females at only 3.9 m distance. The irises of adult males are surrounded by black feathers while the irises of adult females are surrounded by brown feathers. And, during daylight conditions, grackles could discriminate the iris versus feathers using chromatic information of conspecifics with longer wings at farther distances compared to conspecifics with shorter wings (Table 3; Fig. 8). There were no changes in the ability of grackles to discriminate between the iris versus pupil or iris versus feathers after the birds were in captivity (chromatic iris versus pupil: $F_{1,19} = 3.29$, $p = 0.086$; chromatic iris versus feathers: $F_{1,18} = 0.00$, $p = 0.99$; achromatic iris versus pupil:

$F_{1,11} = 2.07$, $p = 0.18$; achromatic iris versus feathers: $F_{1,8} = 1.73$, $p = 0.23$).

3.2. Low-light visual models

Based on the low-light visual models, grackles could discriminate between the iris versus pupil as well as the iris versus feathers at relatively low light levels under ALAN (using chromatic information). The grackles could discriminate between the iris versus pupil when the light level was above approximately 4 lux (mean \pm SE: 3.6 ± 0.31 lux; range: 2–8 lux). Similarly, they could discriminate between the iris versus feathers when the light level was above approximately 21 lux (mean \pm SE: 21.3 ± 7.0 lux; range: 2–159 lux; excluding the five birds with irises and feathers that were not discriminable under any luminance level; Table 2). The minimum light level at which grackles could discriminate the iris versus pupil as well as the iris versus feathers was unaffected by sex, wing length, or their interaction ($p > 0.25$).

4. Discussion

Based on a visual modelling approach, we found that great-tailed grackles can detect the eyes of conspecifics under both daylight and ALAN, although the detection distance is reduced under ALAN. Furthermore, during daylight conditions, grackles can detect the eyes of larger (and likely older) conspecifics at farther distances than they can detect the eyes of smaller (and likely younger) conspecifics. The ability of grackles to detect conspecific eyes has important implications for their social interactions.

Despite variation in iris colors, grackles can detect the eyes of conspecifics under varying lighting conditions. During daylight conditions, on average, we found that they can discriminate the iris from the pupil when they are as far away as 2.3 m; similarly, we found that they can discriminate the iris from the surrounding feathers when they are 5 m away. Their ability to make these discriminations is better when they are using chromatic rather than achromatic information. And, they can discriminate the iris from the feathers at farther distances when the conspecifics are larger (and therefore have more yellow eyes). Even during ALAN conditions, the grackles are still efficient at detecting the eyes. On average, we found that they can distinguish the iris from the pupil or surrounding feathers when they are 2.0 and 2.1 m away, respectively. In line with our hypothesis, the grackles are modeled to be slightly worse at detecting conspecific eyes at farther distances during ALAN compared with daylight conditions, especially when discriminating the iris versus surrounding feathers. This suggests that any social interactions relying on eye detection need to occur at shorter distances under ALAN compared with daylight conditions, which could potentially alter the benefits and costs of signaling. For example, grackles approaching another conspecific at this closer distance under ALAN may have a higher risk of contracting a disease or less time to escape from a conspecific attack. In addition, the artificial light is lacking UV wavelengths, thereby disguising the UV information contained within the grackles' feathers and eyes (Eaton, 2006; Toomey et al., 2010); the lack of UV information under ALAN could disrupt social interactions that rely on UV signaling. Furthermore, the grackles can discriminate conspecific eyes even when the light intensity of artificial sources is low: they can discriminate the pupil from the iris when the artificial light is as low as approximately 4 lux, on average. This low intensity of artificial light is still substantially higher than bright moonlight (Kyba et al., 2017).

The ability to detect the eyes of conspecifics likely promotes social behaviors (Emery, 2000). Grackles can potentially use information from conspecific eyes to evaluate gaze direction. The ability to evaluate gaze direction can aid in many activities, such as avoiding predators (Carter et al., 2008), finding food (Burkart & Heschl, 2006), and responding to conspecific threats (Maestripieri & Wallen, 1997). Given that grackles exhibit a wide range of eye movements (Yorzinski, 2021), individuals could use the eye direction of conspecifics to guide their decisions. In

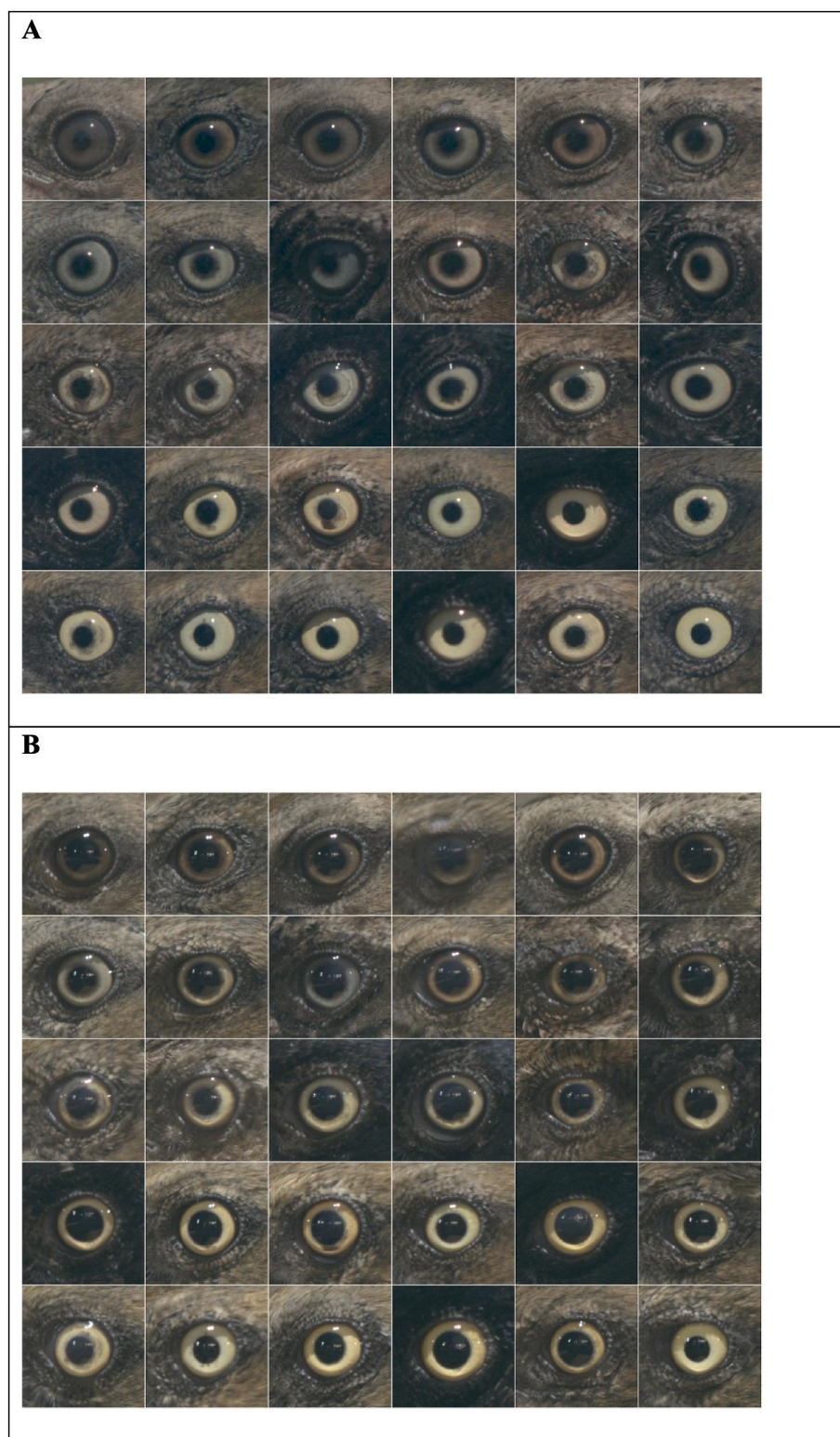


Fig. 3. The eyes of female and male great-tailed grackles ($n = 30$) at a simulated distance of 0 using the avian vision phenotype during (A) daylight and (B) ALAN conditions. For illustration purposes, UV information is not displayed.

addition, grackles could evaluate conspecific eyes to assess age (Selander, 1958; Bortolotti et al., 2003; Polakowski et al., 2020; Passarotto et al., 2020). Because young individuals have browner eyes than adults (Selander, 1958; this study), individuals could benefit by assessing eye color to inform aggressive and courtship decisions. Grackles could also examine conspecific eyes to evaluate the health of

conspecifics (Bouwman & Hawley, 2010; Griggs, 2019). Birds can suffer from ocular diseases and trauma, and the appearance of their eyes can reflect this (Griggs, 2019). Based on eye appearances, individuals could avoid interacting with unhealthy or injured conspecifics (Bouwman & Hawley, 2010), and possibly do so at distances that limit disease transmission.

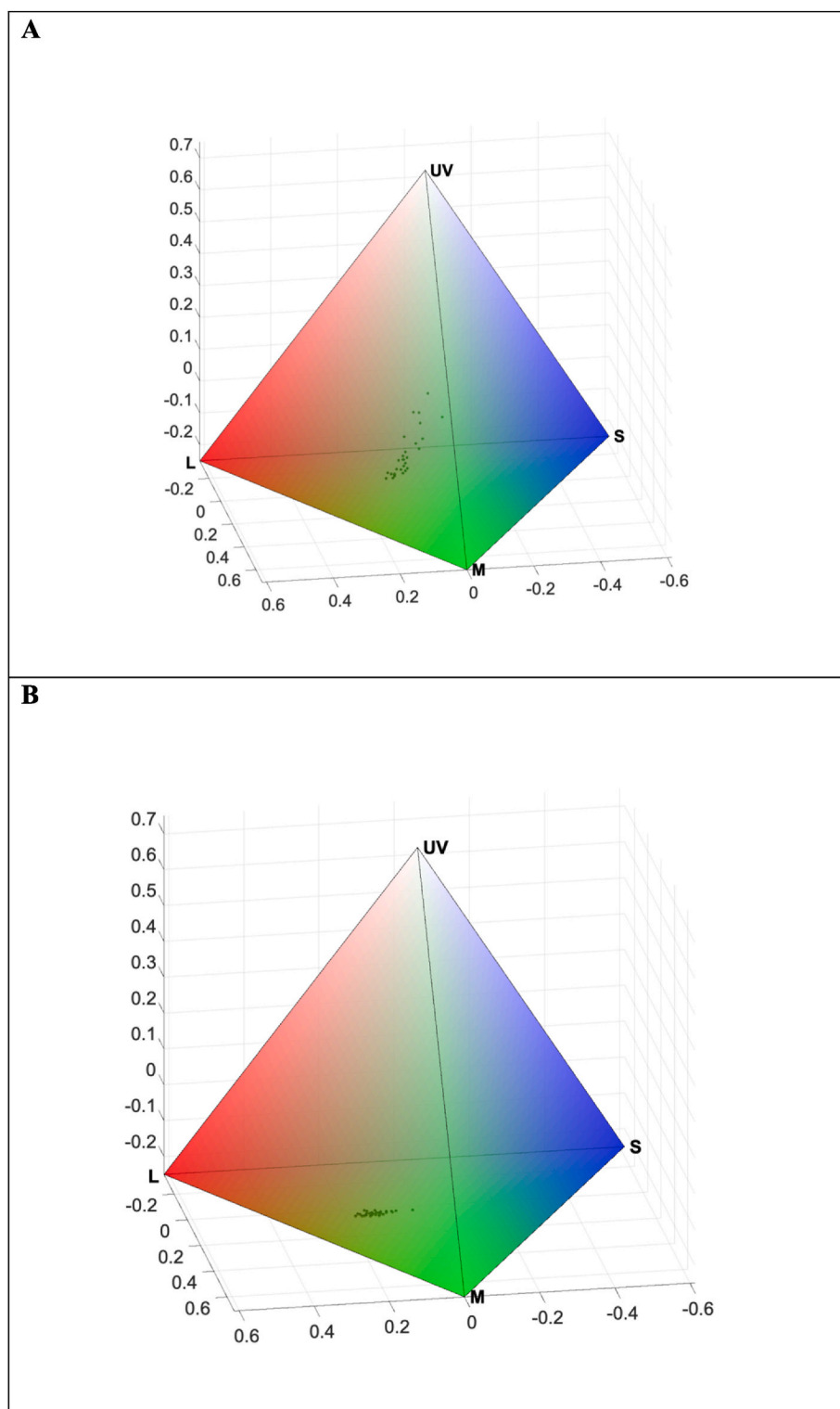


Fig. 4. Distribution of perceived coloration of female and male irises in tetrahedral color space (created using [Stoddard & Prum, 2008](#)) during (A) daylight and (B) ALAN conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1

The influence of wing length (normalized) and sex on iris color (hue and chroma) and luminance. F values with p-values in parentheses are displayed. Numerator degrees of freedom is 1, denominator degrees of freedom is 26.

	Hue	Chroma	Luminance
Wing Length	20.35 (<0.0001)*	23.93 (<0.0001)*	9.27 (0.0053)*
Sex	2.73 (0.11)	3.22 (0.084)	2.75 (0.11)
Wing Length*Sex	0.70 (0.41)	0.92 (0.35)	1.38 (0.25)

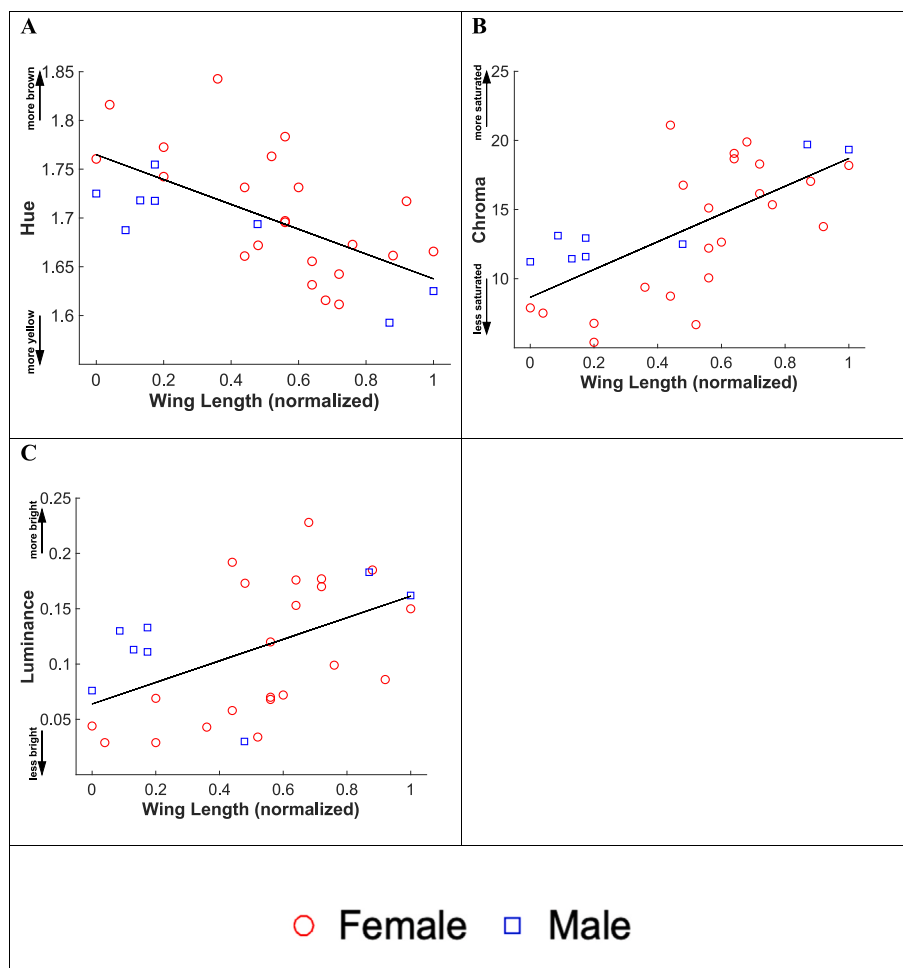


Fig. 5. The relationship between wing length versus iris color and luminance. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2

The number of grackles (out of 30) whose ROIs could be discriminated at some distance based on chromatic or achromatic information in daylight and high levels of ALAN.

	Chromatic		Achromatic	
	Iris vs. Pupil	Iris vs. Feathers	Iris vs. Pupil	Iris vs. Feathers
Daylight	30	30	29	17
ALAN	30	25	28	15

Birds can potentially benefit from detecting conspecific eyes during both daylight and nighttime conditions. Grackles are highly social, often foraging in large flocks (sometimes larger than 200 individuals) during

the daytime (Hanson, 1976) and gathering with hundreds of other conspecifics at nocturnal roosts (Hall & Harvey, 2007). Before artificial light was prevalent at night, interactions using visual information would have been limited because grackles likely cannot see well under those conditions (Martin, 1993; this study). Grackles' light-gathering ability is estimated to be similar to other diurnal avian species and therefore they do not likely see well in low-light conditions (Wilson et al., 2021). However, ALAN has the potential to increase the opportunities for intraspecific communication (Kurvers & Hölker, 2015). Because of the increased light from artificial sources, individuals can potentially exchange visual signals and cues throughout the night that would otherwise be undetectable. These additional exchanges, however, could be costly if they disrupt normal sleep cycles (Aulsebrook et al., 2021) or

Table 3

The impact of lighting condition, sex, and wing length (normalized) on the maximum distance at which grackles can discriminate between the pupil versus iris as well as the iris versus feathers using chromatic and achromatic information. F values are displayed with p-values in parentheses. The numerator degrees of freedom is one. The denominator degrees of freedom is 27, 22, 25, and 11 for the chromatic iris versus pupil, chromatic iris versus feathers, achromatic iris versus pupil, and achromatic iris versus feathers, respectively.

	Chromatic		Achromatic	
	Iris vs. Pupil	Iris vs. Feathers	Iris vs. Pupil	Iris vs. Feathers
Lighting condition	8.84 (0.0061)*	20.70 (0.0002)*	9.07 (0.0059)*	8.48 (0.014)*
Sex	2.20 (0.15)	9.81 (0.0048)*	1.66 (0.21)	0.030 (0.86)
Wing Length	2.26 (0.14)	3.85 (0.062)	0.41 (0.53)	1.13 (0.31)
Lighting condition*Sex	2.85 (0.10)	29.63 (<0.0001)*	5.61 (0.026)*	1.29 (0.28)
Lighting condition* Wing Length	2.20 (0.15)	9.19 (0.0061)*	0.79 (0.38)	0.05 (0.82)
Sex* Wing Length	0.94 (0.34)	0.74 (0.40)	1.55 (0.22)	4.69 (0.53)

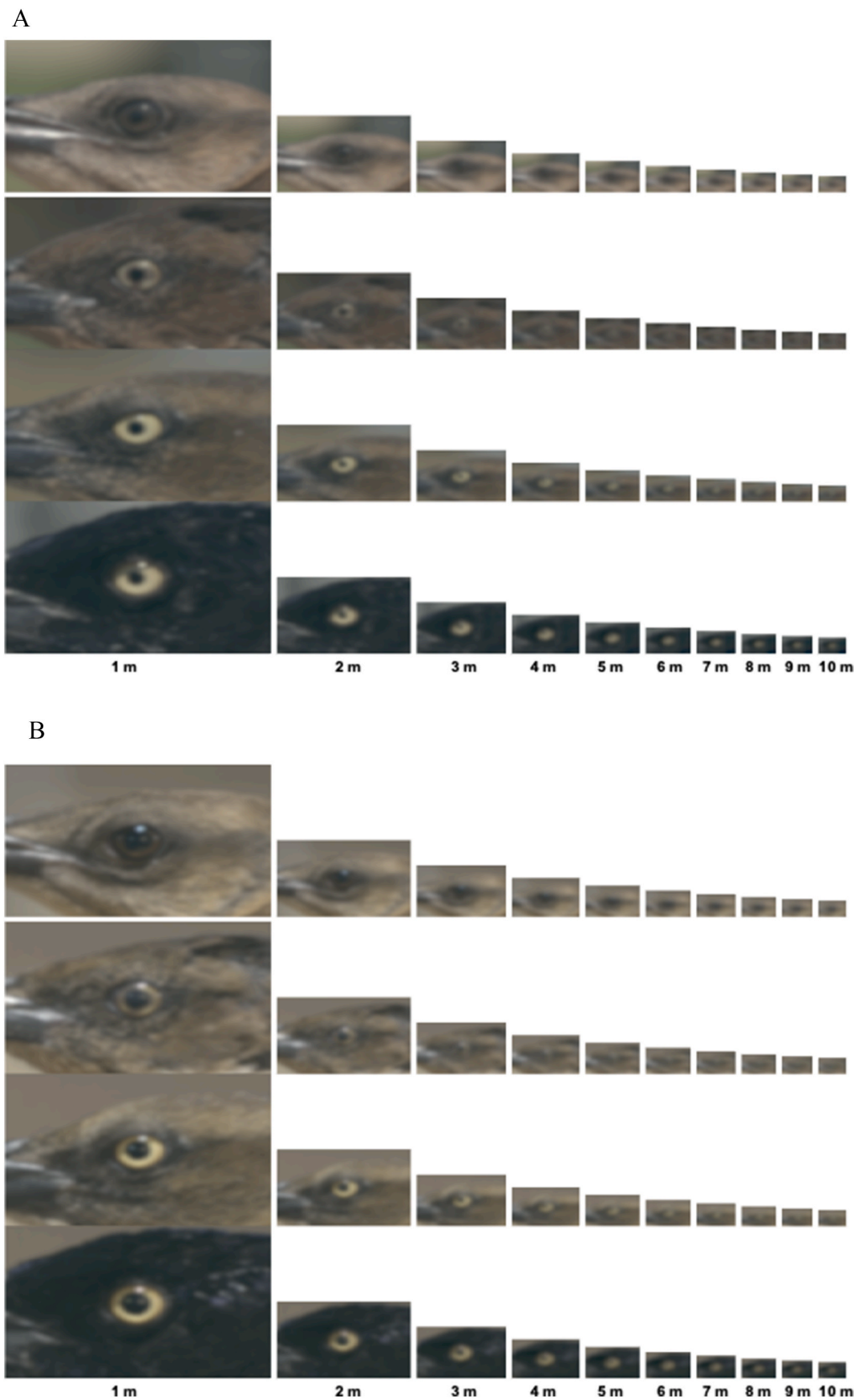


Fig. 6. The eyes of a brown, brown speckled, and yellow eyed female as well as a yellow eyed male at varying distances using the avian vision phenotype during (A) daylight and (B) ALAN conditions. For illustration purposes, UV information is not displayed. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

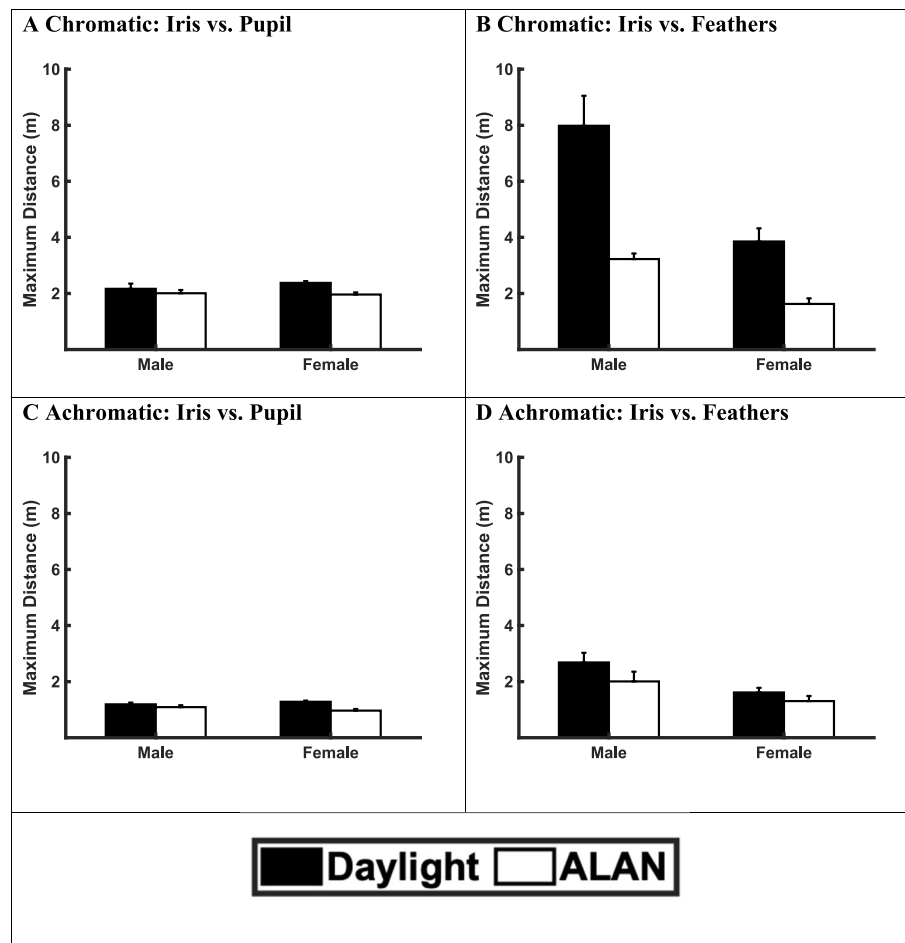


Fig. 7. The maximum distance at which grackles can discriminate between (A) pupil versus iris (chromatic), (B) iris versus feathers (chromatic), (C) pupil versus iris (achromatic), and (D) iris versus feathers (achromatic) relative to the lighting condition. Means \pm standard errors are displayed.

have high energetic costs (Vehrencamp et al., 1989). There is some evidence suggesting that opportunities for social communication could be enhanced by ALAN. Recent work modelling the color vision of a nocturnal hawkmoth suggests some types of artificial lights may enhance color contrasts in conspecific wing patterns (Briolat et al., 2021), potentially facilitating intraspecific communication if these color signals are involved. Similarly, based on a visual modelling approach, we found that grackles can detect the eyes of conspecifics at night when there is artificial lighting. This ability potentially allows them to engage in social behaviors, such as courtship and competition, throughout the night in areas with artificial lighting (although there may be costs associated with these behaviors, such as energy expenditures). Additional studies that document their social interactions under artificial versus natural light at night would be informative.

We also found that great-tailed grackles exhibit iris colors ranging from dull brown to bright yellow. A previous study on a closely-related species (boat-tailed grackles (*Quiscalus major*)) has suggested that iris color in grackles changes during development, with younger birds displaying brown eyes and older birds exhibiting yellow eyes (Gillespie & Gillespie, 1932; Selander, 1958). Our results are consistent with this developmental hypothesis, as we found that smaller (and presumably younger; Selander, 1958) grackles generally had irises that were browner, while larger (and presumably older) grackles had yellower irises. The grackles could discriminate between the iris and surrounding feathers of larger (older) birds at greater distances than smaller (younger) birds in daylight; this is not necessarily surprising given the sharper contrast between the yellow iris and brown/black feathers versus the milder contrast between the brown iris and brown/black

feathers. Similarly, the grackles could discriminate between the iris and surrounding feathers of males at greater distances than females. Given that adults are likely more aggressive than juveniles and males engage in costly fights with each other (Johnson & Peer, 2001), it might benefit grackles to gauge the intention of adults (especially other males) at a distance before approaching too closely. Additional studies will be necessary to confirm age and sex differences, and what, if any, functional consequences they have.

While our study provides a first step toward understanding eye detection in an avian species under both daylight and ALAN conditions, there are several noteworthy limitations. First, our study is based on a visual modeling approach that estimates the ability of birds to make visual discriminations. These estimates were based on parameters from closely-related species because the color vision and acuity of grackles are unknown. Among birds with ultraviolet vision, there is surprisingly little difference among species in their color vision (e.g. Hart & Hunt, 2007; Kelber, 2019). Similarly, acuity scales closely with eye size (Kiltie, 2000; Martin, 2017) such that grackle acuity can be well estimated. Experimental studies will also be necessary to confirm our findings to demonstrate that the grackles can detect conspecific eyes under different light conditions at specific distances and use that information to guide their decisions. Second, we used one location with LED lights on lampposts at a single shopping center to represent nighttime conditions under artificial light. Given that LED lights are increasingly being used for nighttime lighting (Gaston et al., 2015), this type of lighting is likely common at other locations where grackles roost. The specific type of artificial lighting is generally important for assessing the impacts of ALAN on animal visual ecology and behavior (Longcore et al., 2018;

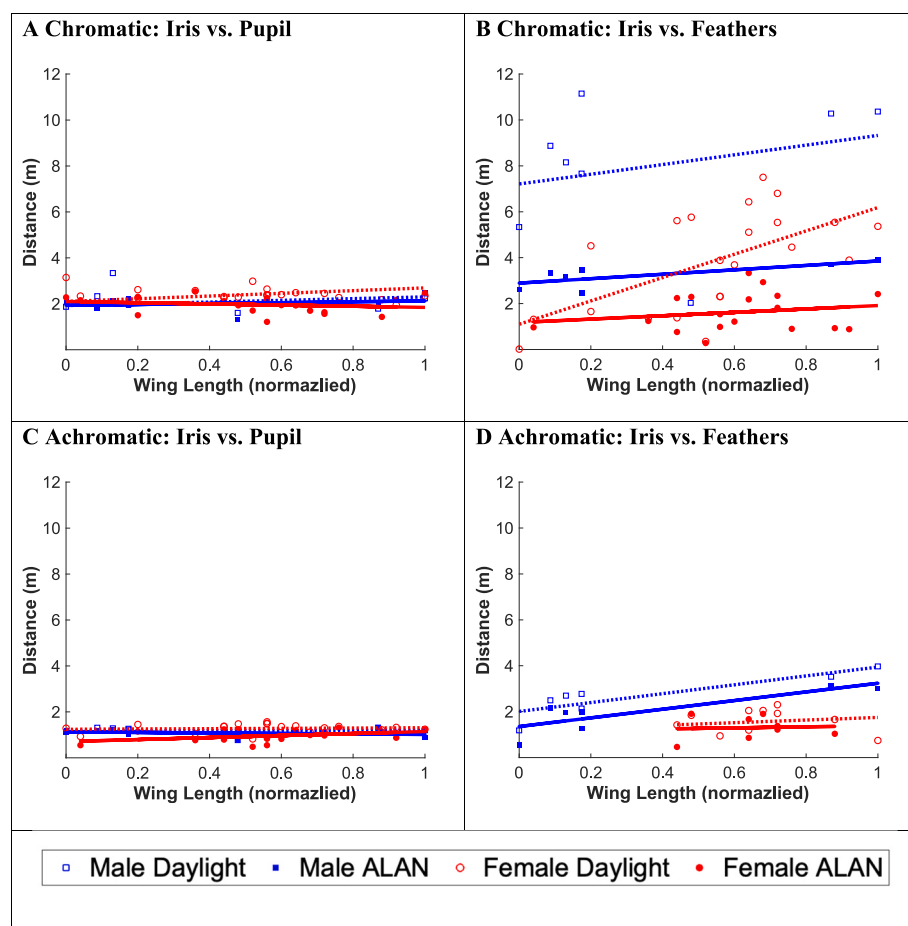


Fig. 8. The maximum distance at which grackles can discriminate between (A) pupil versus iris (chromatic), (B) iris versus feathers (chromatic), (C) pupil versus iris (achromatic), and (D) iris versus feathers (achromatic) relative to wing length. The blue dashed line represents males under daylight, blue solid line represents males under ALAN, red dashed line represents females under daylight, and red solid line represents females under ALAN. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Briolat et al., 2021). However, previous modelling suggests avian vision is not strongly impacted by the shape of broadband lighting irradiance spectra (such as those typically used in modern streetlights), because of their extremely wide range of wavelength sensitivity (Briolat et al., 2021); therefore, different types of artificial light would likely have minimal effects on their ability to discriminate colors.

5. Conclusion

We found that great-tailed grackles can detect conspecific eyes under low and high levels of ALAN using a visual modelling approach. Because conspecific eyes often convey important information about social and environmental factors, grackles can potentially use this information throughout the night in areas with artificial lighting. Additional research is needed to test whether grackles can behaviorally detect conspecific eyes under ALAN and use information from conspecific eyes to inform their decisions.

Author statement

Yorzinski: Conceptualization, Methodology, Software, Formal analysis, Investigation, Resources, Writing - Original Draft, Writing - Review & Editing; Troscianko: Conceptualization, Methodology, Software, Writing - Review & Editing; Briolat: Conceptualization, Methodology, Software, Writing - Review & Editing; Schapiro: Writing - Review & Editing; Whitham: Conceptualization, Methodology, Software, Writing - Review & Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data are uploaded as a supplement.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envpol.2022.120000>.

References

Aulsebrook, A.E., Johnsson, R.D., Lesku, J.A., 2021. Light, sleep and performance in diurnal birds. *Clocks & Sleep* 3, 115–131.

- Baldwin, S.P., Oberholser, H.C., Worley, L.G., 1933. Measurements of Birds, vol. 2. Scientific Publications of the Cleveland Museum of Natural History, Cleveland OH.
- Bortolotti, G.R., Smits, J.E., Bird, D.M., 2003. Iris colour of American Kestrels varies with age, sex and exposure to PCBs. *Biochem. Physiol. Zool.* 76, 99–104.
- Bouwman, K.M., Hawley, D.M., 2010. Sickness behaviour acting as an evolutionary trap? Male house finches preferentially feed near diseased conspecifics. *Biol. Lett.* 6, 462–465.
- Briolat, E.S., Gaston, K.J., Bennie, J., Rosenfeld, E.J., Troscianko, J., 2021. Artificial nighttime lighting impacts visual ecology links between flowers, pollinators and predators. *Nat. Commun.* 12, 4163.
- Burkart, J., Heschl, A., 2006. Geometrical gaze following in common marmosets (*Callithrix jacchus*). *J. Comp. Psychol.* 120 (2), 120–130.
- Carter, J., Lyons, N.J., Cole, H.L., Goldsmith, A.R., 2008. Subtle cues of predation risk: starlings respond to a predator's direction of eye-gaze. *Proc. Biol. Sci.* 275, 1709–1715.
- Caves, E.M., Johnsen, S., 2018. AcuityView: an R package for portraying the effects of visual acuity on scenes observed by an animal. *Methods Ecol. Evol.* 9 (3), 793–797.
- Debrot, A.O., 2014. Nocturnal foraging by artificial light in three Caribbean bird species. *J. Caribbean Ornithol.* 27, 40–41.
- Dell'Aglio, D.D., Troscianko, J., McMillan, W.O., Stevens, M., Jiggins, C.D., 2018. The appearance of mimetic *Heliconius* butterflies to predators and conspecifics. *Evolution* 72 (10), 2156–2166.
- Donner, K.O., 1951. The visual acuity of some passerine birds. *Acta Zool. Fennica* 66, 1–40.
- Eaton, M.D., 2006. A phylogenetic perspective on the evolution of chromatic ultraviolet plumage coloration in grackles and allies (Icteridae). *Auk* 123 (1), 211–234.
- Emery, N.J., 2000. The eyes have it: the neuroethology, function and evolution of social gaze. *Neurosci. Biobehav. Rev.* 24, 581–604.
- Feldmann, K.B., Grabenstein, K.C., Taylor, S.A., 2021. Achromatic plumage variation between and within hybridizing Black-capped and Mountain chickadees. *J. Field Ornithol.* 92 (2), 184–202.
- Gaston, K.J., Visser, E.M.E., Hölker, F., 2015. The biological impacts of artificial light at night: the research challenge. *Phil. Transact. Royal Soc.* 370, 20140133.
- Gillespie, M., Gillespie, J.A., 1932. Color of the iris in grackles. *Auk* 96, 96.
- Griggs, A., 2019. Ocular surface disease in birds. *Vet. Clin. Exot. Anim. Pract.* 22 (1), 53–68.
- Hall, D.W., Harvey, T.M., 2007. Mortality at a night roost of great-tailed grackles and European starlings during a spring hail storm. *Wilson J. Ornithol.* 199, 309–312.
- Hanson, M.T., 1976. Movement Patterns, Flock Parameters, and Habitat Selection in the Great-Tailed Grackle. Ph.D. dissertation. Texas A&M University, College Station, Texas.
- Hart, N.S., Partridge, J.C., Cuthill, I.C., Bennett, A., 2000. Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (*Parus caeruleus* L.) and the blackbird (*Turdus merula* L.). *J. Comp. Physiol.* 186, 375–387.
- Hart, N.S., Hunt, D.M., 2007. Avian visual pigments: characteristics, spectral tuning, and evolution. *Am. Nat.* 169, S7–S26.
- Johnson, K., Peer, B.D., 2001. Great-tailed grackle (*Quiscalus mexicanus*), version 2.0. In: Poole, A.F., Gill, F.B. (Eds.), *The Birds of North America*. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Kelber, A., 2019. Bird colour vision – from cones to perception. *Curr. Opin. Behav. Sci.* 30, 34–40.
- Kiltie, R.A., 2000. Scaling of visual acuity with body size in mammals and birds. *Funct. Ecol.* 14, 226–234.
- Komdeur, J., Oorebeek, M., van Overveld, T., Cuthill, I., 2005. Mutual ornamentation, age, and reproductive performance in the European starling. *Behav. Ecol.* 16 (4), 805–817.
- Kret, M.E., 2017. The role of pupil size in communication. Is there room for learning? *Cognit. Emot.* 32, 1139–1145.
- Kurvers, R.H.J.M., Hölker, F., 2015. Bright nights and social interactions: a neglected issue. *Behav. Ecol.* 26, 334–339.
- Kyba, C.C.M., Posch, T., Mohar, A., 2017. How bright is full moonlight? *Astron. Geophys.* 58, 1.31–1.32.
- Langmore, N.E., Stevens, M., Maurer, G., Heinsohn, R., Hall, M.L., Peters, A., Kilner, R.A., 2011. Visual mimicry of host nestlings by cuckoos. *Proc. Biol. Sci.* 278, 2455–2463.
- Longcore, T., Rodríguez, A., Witherington, B., Penniman, J.F., Herf, L., Herf, M., 2018. Rapid assessment of lamp spectrum to quantify ecological effects of light at night. *J. Exp. Zool. Part A: Ecological and Integrative Physiology* 329, 511–521.
- Maestripieri, D., Wallen, K., 1997. Affiliative and submissive communication in rhesus macaques. *Primates* 38, 127–138.
- Martin, G.R., 1993. Producing the image. In: Zeigler, H.P., Bischof, H.-J. (Eds.), *Vision, Brain and Behaviour in Birds*. MIT Press, Cambridge, pp. 5–24.
- Martin, G.R., 2017. *The Sensory Ecology of Birds*. Oxford University Press, New York, NY.
- Nokelainen, O., Scott-Samuel, N.E., Nie, Y., Wei, F., Caro, T., 2021. The giant panda is cryptic. *Sci. Rep.* 11, 21287.
- Ödeen, A., Håstad, O., 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Mol. Biol. Evol.* 20, 855–861.
- Ödeen, A., Håstad, O., 2010. Pollinating birds differ in spectral sensitivity. *J. Comp. Physiol.* 196, 91–96.
- Olsson, P., Lind, O., Kelber, A., 2015. Bird colour vision: behavioural thresholds reveal receptor noise. *J. Exp. Biol.* 218, 184–193.
- Olsson, P., Lind, O., Kelber, A., 2017. Chromatic and achromatic vision: parameter choice and limitations for reliable model predictions. *Behav. Ecol.* 29, 273–282.
- Passarotto, A., Cruz-Mirallas, A., Avilés, J.M., 2020. Iris yellowness relates to age and individual quality in two owl species. *J. Raptor Res.* 54, 233–244.
- Polakowski, M., Stepniewski, K., Śliwa-Dominiak, J., Remisiewicz, M., 2020. Age-dependent differences in iris colouration of passerines during autumn migration in Central Europe. *PeerJ* 8, e9188.
- Provine, R.R., Cabrera, M.O., Nave-Blodgett, J., 2013. Red, yellow, and super-white sclera: uniquely human cues for healthiness, attractiveness, and age. *Hum. Nat.* 24, 126–136.
- Rasband, W.S., 1997. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA.
- Renoult, J.P., Kelber, A., Schaefer, H.M., 2017. Colour spaces in ecology and evolutionary biology. *Biol. Rev. Camb. Phil. Soc.* 92, 292–315.
- Rodríguez-Morales, D., Tapia-McClung, H., Robledo-Ospina, L.E., Rao, D., 2021. Colour and motion affect a dune wasp's ability to detect its cryptic spider predators. *Sci. Rep.* 11, 15442.
- Russ, A., Ruger, A., Klenke, R., 2015. Seize the night: European Blackbirds (*Turdus merula*) extend their foraging activity under artificial illumination. *J. Ornithol.* 123–131.
- Sanders, D., Frago, E., Kehoe, R., Patterson, C., Gaston, K., 2021. A meta-analysis of biological impacts of artificial light at night. *Nature Ecol. Evol.* 5, 74–81.
- Selander, R.K., 1958. Age determination and molt in the boat-tailed grackle. *Condor* 60, 355–376.
- Siddiqi, A., Cronin, T.W., Loew, E.R., Vorobyev, M., Summers, K., 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *J. Exp. Biol.* 207 (14), 2471–2485.
- Spottiswoode, C.N., Stevens, M., 2011. How to evade a coevolving brood parasite: egg discrimination versus egg variability as host defences. *Proc. Biol. Sci.* 278, 3566–3573.
- Stevens, M., Párraga, C.A., Cuthill, I.C., Partridge, J.C., Troscianko, T.S., 2007. Using digital photography to study animal coloration. *Biol. J. Linn. Soc.* 90, 211–237.
- Stoddard, M.C., Prum, R.O., 2008. Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of new world buntings. *Am. Nat.* 171, 755–776.
- Toomey, M.B., Butler, M.W., Meadows, M.G., Taylor, L.A., Fokidis, H.B., McGraw, K.J., 2010. A novel method for quantifying the glossiness of animals. *Behav. Ecol. Sociobiol.* 64, 1047–1055.
- Troscianko, J., Stevens, M., 2015. Image calibration and analysis toolbox – a free software suite for objectively measuring reflectance, colour and pattern. *Methods Ecol. Evol.* 6, 1320–1331.
- van den Berg, C.P., Troscianko, J., Endler, J.A., Marshall, N.J., Cheney, K.L., 2020a. Quantitative colour pattern analysis (QCPA): a comprehensive framework for the analysis of colour patterns in nature. *Methods Ecol. Evol.* 11 (2), 316–332.
- van den Berg, C.P., Hollenkamp, M., Mitchell, L.J., Watson, E.J., Green, N.F., Marshall, N.J., Cheney, K.L., 2020b. More than noise: context-dependent luminance contrast discrimination in a coral reef fish (*Rhinecanthus aculeatus*). *J. Exp. Biol.* 223, jeb232090.
- Vehrencamp, S.L., Bradbury, J.W., Gibson, R.M., 1989. The energetic cost of display in male sage grouse. *Anim. Behav.* 38, 885–888.
- Vorobyev, M., Osorio, D., 1998. Receptor noise as a determinant of colour thresholds. *Proc. Biol. Sci.* 265 (1394), 351–358.
- Wilson, A.A., Dittmer, M.A., Barber, J.R., Carter, N.H., Miller, E.T., Tyrrell, L.P., Francis, C.D., 2021. Artificial night light and anthropogenic noise interact to influence bird abundance over a continental scale. *Global Change Biol.* 27, 3987–4004.
- Winters, A.E., Stevens, M., Mitchell, C., Blomberg, S.P., Blount, J.D., 2014. Maternal effects and warning signal honesty in eggs and offspring of an aposematic ladybird beetle. *Funct. Ecol.* 28, 1187–1196.
- Whitham, W., Schapiro, S.J., Troscianko, J., Yorzinski, J.L., 2022a. Chimpanzee (*Pan troglodytes*) gaze is conspicuous at ecologically-relevant distances. *Sci. Rep.* 12, 9249.
- Whitham, W., Schapiro, S.J., Troscianko, J., Yorzinski, J.L., 2022b. The gaze of a social monkey is perceptible to conspecifics and predators but not prey. *Proc. Biol. Sci.* 289, 20220194.
- Yorzinski, J.L., Platt, M.L., 2014. Selective attention in peacocks during predator detection. *Anim. Cognit.* 17, 767–777.
- Yorzinski, J.L., 2021. Great-tailed grackles can independently direct their eyes toward different targets. *Exp. Brain Res.* 239 (7), 2119–2126.
- Yorzinski, J.L., Chisholm, S., Byerley, S., Coy, J.R., Aziz, A.B., Wolf, J.A., Gnerlich, A., 2015. Artificial light pollution increases nocturnal vigilance in peahens. *PeerJ* 3, e1174.