Predator Detection is Limited in Microhabitats with High Light Intensity: An Experiment with Brown-Headed Cowbirds

Esteban Fernández-Juricic, Marcella Deisher, Amy C. Stark & Jacquelyn Randolet

Department of Biological Sciences, Purdue University, West Lafayette, IN, USA

Correspondence
Esteban Fernández-Juricic, Department of Biological Sciences, Purdue University, 915 W State Street, West Lafayette, IN 47907, USA.
E-mail: efernan@purdue.edu

Abstract

Variations in ambient light conditions across different microhabitats can modify the detectability of predators and prey. Prey have been shown to be more visible in sunlit than in shaded patches, leading to higher predation risk and more investment in vigilance (predation risk hypothesis). Additionally, prey have been hypothesized to take longer to detect predators in sunlit compared to shaded patches because of the excess of sunlight causing glare effects (disability glare hypothesis). We tested the predictions of these two non-mutually exclusive hypotheses in a semi-natural experiment with brown-headed cowbirds by measuring vigilance behavior and detection of a ground predator in patches under the shade of vegetation and in the open. Light intensity and achromatic contrast were higher in the sunlit patches, which could enhance glare effects, but chromatic contrast was higher in the shaded patches. Brown-headed cowbirds took longer to show alert reactions to and flee from a ground predator in sunlit compared to shaded patches. However, the two parameters associated with perceived predation risk (vigilance prior to the predator exposure and time to resume foraging after the attack) did not differ between sunlit and shaded patches. Our findings support to a greater extent the disability glare hypothesis than the predation risk hypothesis. Overall, ambient light conditions can affect two critical components of behavioral predator–prey interactions in terrestrial habitats: detection of and escape from predators. The effects of disability glare are expected to be more pronounced in bird species with wider visual fields or without sun-shading structures; however, species may compensate through various behaviors (e.g. avoidance of sunlit patches and changes in head orientation).

Introduction

Predators and prey can enhance capture success or avoidance, respectively, through early detection (Lima & Dill 1990). Ambient light conditions can affect detection by varying the visibility of objects in relation to the background (Endler 1987). For instance, in some systems, high light intensity can increase the distance at which predators detect prey (e.g. Richmond et al. 2004; Meager et al. 2010), and consequently enhance the prey's perceived predation risk (Clark & Levy 1988; Kotler et al. 1988, 1994). On the other hand, at very low light intensity levels (e.g. dawn, dusk), prey may have a lower ability to detect an approaching predator, leading to an increase in predation risk. For example, under low light conditions, semipalmated sandpipers (*Calidris pusilla*) are more flighty (Beauchamp & Ruxton 2008) and dark-eyed juncos (*Junco hyemalis*) increase their investment in vigilance (Lima 1988).

The effects of ambient light conditions on predation risk can also be manifested as variations in

activity patterns and patch use in different micro-habitats (e.g. Braña et al. 2010). For instance, patch use in short-toed treecreepers (*Certhia brachydactyla*) is influenced by a trade-off between thermoregulation and predation risk (Carrascal et al. 2001). Treecreepers prefer sunlit patches when temperature in shaded patches is <4°C for thermoregulatory reasons (e.g. reducing metabolic costs), but they switch to shaded patches when patch temperature is >9°C because visibility to predators is higher and crypsis is lower in sunlit patches. Furthermore, when in sunlit patches, treecreepers and house finches (*Carpodacus mexicanus)* have been found to increase vigilance compared to shaded patches (Carrascal et al. 2001; Fernández-Juricic & Tran 2007) likely to compensate for the higher risk of predation because of the greater visual exposure to predators (Endler 1987; hereafter, predation risk hypothesis).

Additionally, the ability of prey to visually detect predators may be limited in sunlit patches. A recent study found that house finches take longer to detect an aerial predator when foraging in sunlit compared to shaded patches (Fernández-Juricic & Tran 2007). This finding was explained as a result of an excess of sunlight in the eye chamber, which reduces retinal image contrast and visual resolution (Koch 1989; hereafter, disability glare hypothesis). Birds can compensate for disability glare through morphological traits and/or behavioral responses. Morphologically, some bird species have sun-shading structures (e.g. large eyebrows, feathers on the eye lids, large blind areas at the rear of the head) to reduce the incidence of light on the retina (Martin & Katzir 2000). Behaviorally, some species reduce foraging time in sunlit patches (Carrascal et al. 2001; Fernández-Juricic & Tran 2007; Gall & Fernández-Juricic 2009).

The predation risk and disability glare hypotheses are not mutually exclusive, as they explain different aspects of anti-predator responses (vigilance and predator detection, respectively) in patches with different levels of ambient light. The predation risk hypothesis predicts that animals should increase vigilance efforts (hence, reducing foraging behavior) in sunlit compared to shaded patches (Carrascal et al. 2001). The disability glare hypothesis predicts that the responses (e.g. detection, flushing) to a predator attack would be delayed in sunlit compared to shaded patches (Fernández-Juricic & Tran 2007). Furthermore, in species that forage in groups, the disability glare hypothesis predicts that individuals in sunlit patches would have more difficulty detecting cues from group mates related to a predator attack (e.g. group mates escaping; Fernández-Juricic & Tran 2007). This will lead to a higher difference in the time to respond to the predator between group mates in sunlit compared to shaded patches. To our knowledge, no study has tested the predictions of both hypotheses in relation to ground predators in a semi-controlled scenario (considering individual identity, food deprivation, food availability, and vigilance time).

Our goal was to assess the responses of the brown-headed cowbird (*Molothrus ater*) to a ground predator while foraging in sunlit and shaded patches. The brown-headed cowbird is a good study species as it inhabits ecotones between closed and open habitats (e.g. edges between forests and meadows; Lowther 1993). Brown-headed cowbirds are brood parasites that during the breeding season spend time in closed habitats parasitizing nests as well as in open habitats foraging on the ground (Curson et al. 2000). Given this breeding strategy, brown-headed cowbirds are exposed to a wide variety of microhabitats and hence different ambient light levels. We conducted a seminatural experiment in which we manipulated whether pairs of cowbirds (males and females) foraged under tree shade or in the open.

We tested the predictions of the predation risk hypothesis by measuring the proportion of time scanning before the predator attack and the time to resume foraging behavior after the predator attack. These behaviors have been associated with changes in the perceived risk of predation (e.g. Gluck 1987; Lima 1998). We tested the predictions of the disability glare hypothesis by measuring reaction time (i.e. time to show alert responses to the predator) and flight initiation time (i.e. time to take flight in response to the predator). These behaviors have been associated with predator detection (e.g. Kaby & Lind 2003; Blackwell et al. 2009). Additionally, we assessed a key assumption of the disability glare hypothesis related to the ability of cowbirds to visually perceive the predator model in sunlit and shaded patches. We estimated the chromatic (based on hues) and achromatic (based on brightness) contrasts of the predator in relation to the visual background using avian vision models (Vorobyev & Osorio 1998; Endler & Mielke 2005; Montgomerie 2006).

Methods

The experiment was conducted from April 20 to September 7, 2010, at the Ross Biological Reserve (Tippecanoe County, Indiana, IN, USA; N: 40°24′

34.4″, W: 087°04′ 02.1″). The Ross Biological Reserve has restricted access, so our experiment was not affected by human disturbance. Within the reserve, we used two areas: one located under a closed canopy of black locust (*Robinia pseudoacacia*), honey locust (*Gleditsia triacanthos*), and white ash (*Fraxinus americana*) trees (shaded patch), and the other one located on a grassy area approximately 10 m away from the woods (sunlit patch). We acknowledge that the ambient light level effects are confounded with those of microhabitat, as our treatments also differ in the presence of vegetation over the study subjects. However, we blocked most of the view of the surroundings with a screen (see below) to reduce the effects of protective/obstructive cover (e.g. Lazarus & Symonds 1992). Therefore, our design mimicked the natural conditions where this species is expected to find variations in ambient light levels by using different microhabitats (Lowther 1993).

Experimental procedures were approved by the Purdue Animal Care and Use Committee (protocol no. 09-018). We captured brown-headed cowbirds from different populations in Tippecanoe County, Indiana. Eighty-four birds (42 males, 42 females) were banded and housed in indoor enclosures (0.61 m × 0.76 m × 0.60 m) under a 14:10-h light–dark cycle (lights on at 0700 and off at 2100) at the Purdue Life Science Animal Building. Birds were in visual, auditory, and physical contact with generally three to six individuals per enclosure. Approximately 24 h prior to trials, birds were moved to the Ross Biological Reserve, where they were housed in covered outdoor aviaries (1.8 m × 1.8 m × 2.5 m). Between two and ten birds were housed per aviary. Food (Kaytee midwest regional blend wild bird food; Chilton, Wisconsin, WI, USA) was available *ad libitum*, except during trials and the preceding periods of food deprivation. Water was always available. Individuals were food-deprived for approximately 10–12 h prior to trials to increase the chances they would forage under the experimental conditions (following Morgan & Fernández-Juricic 2007). Right after the trials, each bird was provided with food.

We used a 0.61-m-diameter cylindrical mesh-wire enclosure (2.5-cm openings). This 0.48-m-high enclosure was placed on top of a round wooden base with sawdust as a substrate (Fig. 1). We kept food availability constant across trials by mixing the sawdust with 20 g of mixed birdseed (Kaytee midwest regional blend wild bird food; Chilton). The area surrounding the enclosure was screened with 2-m-high brown tarp hanging from shepherd hooks to avoid
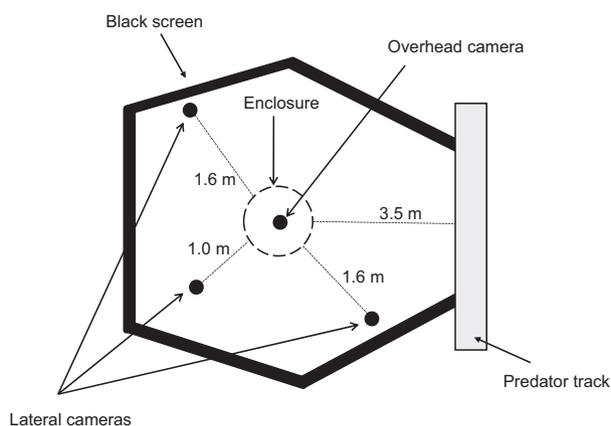
Fig. 1: Schematic representation of the experimental setup showing the placement of the enclosure, the track used to expose brown-headed cowbirds to the stuffed cat, and the position of four cameras.

visual disturbance (Fig. 1). We left a 1.9-m-wide opening between the tarp panels. A 3.2-m-long and 0.32-m-wide wooden track covered in rubber was placed 3.5 m in front of the enclosure. The ground predator model was a stuffed domestic black cat (Blue Russian Model, Piutrè Animal Collection 63.5 cm from nose to tail; Piutrè USA, Ltd., Falls Church, VA, USA) attached to a skateboard (see also Jones et al. 2007; Fernández-Juricic et al. 2009). Our predator model was representative of an introduced species; nevertheless, domestic cats have been shown to be a source of predation to birds in a wide variety of habitats (e.g. Crooks & Soulé 1999; van Heezik et al. 2010; Tschanz et al. 2011). Given the diversity of habitats cowbirds use, we expected them to show anti-predator behavior to the cat.

The head of the predator model was facing toward the enclosure. A string was attached to the skateboard and stretched across the track so that the predator model could be rolled smoothly across the opening between the panels producing as little noise as possible (see also Fernández-Juricic et al. 2009). We established that noise did not noticeably affect responses because individuals did not react to the predator model before it became visible through the opening. The skateboard was not visible to the birds because the edges of the track were slightly elevated. The average speed at which the cat was rolled across the track was 0.35 ± 0.02 m/s. The track faced the woods in both patches (sunlit and shaded) to create a similar visual background of trees.

Trials were conducted in the mornings (0700–1200 h). We conducted 21 trials in each patch type (sunlit, shaded). One male and one female were used in each trial; thus, we used a total of 42 individuals

of each sex. The male and the female involved on a given trial were chosen randomly from the cages where individuals were housed. The male cowbirds (42.89 ± 0.66 g) had significantly higher body mass than the females used in this experiment (34.39 ± 0.50 g; paired t-test, $t_{41} = 9.82$, p < 0.001). Individuals were allowed to forage for five min after the first pecking attempt by either of them, and then they were exposed to the ground predator model. Afterward, the predator was not visible to the animals. We ended the trial after either one or both individuals resumed pecking. Each individual was exposed only once to the predator model. We did not use a repeated-measures design to avoid habituation or sensitization effects toward the predator, which could have biased our results.

Male and female cowbirds, as well as the predator model, were recorded through four video cameras (Fig. 1). One camera was set up 0.5 m directly above the center of the enclosure with a camera stand made out of 1-inch PVC pipes. Three other cameras were also set up around the enclosure: the first one facing the track, the second one facing the back of the enclosure, and the third one was facing the front of the enclosure (Fig. 1). The camera facing the track recorded the predator model, and the other three cameras recorded the behavior of the cowbirds from different perspectives.

Videos were coded with Virtual Dub software using frame-by-frame analysis (30 frames per s). We recorded the time at which each bird showed the first reaction to the predator (first reaction time). First reaction time was measured from the first exposure of the predator model (video frame at which the nose of the cat was visible) to the time when the first bird showed one of the following five responses: crouching, head-up movement, head movement toward the track, change in flight path, and freezing. Crouching occurred when the individual was on the ground and visibly moved downward in preparation to fly. Head-up movement occurred when the individual moved its head from below to above the horizontal plane of the body. In some cases, crouching and head-up movements occurred simultaneously when individuals were on the ground (Table 1), and for such trials, both responses were recorded as the first reaction. Moving the head toward the track occurred when the head of the individual was facing away from the track (80–180° away from the track) before the predator was presented, and after its exposure, the head moved laterally in the direction of the track (0–80° from the track). Moving the head

Table 1: First reaction behaviors by brown-headed cowbirds in response to a ground predator: crouching (CR), head-up movement (HUPM), head movement toward the track (HMOV), change in flight path (FPATH), and freezing (FREEZ). CR + HUPM, crouching and head-up movement occurred simultaneously. Each count represents an individual bird (the same individual was never exposed to the predator model more than once). Definitions in Methods

	CR	HUPM	CR+HUPM	HMOV	FPATH	FREEZ
Sunlit patches						
Males	11	3	0	5	0	2
Females	11	1	0	7	1	0
Totals	22	4	0	12	1	2
Shaded patches						
Males	15	4	1	1	0	0
Females	11	6	2	2	0	0
Totals	26	10	3	3	0	0

toward the track was recorded when individuals were either on the ground or hanging from the enclosure walls. A change in flight path occurred when individuals that were flying parallel to the ground shifted the trajectory of the path upwards after the exposure to the predator. Freezing occurred when the individual suddenly stopped the behavior it was engaged in and remained motionless either on the ground or hanging from the walls of the enclosure.

The other metric we recorded was flight initiation time: the time period between the first exposure of the predator model (video frame at which the nose of the cat was visible) and the point when individuals flushed from the ground or flew away from the enclosure walls (video frame at which the feet visibly left the ground or the side of the enclosure). Finally, we recorded the time to resume foraging between the first exposure of the predator model (video frame at which the nose of the cat was visible) and the time when individuals pecked on the ground after the exposure. First reaction time, flight initiation time, and time to resume foraging were all recorded in frames.

We measured scanning behavior of each individual using JWatcher (Blumstein & Daniel 2007). A student (M. Hoover) coded all the videos after she reached an intra-observer error <5% between repeated measurements on the same video sequences. Scanning behavior was recorded 3–4 min before the exposure of the predator model. We recorded the proportion of time individuals spent scanning (head moving and raised above the horizontal plane of the body) on the ground and hanging from the enclosure walls.

Before the beginning of the trials, we measured light intensity at the center of the enclosure with a Mastech digital illuminance/light meter LX1330B (0–200 000 lux range), and ambient temperature with a Kestrel 3500 pocket weather meter. These measurements allowed us to establish the putative differences in light intensity between patch types, and whether they were matched by temperature differences.

Differences in the responses of cowbirds between sunlit and shaded patches could be related to variations in the brightness (achromatic) and/or color (chromatic) contrast between the ground predator and the visual background. We estimated the chromatic and achromatic contrasts of the ground predator in sunlit and shaded patches using Vorobyev and Osorio's physiological model (Vorobyev & Osorio 1998). Because the color sensitivity of the brown-headed cowbird's visual system is not known, we used the ultraviolet- and violet-sensitive visual systems in the calculations of visual contrast (for a similar approach see Igic et al. 2010). Details of the calculations are presented in Appendix S1. The output of the chromatic and achromatic contrast calculations is in 'just noticeable differences' (JND) units (e.g. Siddiqi et al. 2004; Cassey et al. 2009). A JND = 1 is considered the threshold of discrimination. When JND < 1, an object is indistinguishable from the background. When JND varies from 1 to 3, the visual system could discriminate between the object and the background but with difficulty. JND values >3 indicate that the visual stimuli can be easily discriminated.

Statistical Analysis

We used general linear models (GLM) to analyze the differences in light intensity, temperature, and chromatic and achromatic contrasts between sunlit and shaded patches. With a similar analysis, we assessed differences in scanning behavior between patches and sexes. We also used GLMs to analyze the effects of patch type and sex (and their interaction) on first reaction time, flight initiation time, and time to resume foraging. We included the proportion of time scanning on the ground and hanging from the enclosure walls as covariates in these models, as vigilance behavior can affect the probabilities of predator detection (Lima & Bednekoff 1999; Cresswell et al. 2003). We checked the data for normality and homogeneity of the variance with normal probability plots and residual plots, respectively. We present means ± SE throughout. Statistical analyses were run with Statistica 9.2 (Tulsa, OK, USA).

Results

Ambient Light, Temperature, and Visual Contrast

Sunlit patches (27,642.54 ± 6,399.53 lux) had significantly higher light intensity than shaded patches (1,110.43 ± 145.95 lux; $F_{1,40} = 17.18$, p < 0.001). However, there were no significant differences in temperature ($F_{1,40} = 0.26$, p = 0.612) between sunlit (21.04 ± 1.81°C) and shaded (19.89 ± 1.34°C) patches during the trials.

Achromatic contrast of the predator was significantly higher in the sunlit than in the shaded patches (violet-sensitive system, $F_{1,39} = 226.51$, p < 0.001; ultraviolet-sensitive system, $F_{1,39} = 223.68$, p < 0.001; Fig. 2a), which is in agreement with the light intensity results presented above. However, chromatic contrast of the predator was significantly higher in the shaded than in the sunlit patches (violet-sensitive system, $F_{1,39} = 19.71$, p < 0.001; ultraviolet-sensitive system, $F_{1,39} = 23.74$, p < 0.001; Fig. 2b).
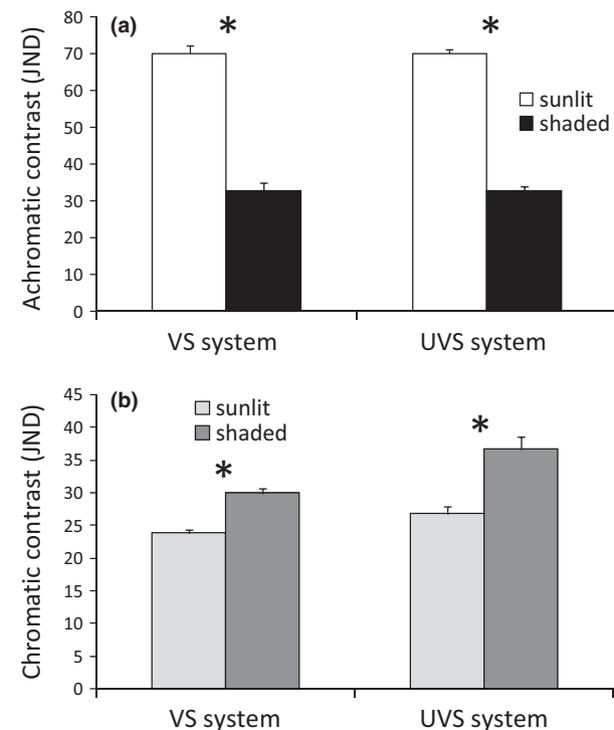
Fig. 2: (a) Achromatic and (b) chromatic contrast values of a ground predator based on violet-sensitive (VS) and ultraviolet-sensitive (UVS) avian visual systems. Units are in just noticeable differences (JND; see text for details). Stars denote significant differences.

Predation Risk Hypothesis

Before the exposure to the predator, the proportion of time spent head-up scanning on the ground did not vary significantly between sunlit (0.62 ± 0.04) and shaded (0.59 ± 0.03) patches ($F_{1,80} = 0.49$; $p = 0.488$), nor was it affected by sex ($F_{1,80} = 0.60$; $p = 0.441$) or the interaction between patch type and sex ($F_{1,80} = 0.26$; $p = 0.610$). The proportion of time spent scanning from the enclosure walls did not vary significantly between sunlit (0.09 ± 0.03) and shaded (0.05 ± 0.03) patches ($F_{1,80} = 0.80$; $p = 0.373$), nor was it affected by sex ($F_{1,80} = 0.06$; $p = 0.810$) or the interaction between patch type and sex ($F_{1,80} = 1.31$; $p = 0.256$).

The time to resume foraging after the predator exposure did not vary significantly between sunlit ($4,167.48 \pm 1,226.46$ frames) and shaded ($3,535.46 \pm 1,225.87$ frames) patches (Table 2), controlling for the proportion of time scanning on the ground and hanging from the enclosure walls. Sex and the interaction between patch type and sex were not significant (Table 2).

Disability Glare Hypothesis

The most frequent first reaction toward the predator in both sunlit and shaded patches was crouching (Table 1). The second most frequent first reaction was moving the head toward the track in sunlit patches, and head-up movement in shaded patches (Table 1). Within each patch condition, the frequency of responses of males and females was similar across different reaction behaviors (Table 1). One female in the sunlit patch condition reacted first with a flushing behavior, and thus was not considered in the analysis of the first reaction to the predator (see criteria in Methods).

The first reaction to the predator was significantly quicker in shaded than in sunlit patches (Table 2; Fig. 3a), considering in the model the proportion of time scanning on the ground and hanging from the enclosure walls (Table 2). There was no significant difference in the time of the first response to the predator between males (8.03 ± 0.73 frames) and females (8.51 ± 0.74 frames; Table 2). Additionally, the responses of males and females did not vary significantly between sunlit and shaded patches (Table 2).

The flush initiation time was significantly quicker in shaded than in sunlit patches (Table 2; Fig. 3b). The proportion of time scanning on the ground did not influence flight initiation time, but the proportion of time hanging from the enclosure walls was negatively and significantly associated with flight initiation time (coefficient = -16.71; Table 2). There

Table 2: Responses of brown-headed cowbirds to a ground predator (first reaction time, flight initiation time, and time to resume foraging) in relation to treatment (sunlit, shaded foraging patches), sex, and proportion of time scanning on the ground and on the enclosure walls. Results from general linear models. Degrees of freedom differ between response variables because not all individuals showed all three behaviors in response to the predator

	F	df	p
Time to resume foraging			
Treatment	0.14	1,49	0.708
Sex	0.95	1,49	0.335
Treatment x Sex	2.17	1,49	0.147
Proportion of time scanning on the ground	3.92	1,49	0.053
Proportion of time scanning on the enclosure walls	2.40	1,49	0.127
First reaction time			
Treatment	3.99	1,77	**0.049**
Sex	0.20	1,77	0.652
Treatment x Sex	0.03	1,77	0.856
Proportion of time scanning on the ground	0.87	1,77	0.354
Proportion of time scanning on the enclosure walls	2.53	1,77	0.116
Flight initiation time			
Treatment	4.12	1,68	**0.046**
Sex	0.01	1,68	0.954
Treatment x Sex	0.01	1,68	0.963
Proportion of time scanning on the ground	0.27	1,68	0.603
Proportion of time scanning on the enclosure walls	5.52	1,68	**0.022**

Significant results are marked in bold.
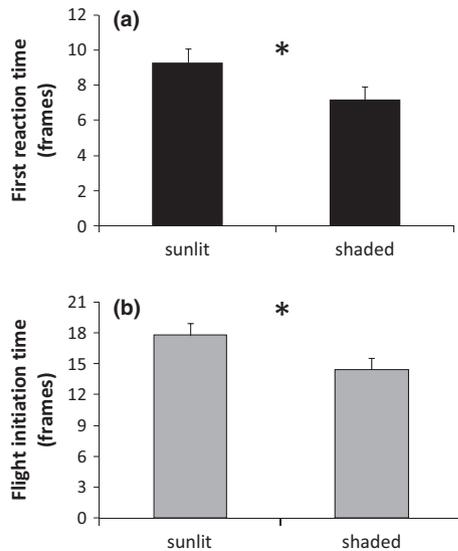
Fig. 3: (a) First reaction time and (b) flight initiation time of brown-headed cowbirds in response to a ground predator (stuffed cat) in sunlit and shaded patches. Measurements made in frames. Stars denote significant differences.

was no significant difference in the flight initiation time between males (16.16 ± 1.16 frames) and females (16.07 ± 1.09 frames; Table 2).

Discussion

We tested the predictions of two non-mutually exclusive hypotheses on the behavioral responses (perceived predation risk and predator detection) of cowbirds in microhabitats with different levels of ambient light. Our findings appear to support to a greater extent the disability glare hypothesis than the predation risk hypothesis under the seminatural experimental conditions used in this study. Brown-headed cowbirds took longer to respond to a ground predator in sunlit compared to shaded patches. The two parameters associated with perceived predation risk (vigilance prior to the predator exposure and time to resume foraging after the attack) did not differ between sunlit and shaded patches.

Although previous studies found that individuals increase their vigilance efforts in sunlit in relation to shaded patches (Carrascal et al. 2001; Fernández-Juricic & Tran 2007), brown-headed cowbird did not show this level of variation under our experimental conditions. Our study differs from the previous ones in that cowbirds were in close physical contact, which may have led to an increase in mimicking any increase in vigilance behavior by the flock mate

(Fernández-Juricic et al. 2004), minimizing differences in vigilance between patch types. Alternatively, we may have failed to detect a significant difference owing to sample size issues. Despite this lack of a significant effect, we cannot rule out that brown-headed cowbirds vary their perception of risk in patches with different vegetation structure. For instance, under seminatural conditions, cowbirds seek cover in patches with more vegetation complexity when predation risk increases (Morgan & Fernández-Juricic 2007). This suggests that open areas may have an intrinsic higher risk of predation despite the fact that brown-headed cowbirds forage in a broad variety of habitats (e.g. open fields, meadows, and forest edges; Lowther 1993). We attempted to reduce this potential habitat effect in our study by blocking most of the view of the surroundings (with the exception of the track where the predator was exposed), but simultaneously keeping conditions as natural as possible (presence/absence of vegetation above the enclosure).

When analyzing predator detection, we controlled for individual variation in perceived predation risk in the models by including the proportion of time spent vigilant by each individual. We found that individuals that spent more time scanning while hanging from the enclosure walls took flight more quickly likely because they had a better viewpoint of the surroundings. This corroborates the positive relationship between vigilance effort and predator detection abilities (Cresswell et al. 2003).

Despite the individual variation in vigilance, predator detection varied between sunlit and shaded patches. In sunlit patches, brown-headed cowbirds took 22.5% longer to react to the predator, and 18.7% longer to flush away from the predator compared to shaded patches. Based on the number of frames recorded, the averaged difference between patches considering both reaction and flushing was approximately 0.17 s. Although this difference does not seem large, it seems sufficient for an individual to get an early edge on a successful escape strategy (Hilton et al. 1999; Cresswell et al. 2003; Quinn & Cresswell 2005). Although this response can only be considered in relation to ground predators, similar results were also found in house finches in relation to aerial predator attacks (Fernández-Juricic & Tran 2007). This suggests that for at least some species, foraging in sunlit patches may reduce the ability to detect predators, which could potentially increase mortality, despite some potential benefits (e.g. improved thermoregulation; Carrascal et al. 2001).

One of the predictions of the disability glare hypothesis is that individuals would have a more difficult time detecting group mates escaping in sunlit patches (Fernández-Juricic & Tran 2007). This would lead to a greater difference in reaction and flight initiation times between group mates in sunlit compared to shaded patches. However, we did not find support for this prediction in our study. One explanation is the fact that individuals were very close to the predator and to each other (<1 m), which may have led to each individual detecting the predator on its own or through the close positioned companion despite the potential glare effects. A few studies have shown that delays in social information flow about predation are more pronounced when group mates are farther than in the present study (Fernández-Juricic et al. 2004; Fernández-Juricic & Beauchamp 2008).

Our results suggest that high ambient light levels may affect the ability to discriminate predators from the visual background. This could be caused by disability glare, by which imperfections in the optical media (e.g. cornea and lens) cause sunlight to scatter within the eye chamber (Vos 2003). Disability glare can lead to a visual veil that reduces overall contrast (Rubin & Stark 1995), and thus the ability to detect an object in the visual field. Disability glare has been shown to negatively affect important behavioral functions in humans, such as driving performance when the viewer is subject to other incoming light sources (e.g. sunlight and headlights of vehicles; Ranney et al. 2000; Babizhayev 2003; Gray & Regan 2007).

Animals are expected to use achromatic cues to quickly detect changes in the shape and motion of objects (Osorio et al. 1999; Burton 2000). These cues are generally used in predator detection (Cronin 2005). We found that achromatic contrast of the ground predator was higher in sunlit than in shaded patches, but the ability of individuals to make use of an increase in the predator brightness for detection may have actually been constrained by the greater light intensity leading to the glare effects. In the shaded conditions, however, it is possible that individuals may have used chromatic cues to enhance the detection of the ground predator (Fig. 2). Previous studies have found that birds may use chromatic cues to detect cryptic objects in their environment (e.g. Stobbe et al. 2009; Lindstedt et al. 2011).

At least in humans, the effects of disability glare are expected to increase when the angle of sunlight reaching the eye is closer to the position of the fovea (Aslam et al. 2007). Brown-headed cowbirds have a fovea located approximately at the center of their retina (Dolan & Fernández-Juricic 2010), but they have wide lateral visual fields and a binocular area that extends above and half way behind their heads (Blackwell et al. 2009). This visual configuration increases visual coverage, and hence facilitates imaging the sunlight when the sun is at different angles over the horizon, as cowbirds do not have sun-shading structures (Martin & Katzir 2000). Another species without sun-shading structures, the black phoebe (*Sayornis nigricans*), has been shown to prefer territories with lower ambient light intensities likely to reduce the potential effects of disability glare when catching insects (Gall & Fernández-Juricic 2009).

Our findings suggest that ambient light conditions can affect some critical components of behavioral predator–prey interactions in terrestrial habitats. We propose that disability glare may be one of the mechanisms involved in limiting predator detection in microhabitats with high light intensity levels. The effects of disability glare are expected to be more pronounced in bird species with wider visual fields or without sun-shading structures (Martin & Katzir 2000). However, these effects are expected to be dynamic, and consequently they could be compensated through different behaviors such as short residence times in sunlit patches (Fernández-Juricic & Tran 2007; Gall & Fernández-Juricic 2009), increase in vigilance behavior while in sunlit patches (Carrascal et al. 2001; Fernández-Juricic & Tran 2007), changes in head orientation to reduce sun imaging (e.g. aligning the blind area toward the sun), and joining larger groups to reduce predation risk in sunlit patches. Future studies should test these predictions in microhabitats with different ambient light intensities. Finally, from a methodological perspective, our results suggest that future behavioral studies on anti-predator behavior should at least control statistically for the effects of ambient light intensity as it can affect vigilance behavior (Carrascal et al. 2001; Fernández-Juricic & Tran 2007) and predator detection (this study).

Acknowledgements

Literature Cited

Aslam, T. M., Haider, D. & Murray, I. J. 2007: Principles of disability glare measurement: an ophthalmological perspective. Acta Ophthalmol. Scand. 85, 354—360.

Babizhayev, M. A. 2003: Glare disability and driving safety. Ophthalmic Res. 35, 19—25.

Beauchamp, G. & Ruxton, G. D. 2008: Time of day and flightiness in flocks of semipalmated sandpipers. Condor 110, 269—275.

Blackwell, B. F., Fernández-Juricic, E., Seamans, T. W. & Dolan, T. 2009: Avian visual system configuration and behavioural response to object approach. Anim. Behav. 77, 673—684.

Blumstein, D. T. & Daniel, J. C. 2007: Quantifying Behavior the JWatcher Way. Sinauer, Sunderland, Massachusetts.

Braña, F., Prieto, L. & González-Quirós, P. 2010: Habitat change and timing of dusk flight in the Eurasian woodcock: a trade-off between feeding and predator avoidance? Ann. Zool. Fenn. 47, 206—214.

Burton, B. G. 2000: Problems and solutions in early visual processing. In: Information Theory and the Brain (Baddeley, R. J., Hancock, P. J. & Földiák, P., eds). Cambridge University Press, Cambridge, pp. 25—40.

Carrascal, L. M., Díaz, J. A., Huertas, D. L. & Mozetich, I. 2001: Behavioral thermoregulation by treecreepers: trade-off between saving energy and reduced crypsis. Ecology 82, 1642—1654.

Cassey, P., Ewen, J. G., Marshall, N. J., Vorobyev, M., Blackburn, T. M. & Hauber, M. E. 2009: Are avian eggshell colours effective intraspecific communication signals in the Muscicapoidea? Ibis 151, 689—698.

Clark, C. W. & Levy, D. A. 1988: Diel vertical migrations by juvenile sockeye salmon and the antipredation window. Am. Nat. 131, 271—290.

Cresswell, W., Quinn, J. L, Whittingham, M. J. & Butler, S. 2003: Good foragers can also be good at detecting predators. Proc. R. Soc. Lond. B 270, 1069—1076.

Cronin, T. W. 2005: The visual ecology of predator-prey interactions. In: Ecology of Predator-Prey Interactions (Barbosa, P. & Castellanos, I., eds). Oxford University Press, Oxford, pp. 105—138.

Crooks, K. R. & Soulé, M. E. 1999: Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400, 563—566.

Curson, D. R., Goguen, C. B. & Mathews, N. E. 2000: Long-distance commuting by Brown- headed Cowbirds in New Mexico. Auk 117, 795—799.

Dolan, T. & Fernández-Juricic, E. 2010: Retinal ganglion cell topography of five species of ground foraging birds. Brain Behav. Evol. 75, 111—121.

Endler, J. A. 1987: Predation, light intensity and courtship behavior in Poecila reticulate (Pisces, Poeciliidae). Anim. Behav. 35, 1376—1385.

Endler, J. A. & Mielke, P. W. Jr. 2005: Comparing entire colour patterns as birds see them. Biol. J. Linn. Soc. 86, 405—431.

Fernández-Juricic, E. & Beauchamp, G. 2008: An experimental analysis of spatial position effects on foraging and vigilance in Brown-headed Cowbird flocks. Ethology 114, 105—114.

Fernández-Juricic, E. & Tran, E. 2007: Changes in vigilance and foraging behaviour with light intensity and their effects on food intake and predator detection in house finches. Anim. Behav. 74, 1381—1390.

Fernández-Juricic, E., Siller, S. & Kacelnik, A. 2004: Flock density, social foraging and scanning: an experiment with starlings. Behav. Ecol. 15, 371—379.

Fernández-Juricic, E., Delgado Sáez, J. A., Remacha, C., Jiménez, M. D., Garcia, V. & Hori, K. 2009: Can a solitary avian species use collective detection? An assay in semi-natural conditions. Behav. Process 82, 67—74.

Gall, M. D. & Fernández-Juricic, E. 2009: Effects of physical and visual access to prey on patch selection and food search effort in a sit-and-wait predator, the Black Phoebe. Condor 111, 150—158.

Gluck, E. 1987: An experimental study of feeding, vigilance and predator avoidance in a single bird. Oecologia 71, 268—272.

Gomez, D. 2006. AVICOL, a program to analyse spectrometric data. Free executable available at http://sites. google.com/site/avicolprogram/ or from the author at dodogomez@yahoo.fr

Gray, R. & Regan, D. 2007: Glare susceptibility test results correlate with temporal safety margin when executing turns across approaching vehicles in simulated low-sun conditions. Ophthal. Physl. Opt. 27, 440—450.

Hart, N. S. & Vorobyev, M. 2005: Modeling oil droplet absorption spectra and spectral sensitivities of bird cone photoreceptors. J Comp Physiol A. 191, 381—392.

Hart, N. S. & Hunt, D. M. 2007: Avian visual pigments: characteristics, spectral tuning, and evolution. American Naturalist 169, S7—S26.

van Heezik, Y., Smyth, A., Adams, A. & Gordon, J. 2010: Do domestic cats impose an unsustainable harvest on urban bird populations? Biol. Conserv. 143, 121—130.

Hilton, G. M., Cresswell, W. & Ruxton, G. D. 1999: Intraflock variation in the speed of escape-flight response on attack by an avian predator. Behav. Ecol. 10, 391—395.

Igic, B., Leuschner, N., Parker, K. A., Ismar, S. M. H., Gill, B. J., Lovegrove, T. G., Millar, C. D. & Hauber, M. E. 2010: Size dimorphism and avian-perceived sexual dichromatism in a New Zealand endemic, the whitehead (Mohoua albicilla). J Morphol 271, 697—704.

Jones, K. A., Krebs, J. R. & Whittingham, M. J. 2007: Vigilance in the third dimension: head movement not

scan duration varies in response to different predator models. Anim. Behav. **74**, 1181—1187.

Kaby, U. & Lind, J. 2003: What limits predator detection in blue tits (*Parus caeruleus*): posture, task or orientation? Behav. Ecol. Sociobiol. **54**, 534—538.

Koch, D. D. 1989: Glare and contrast sensitivity testing in cataract patients. J. Cataract Ref. Surg. **15**, 158—164.

Kotler, B. P., Brown, J. S., Smith, R. J. & Wirtz, W. O. 1988: The effects of morphology and body size on rates of owl predation on desert rodents. Oikos **53**, 145—152.

Kotler, B. P., Ayal, Y. & Subach, A. 1994: Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. Oecologia **100**, 391—396.

Lazarus, J. & Symonds, M. 1992: Contrasting effects of protective and obstructive cover on avian vigilance. Anim. Behav. **43**, 519—521.

Lima, S. L. 1988: Vigilance during the initiation of daily feeding in Dark-eyed Juncos. Oikos **53**, 12—16.

Lima, S. L. 1998: Nonlethal effects in the ecology of predator-prey interactions - What are the ecological effects of anti-predator decision-making? Bioscience **48**, 25—34.

Lima, S. L. & Bednekoff, P. A. 1999: Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? Anim. Behav. **58**, 537—543.

Lima, S. L. & Dill, L. M. 1990: Behavioural decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**, 619—640.

Lindstedt, C., Eager, H., Ihalainen, E., Kahilainen, A., Stevens, M. & Mappes, J. 2011: Direction and strength of selection by predators for the color of the aposematic wood tiger moth. Behav. Ecol. **22**, 580—587.

Lowther, P. E. 1993: Brown-headed Cowbird (*Molothrus ater*), The Birds of North America Online (Poole, A., ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/047.

Martin, G. R. & Katzir, G. 2000: Sun shades and eye size in birds. Brain Behav. Evol. **56**, 340—344.

Meager, J. J., Moberg, O., Strand, E. & Utne-Palm, A. C. 2010: Effects of light intensity on visual prey detection by juvenile Atlantic cod (*Gadus morhua L.*). Mar. Freshw. Behav. Phy. **43**, 99—108.

Montgomerie, R. 2006: Analyzing colors. In: Bird Coloration: Mechanisms and Measurements (Hill, G. E. & McGraw, K. J., eds). Harvard University Press, Cambridge, pp. 90—147.

Morgan, T. & Fernández-Juricic, E. 2007: The effects of predation risk, food abundance, and population size on group size of brown-headed cowbirds (*Molothrus ater*). Ethology **113**, 1173—1184.

Osorio, D., Miklosi, A. & Gonda, Z. 1999: Visual ecology and perception of coloration patterns by domestic chicks. Evol. Ecol. **13**, 673—689.

Quinn, J. L. & Cresswell, W. 2005: Escape response delays in wintering redshank, *Tringa totanus*, flocks: perceptual limits and economic decisions. Anim. Behav. **69**, 1285—1292.

Ranney, T. A., Simmons, L. A. & Masalonis, A. J. 2000: The immediate effects of glare and electrochromic glare-reducing mirrors in simulated truck driving. Hum. Factors **42**, 337—347.

Richmond, H. E., Hrabik, T. R. & Mensiger, A. F. 2004: Light intensity, prey detection and foraging mechanisms of age 0 year yellow perch. J. Fish Biol. **65**, 195—205.

Rubin, G. S. & Stark, W. J. 1995: Current status of contrast sensitivity and glare testing in evaluation of the cataract patient. Ophthalmol. Clin. North Am. **8**, 539—546.

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**, 2471—2485.

Stobbe, N., Dimitrova, M., Merilaita, S. & Schaefer, H. M. 2009: Chromaticity in the UV/blue range facilitates the search for achromatically background-matching prey in birds. Phil. Trans. R. Soc. B **364**, 511—517.

Tschanz, B., Hegglin, D., Gloor, S. & Bontadina, F. 2011: Hunters and non-hunters: skewed predation rate by domestic cats in a rural village. Eur. J. Wildlife Res. **57**, 597—602.

Vorobyev, M. & Osorio, D. 1998: Receptor noise as a determinant of colour thresholds. Proc. R. Soc. Lond. B **265**, 351—358.

Vos, J. J. 2003: On the cause of disability glare and its dependence on glare angle, age and ocular pigmentation. Clin. Exp. Optom. **86**, 363—370.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1: Chromatic and achromatic contrast calculations.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.