Forward-Facing Predators Attract Attention in Humans (*Homo sapiens*)

Jessica L. Yorzinski and Maria E. Tovar
Texas A&M University

Richard G. Coss
University of California, Davis

Even prey that successfully evade attack incur costs when responding to predators. These nonlethal costs can impact their reproductive success and survival. One strategy that prey can use to minimize these costs is to adjust their antipredator behavior based on the perceived level of risk. We tested whether humans adopt this strategy by presenting participants with photographic arrays of predators (lions) that varied in their level of risk. While their eye movements were recorded, the participants searched for a forward-facing predator (signifying potential predator interest; high-risk target) among an array of inattentive predators that were facing away (low-risk distractors) or searched for a predator that was facing away from them among an array of forward-facing predators. As a control, participants also searched through similar arrays that displayed a potential prey species (impalas) rather than predators. Participants detected forward-facing predators more quickly than predators facing away from them. Unexpectedly, they were also quicker at detecting forward-facing prey versus prey facing away from them, but slower to detect these forward-facing prey compared with forward-facing predators. They were slower to detect predators and prey facing away from them because they spent more time looking at the forward-facing distractors and looked at more of those distractors. The results indicate that human attention is drawn toward dangerous predators with forward-facing orientations, and this could allow humans to quickly assess predator intentions.

Keywords: attention, delayed disengagement, eye-tracking, predator detection, prey

Prey incur costs when responding to predators even when they successfully evade attack (Creel & Christianson, 2008; Cresswell, 2008; Lima, 1998; Peckarsky et al., 2008). These costs include lower energy intake, higher energetic expenditure, reduced mating success, higher risk to additional predators, and emigration (Preisser, Bolnick, & Benard, 2005). Because of these nonlethal costs, it is not always adaptive for prey to flee immediately (Dugatkin & Godin, 1992). Instead, they can assess the level of threat and then decide whether to engage in defensive action (Ydenberg & Dill, 1986).

One way that individuals can assess risk is by evaluating predator behavior. A particularly informative behavior of predators is their orientation. Prey are at high risk when predators are oriented toward them because the prey have likely been detected (Cooper, 1998; Kyle & Freeberg, 2016; Stankowich & Coss, 2006). Prey that rapidly detect these high-risk predators are more likely to avoid attack because they can initiate their escape response sooner (Lind, 2004). Attentional mechanisms that allow prey to direct their attention quickly toward highly dangerous predators (and subsequently respond rapidly) are likely favored by natural selection (Coss, 2003; Isbell, 2006; Yorzinski, Penkunas, Platt, & Coss, 2014).

Previous work has shown that prey are sensitive to the orientation of predators. For example, lizards (*Holbrookia propinqua*) are more likely to flee from a predator that turns its head toward versus away from them (Cooper, 1998). Similarly, house sparrows (*Passer domesticus*) more often flee from predators that are facing toward versus away from them (Hampton, 1994). Furthermore, hadeda ibises (*Bostrychia hagedash*) not only flee more quickly in response to a forward-facing predator but also become alert sooner, suggesting that attentional mechanisms (such as bottom-up mechanisms that are driven by stimuli saliency; Itti & Koch, 2001) favor the detection of forward-facing threats (their gaze behavior was not, however, monitored; Bateman & Fleming, 2011). Prey even exhibit differential physiological arousal in response to predator orientation: Humans have larger pupil sizes when viewing animals with a forward-facing versus averted gaze (Coss & Towers, 1990). Prey tend to use the orientation of a predator's head rather than its eyes (Hampton, 1994) or body (Kyle & Freeberg, 2016) to make their escape decisions. Although many animals detect predators quickly and even adjust their escape response relative to the orientation of predators (reviewed in Bateman & Fleming, 2011), we are unaware of any studies that have directly explored whether predator orientation impacts attention.

The aim of this study was to test the hypothesis that predators exhibiting dangerous orientations attract more attention than pred-

Jessica L. Yorzinski and Maria E. Tovar, Department of Wildlife and Fisheries Sciences, Texas A&M University; Richard G. Coss, Department of Psychology, University of California, Davis.

Correspondence concerning this article should be addressed to Jessica L. Yorzinski, Department of Wildlife and Fisheries Sciences, Texas A&M University, 534 John Kimbrough Boulevard, College Station, TX 77843. E-mail: jyorzinski@tamu.edu

ators exhibiting less dangerous orientations. We tested this hypothesis in human participants because our previous work found that human participants are faster at detecting predators compared with nonpredators (both of which were facing away from the participants), but the impact of different predator orientations on these detection abilities was not examined (Yorzinski et al., 2014). We recorded the eye movements of human participants as they searched for predators (lions). They searched for an image of a predator that was oriented toward the participants (signifying potential predator interest; high-risk target) embedded in an array of inattentive predators that were oriented away from the participants (low-risk distractors) or searched for an image of a predator that was oriented away from the participants (target) embedded in an array of predators that were facing toward the participants (distractors). To determine whether their detection abilities were specific to predators or generalized to other animals, the participants also searched through similar arrays that displayed a historical game species (attentive or inattentive impalas) rather than predators. We presented the participants with color images and images in which low-level features were minimized (spatial frequency and luminance were controlled).

If predators exhibiting dangerous orientations attract more attention than predators exhibiting less dangerous orientations, we expected that participants would be faster to detect high-risk predators oriented toward them versus low-risk predators oriented away from them. If predator orientation does not impact the attention of prey, we expected that participants would detect predators oriented toward them and oriented away from them at similar speeds. In addition, we examined the visual-scanning process that participants used while searching through the predator and prey arrays. We tested whether high-risk predators (a) maintain attention or "delay disengagement" during visual search (Fox, Russo, & Dutton, 2002) and/or (b) exogenously attract attention through low-level features (e.g., luminance or contrast; Simons, 2000). If high-risk predators are effective at maintaining attention, we predicted that humans would spend more time looking at distractors when the distractors were high-risk predators compared with low-risk predators. If high-risk predators capture attention through low-level features, we predicted that humans would look at a larger number of distractors when the distractors were high-risk predators compared with low-risk predators.

Method

Participants

Thirty men and 30 women participated in this study at Texas A&M University from February through May, 2017. They were of European heritage and between the ages of 18 and 30 years old ($M = 20.2$, $SE = 0.28$ years). Flyers and e-mails were used to recruit participants. The participants were told that they would be participating in a study that explored predator recognition and they earned $10 for their participation. The institutional review board of Texas A&M University (2016-0575D) approved this study; written consent was obtained from all participants.

Animal Images

We created two sets of 96 matrices that displayed images of predators and prey. The predator set showed images of lions (*Panthera leo*), and the prey set showed images of impalas (*Aepyceros melampus*). The lion and impala images consisted of adult males with manes and adult females, respectively. The displayed animals were standing with all four legs on the ground, depicted in a natural scene, and not displaying threatening or defensive postures; the images were obtained from online sources. With the exception of four images (4.2%; two lions and two impalas), all of the animals' bodies were oriented sideways. The animals' heads were facing toward the left in 47.9% of the images in which the animals were facing away from the camera (see the following text) and facing toward the right in the remaining 52.1% of those images. Among the images in which the animals' heads were facing away from the camera, all of the animals' bodies were oriented in the same direction as their heads except in two lion images (4.2%).

Each set included four treatment blocks (Toward, Toward Control, Away, and Away Control), each of which had 24 matrices. In the first set, the first treatment block (Target Lion Toward) consisted of 24 matrices that were created from 24 images of lions. Each matrix consisted of a 3×3 array of photographs in which one lion was facing toward the camera (head directed toward camera; target) and seven lions were facing away from the camera (head directed to the side; distractors; the middle matrix position was left empty; Figure 1A). Each matrix was 2560×1440 pixels (dpi = 96) and filled the entire screen. Images within the matrices were 293×208 pixels (~7.4 degrees wide and 5.2 degrees high from the participants' perspective); 100 pixels separated images from each other. A given lion image that was facing the camera appeared three times in each of the eight possible positions across the 24 matrices and only appeared once within each matrix. Lion images that were facing away from the camera appeared in pseudorandomized positions within each matrix such that each image appeared seven times across the 24 matrices but was never in the same matrix position more than once and only appeared once within each matrix.

A second treatment block (Target Lion Toward Control) was created using the 24 matrices that were generated in the first treatment block except that the matrices were processed using the SHINE toolbox (Figure 1B; default settings; Willenbockel et al., 2010) in MATLAB to minimize low-level confounds (images within a matrix were matched for luminance and spatial frequency). The SHINE toolbox first matches the Fourier amplitude spectra of the images (spatial frequency matching) and then matches the luminance histograms (Willenbockel et al., 2010); the low-level features of the resulting images are therefore minimized (because they have the same luminance and spatial frequency) but not entirely eliminated, as the toolbox does not match other low-level features (such as edges or orientation).

We repeated the aforementioned process to generate the third (Figure 1C) and fourth (Figure 1D) treatment blocks (Target Lion Away and Target Lion Away Control) except that one lion image facing away from the camera (target) and seven lion images facing toward the camera (distractors) were used in each matrix. Therefore, there were a total of 96 matrices in the Target Lion Toward, Target Lion Toward Control, Target Lion Away, and Target Lion Away Control treatment blocks.

The second set of 96 matrices was created using the same procedure that we used to create the first set except that we used images of impalas rather than lions. The images were used to
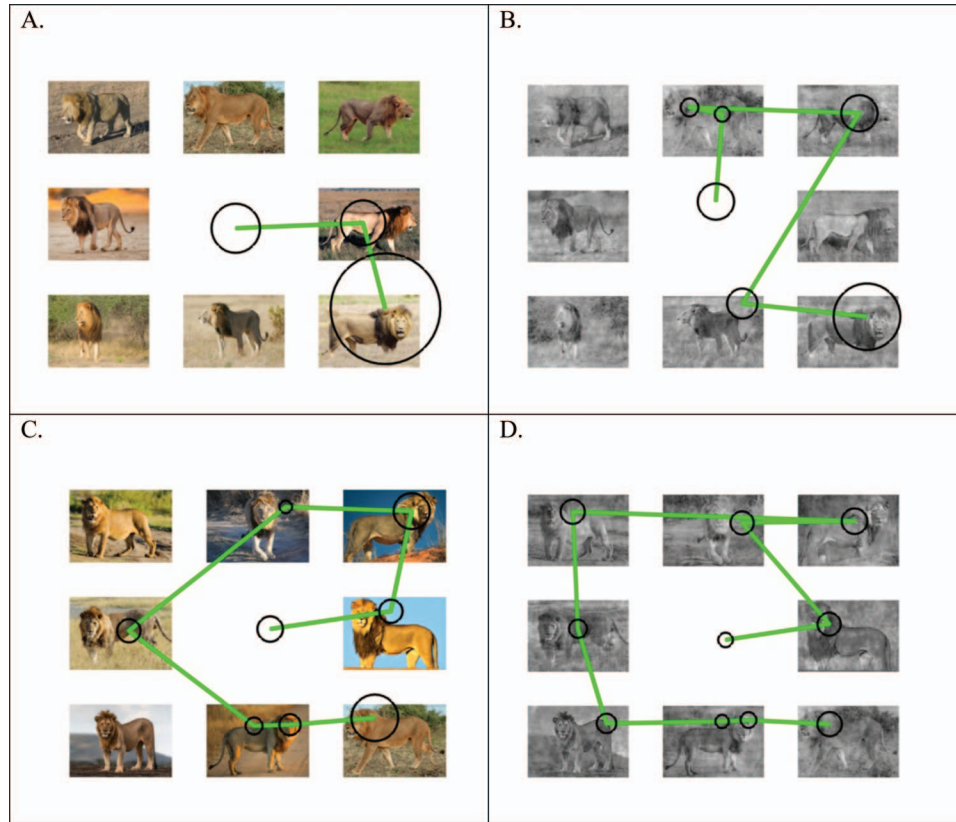
Figure 1. Examples of scanpaths from one participant on matrices from the four treatment blocks of the lion set (A, B target facing toward; C, D target facing away). The participant begins looking at the middle of the images and ends by looking at the target animals. The size of the black circles corresponds to the amount of time the participant spent looking at a given location. See the online article for the color version of this figure.

create the Target Impala Toward, Target Impala Toward Control, Target Impala Away, and Target Impala Away Control treatment blocks.

Eye Tracker

We used a Tobii X2-60 eye tracker along with Tobii Studio 3.4 (Tobii Technology, Inc., Danderyd, Sweden) to present our images and record the gaze of participants (accuracy: 0.4 degrees; data rate: 60 Hz; binocular tracking). Participants were told that we were measuring the size of their pupils but were not told that their eye movements were being monitored until after they completed the trial. The images were displayed on a 63.5-cm Dell UltraSharp UP2516D monitor (2560 × 1440 pixels; Dell Computer Corporation, Round Rock, TX). The luminance of the monitor (sensor positioned in the middle of the monitor and directed toward the screen) displaying a white background was 190 cd/m², and the illuminance of the testing room (sensor positioned in the middle of the monitor and directed toward the participant) was 250 lux (Spectra Cine PhoRad Meter, SC-820, Burbank, California). Participants were positioned ~60 cm from the screen and used a chin cup (UHCOTech HeadSpot, Houston, Texas) to minimize head movements. The equipment was calibrated (5 points) before each trial began. We used the Tobii Velocity-Threshold Identification filter (I-VT filter; gap fill-in: 75 ms; eye selection: average; velocity calculator window: 20 ms; I-VT classifier threshold: 30 degrees/s; merge adjacent time: 75 ms; merge adjacent angle: 0.5 degrees) to classify fixations and saccades. This filter classifies eye movements as fixations or saccades based upon the velocity of eye movements. Eye movements below and above the velocity threshold (30 degrees/s, in this study) are classified as fixations and saccades, respectively. Eye-tracking data consisted of coordinates of where participants were known to be looking during each sampling point.

Experimental Procedures

The experimenter (Maria E. Tovar) first asked participants to perform two practice trials so they could become familiar with the procedure. In the first practice trial, participants fixated a black dot that appeared in the center of the screen for 1 s. They were then presented with a 3 × 3 matrix that consisted of one image of a cat (*Felis catus*) facing the camera and seven images of cats facing away from the camera (arranged in the same manner as described earlier for the predator and prey matrices). They were instructed to press the space bar on the keyboard as soon as they located the cat image that was facing toward them. Once they pressed the space bar, the matrix disappeared and the fixation dot reappeared. They

repeated this process for five matrices. The second practice trial was similar to the first except that the subjects were searching for the cat that was facing away from the camera among images of cats that were facing toward the camera.

After completing the practice trials, participants were then presented with the first set of 24 matrices. As in the practice trials, they were instructed to fixate a central dot; when a matrix appeared, they were asked to press the space bar as soon as they found the target animal. Because the participants fixated this central dot, the middle position of the matrices was left empty (see Figure 1) to ensure that participants had to search for the target. They performed this task for each of the four blocks of matrices within the set (the order of the blocks was randomized across participants). This process was repeated a second time with the second set of matrices (the order of the sets was randomized across participants). By the end of the trial, a participant therefore performed the search task on eight blocks of matrices: Target Lion Toward, Target Lion Toward Control, Target Lion Away, Target Lion Away Control, Target Impala Toward, Target Impala Toward Control, Target Impala Away, and Target Impala Away Control, with the order of the blocks and sets randomized across participants.

Measurements and Statistical Analysis

Using a customized MATLAB program, we drew rectangular regions of interest (ROIs) around each target and distractor (293 × 208 pixels). All target and distractor images were the same size, and their ROIs included the entire rectangular region of each image. For each fixation coordinate, we determined which ROI it fell within to determine whether the participant was looking at the target image, distractor images, or neither the target nor distractor images. We calculated four metrics: the amount of time that elapsed before participants fixated on the target (Latency to Fixate Target), the amount of time that elapsed before participants manually responded by pressing the space bar to indicate they detected the target (Latency to Manual Response), the number of different distractors the participants fixated (Number of Different Distractors Fixated), and the average time that participants spent looking at each distractor, only including distractors that were fixated (Time Viewing Distractors). For each participant, we calculated the mean value of the metrics within each of the eight treatment blocks (Target Lion Toward, Target Lion Toward Control, Target Lion Away, Target Lion Away Control, Target Impala Toward, Target Impala Toward Control, Target Impala Away, and Target Impala Away Control). In matrices where the data indicated a participant never fixated the target, it was not possible to determine whether the participants did not fixate the target (and therefore did not correctly perform the task) or whether the eye-tracker failed to record the participants' gaze when they were fixating the target. We therefore excluded a given matrix from the analysis if a participant's fixations never fell within the target or if more than 10% of the gaze data was missing; only 3.5% of the matrices were discarded due to this restriction.

We analyzed our data using linear mixed-effects models with repeated measures (PROC MIXED) in SAS (Version 9.4; SAS Institute Inc., Cary, NC). Our statistical analyses consisted of four independent (response) variables (latency to fixate the target, latency to respond manually, number of different distractor images fixated, and time viewing each distractor image). The models consisted of a between-subjects dependent variable: gender; the models also consisted of four within-subjects dependent variables: orientation (target facing toward vs. away), animal type (lion vs. impala), type of image (natural image vs. image that controlled for low-level features), and trial order (the order in which the eight treatment blocks were presented). All of the interactions among the dependent variables were included in the models. Participant identity was included within the models to account for repeated measures. We made a priori predictions regarding differences among treatment blocks and created contrasts to evaluate these differences; we performed eight comparisons and used the false discovery rate correction (Benjamini & Hochberg, 1995) to evaluate statistical significance.

We also performed a factor analysis on the four response variables to extract a single factor that explained 76.3% of the variation in the original variables in Minitab (Version 18.1; Minitab Inc., State College, PA). We ran another linear mixed-effects model with repeated measures using this composite factor as the response variable.

Results

Head orientation impacted detection: Participants were faster to visually fixate the target (predator or prey) when the target was facing toward versus facing away (Latency to Fixate Target, Table 1; Figure 2A). In the natural images, participants were 1.24× faster at detecting the forward-facing predator compared with the predator facing away; similarly, they were 1.23× faster at detecting the forward-facing prey versus the prey facing away in the natural images. Animal type also influenced detection. Participants were faster to fixate the predator versus prey targets irrespective of orientation and image type. In particular, they were 1.17× and 1.27× faster at detecting the forward-facing predator compared with the forward-facing prey in the natural and control images, respectively. Participants were slower at detecting the targets in the control versus natural images. Gender of participants and trial order did not impact their ability to detect the targets. The results were similar for the latency to detect the target via a key press (Latency to Manual Response, Table 1; Figure 2B).

Participants looked at more distractors (Number of Different Distractors Fixated, Table 1; Figure 2C) and spent more time looking at those distractors (Time Viewing Distractors, Table 1; Figure 2D) when the distractors (predator or prey) were facing forward versus facing away. When viewing the natural images, participants looked at 1.26 more predator distractors when the distractors were facing forward versus facing away and spent 1.36 more time looking at those forward-facing predator distractors compared with the predator distractors facing away. Participants also looked at more distractors and spent more time looking at those distractors when the distractors were predators rather than prey and when the images were natural rather than control. Gender of participants and trial order did not influence the number of distractors they viewed or the amount of time they viewed them. The results based on the composite variable (Composite Factor, Table 1) were generally similar to the results based on the individual variables (Latency to Fixate Target, Latency to Manual Response, Number of Different Distractors Fixated, Time Viewing Distractors, Table 1).

Table 1

The Effect of Orientation, Animal Type, Image Type, Gender, and Trial Order on the Latency to Locate the Target (via Fixations and Manual Responses), Number of Different Distractors Fixated, Time Viewing Each Distractor, and the Composite Factor While Controlling for Repeated Measures

	Latency to Fixate Target	Latency to Manual Response	Number of Different Distractors Fixated	Time Viewing Distractors	Composite Factor
Overall model					
Orientation	33.77 (<.0001)*	23.59 (<.0001)*	24.42 (<.0001)*	37.45 (<.0001)*	44.89 (<.0001)*
Animal type	35.19 (<.0001)*	19.9 (<.0001)*	32.54 (<.0001)*	7.35 (.01)*	33.73 (<.0001)*
Orientation × Animal Type	0.40 (.53)	1.76 (.19)	1.11 (.30)	0.30 (.59)	0.25 (.62)
Image type	5.97 (.02)*	11.05 (.0015)*	4.51 (.04)*	5.16 (.03)*	10.09 (.0024)*
Orientation × Image Type	0.46 (.50)	0.61 (.44)	0.26 (.61)	0.58 (.45)	0.15 (.70)
Animal Type × Image Type	0.77 (.38)	1.66 (.20)	0.41 (.53)	0.43 (.51)	1.19 (.28)
Orientation × Animal Type × Image Type	0.45 (.51)	0.01 (.93)	2.4 (.13)	2.16 (.15)	0.03 (.85)
Gender	0.56 (.46)	0.18 (.67)	0.29 (.59)	0.12 (.73)	0.02 (.89)
Orientation × Gender	0.53 (.47)	0.07 (.79)	0.34 (.56)	0.32 (.57)	0.10 (.75)
Animal Type × Gender	1.93 (.17)	5.89 (.02)*	8.10 (.01)*	0.26 (.61)	4.99 (.03)*
Orientation × Animal Type × Gender	0.00 (.95)	0.54 (.46)	0.09 (.76)	0.21 (.65)	0.08 (.78)
Image Type × Gender	0.53 (.47)	0.72 (.40)	2.51 (.12)	0.14 (.71)	1.18 (.28)
Orientation × Image Type × Gender	0.23 (.63)	0.74 (.39)	0.32 (.58)	0.3 (.59)	0.19 (.66)
Animal Type × Image Type × Gender	0.18 (.68)	0.02 (.89)	4.56 (.04)*	2.03 (.16)	1.50 (.23)
Orientation × Animal Type × Image Type × Gender	0.00 (.97)	0.07 (.79)	0.18 (.68)	1.61 (.21)	0.13 (.72)
Trial order	0.03 (.86)	1.54 (.21)	3.28 (.07)	3.76 (.053)	2.18 (.14)
Orientation × Trial Order	0.00 (.97)	0.59 (.44)	0.73 (.39)	0.05 (.82)	0.32 (.57)
Animal Type × Trial Order	2.00 (.16)	1.61 (.21)	1.32 (.25)	0.23 (.63)	1.80 (.18)
Orientation × Animal Type × Trial Order	0.53 (.47)	1.27 (.26)	0.17 (.68)	0.01 (.93)	0.57 (.45)
Image Type × Trial Order	0.00 (.95)	0.84 (.36)	1.09 (.30)	0.02 (.90)	0.40 (.53)
Orientation × Image Type × Trial Order	0.11 (.74)	0.38 (.54)	0.71 (.40)	0.64 (.43)	0.10 (.75)
Animal Type × Image Type × Trial Order	0.00 (.95)	0.45 (.50)	0.53 (.47)	0.25 (.62)	0.37 (.54)
Orientation × Animal Type × Image Type × Trial Order	0.14 (.71)	0.11 (.74)	0.33 (.57)	1.71 (.19)	0.05 (.83)
Gender × Trial Order	2.36 (.13)	0.17 (.68)	0.01 (.92)	0.65 (.42)	0.12 (.73)
Orientation × Gender × Trial Order	2.43 (.12)	1.47 (.23)	1.79 (.18)	0.03 (.86)	1.51 (.22)
Animal Type × Gender × Trial Order	0.29 (.59)	3.03 (.08)	5.67 (.02)*	0.05 (.82)	1.91 (.17)
Orientation × Animal Type × Gender × Trial Order	0.52 (.47)	0.08 (.78)	0.15 (.70)	0.00 (.96)	0.05 (.82)
Image Type × Gender × Trial Order	0.91 (.34)	0.87 (.35)	2.4 (.12)	0.32 (.57)	1.52 (.22)
Orientation × Image Type × Gender × Trial Order	0.05 (.82)	0.24 (.63)	0.00 (.98)	0.10 (.76)	0.02 (.89)
Animal Type × Image Type × Gender × Trial Order	0.06 (.81)	0.01 (.94)	3.58 (.06)	1.77 (.18)	1.00 (.32)
Orientation × Animal Type × Image Type × Gender × Trial Order	0.33 (.57)	0.22 (.64)	0.05 (.82)	0.67 (.41)	0.42 (.52)
Comparisons					
Lion Toward vs. Lion Away	5.60 (<.0001)* [1.02]	5.29 (<.0001)* [1.05]	6.99 (<.0001)* [1.35]	6.83 (<.0001)* [1.33]	7.59 (<.0001)* [1.48]
Impala Toward vs. Impala Away	6.35 (<.0001)* [1.37]	6.49 (<.0001)* [1.42]	6.19 (<.0001)* [1.08]	7.27 (<.0001)* [1.51]	8.13 (<.0001)* [1.69]
Lion Toward Control vs. Lion Away Control	7.24 (<.0001)* [1.31]	6.29 (<.0001)* [1.09]	8.80 (<.0001)* [1.66]	6.11 (<.0001)* [1.13]	8.75 (<.0001)* [1.58]
Impala Toward Control vs. Impala Away Control	6.45 (<.0001)* [1.06]	6.52 (<.0001)* [1.04]	3.34 (.0015)* [0.60]	7.82 (<.0001)* [1.29]	7.50 (<.0001)* [1.22]
Lion Toward vs. Impala Toward	3.91 (.0002)* [0.98]	2.35 (.022)* [0.61]	5.63 (<.0001)* [0.99]	2.11 (.040)* [0.48]	4.27 (<.0001)* [0.98]
Lion Toward Control vs. Impala Toward Control	6.49 (<.0001)* [1.25]	4.33 (<.0001)* [0.76]	7.90 (<.0001)* [1.38]	1.91 (.061) [0.35]	6.34 (<.0001)* [1.15]
Lion Away vs. Impala Away	4.59 (<.0001)* [0.80]	3.49 (.0009)* [0.65]	4.76 (<.0001)* [0.94]	2.47 (.016)* [0.42]	4.72 (<.0001)* [0.87]
Lion Away Control vs. Impala Away Control	5.72 (<.0001)* [0.89]	4.59 (<.0001)* [0.70]	2.46 (.017)* [0.45]	3.63 (.0006)* [0.58]	5.11 (<.0001)* [0.81]

Note. F values are displayed; *p*-values are indicated in parentheses and statistically significant comparisons are indicated with an asterisk. Standardized effect size (Cohen's *d*) is reported in brackets. The numerator degrees of freedom is one and the denominator degrees of freedom is 58 in all tests except the denominator degrees of freedom is 390 for any terms containing trial order.
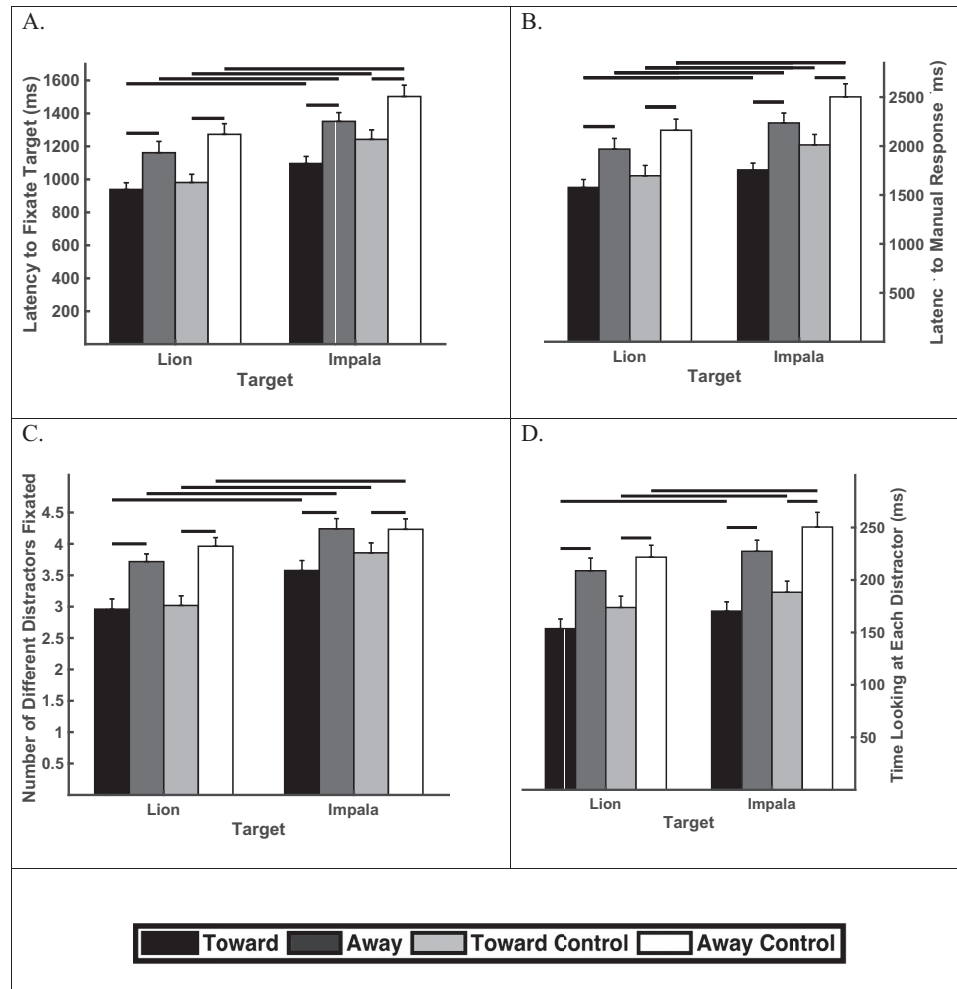
Figure 2. (A) The latency to first fixate the target animal. (B) The latency to respond manually (key press). (C) The number of animal distractors fixated. (D) The duration of time spent looking at animal distractors. Means and 95% confidence intervals are shown; horizontal lines indicate planned comparisons that were statistically significant.

Discussion

Participants were faster to detect predators (lions) and prey (impalas) facing toward versus away from them. Furthermore, they were quicker to detect forward-facing predators than forward-facing prey, supporting the hypothesis that predators exhibiting dangerous orientations attract an increased amount of attention. These results were generally upheld when controlling for some low-level confounds.

We found that humans' attention to predators depends on the level of risk. Human participants were faster to detect (via both visual fixation and manual response) predators that were oriented toward versus away from them. Other species, including lizards and birds, also respond more strongly to predators that are oriented toward them versus oriented away from them (Bateman & Fleming, 2011; Cooper, 1997, 1998, 2003; Freeberg, Krama, Vrublevska, Krams, & Kullberg, 2014; Hampton, 1994). Predators oriented toward a prey individual represent a high level of risk because those predators have likely detected that individual (Coo-

per, 1998; Kyle & Freeberg, 2016; Stankowich & Coss, 2006). Rapidly detecting these highly threatening predators provides more time to take defensive action and evade attack.

Given that human subjects detected forward-facing lions ~220 ms faster than lions facing away, forward-facing lions would be detected when they were 3.1 m farther from the subjects compared with lions facing away (assuming that lions sprint at ~13.9 m/s; Elliot, Cowan, & Holling, 1977; Schaller, 1972). Because lions are less successful in capturing prey that are farther from them (Elliot, Cowan, & Holling, 1977), this extra distance between the lions and humans could lower predation rates. Similarly, avian prey vary in their latency to detect predators such that predators would be 2.5 m farther from individuals that are faster (100 ms) to detect predators; it is likely that these individuals experience lower predation rates compared with individuals that are slower to detect predators (Hilton, Cresswell, & Ruxton, 1999). Because demographic variables can impact predator assessment (Chapman, Kertz, Zurlage, & Woodruff-Borden, 2008; Parsons & Rizzo,

2008), the participants in this study were drawn from a limited subset of the population (European heritage and between the ages of 18 and 30 years old); future studies could test whether demographic variables influence predator detection.

Predators can orient toward prey by directing their eyes, heads, or bodies toward them (Kyle & Freeberg, 2016). In the majority of studies examining predator orientation, the eyes, heads, and bodies of the predators are oriented in the same direction and it is therefore not possible to determine which features (eyes, heads, or bodies) prey are using when making their antipredator decisions. Two studies that independently manipulated predators' head and eye or body orientations found that prey were attending to head orientation rather than eye (Hampton, 1994) or body (Kyle & Freeberg, 2016) orientation. In our study, human participants were instructed to search for the predator that was directing its head toward or away from the participant; in the majority of our predator stimuli, the predators' bodies were oriented to the side. This created a situation in which head and body direction were congruent (oriented in the same direction) in the stimuli in which the predator was facing away from the participant but incongruent (oriented in different directions) in the stimuli in which the predator was facing toward the participant. Given that the participants' search times were actually faster for the incongruent stimuli (head directed toward camera but body directed away from the camera) than the congruent stimuli (head and body directed away from the camera), the results suggest that the participants were ignoring body orientation during their search (as we would expect them to do based on the instructions). Future experiments that systematically manipulate the eye, head, and body direction of predators would provide further insight into the features that humans use to inform their antipredator decisions.

Unexpectedly, we found that human participants were faster to detect (via both visual fixation and manual response) prey oriented toward versus away from them. Given that predators also incur costs when hunting prey (Mukherjee & Heithaus, 2013), this behavior may be evolutionarily adaptive. To minimize costs, predators can avoid prey that are difficult to capture (FitzGibbon, 1989, 1990; Schaller, 1972). Prey that are oriented toward predators are likely harder to capture than prey oriented away from predators (Krause & Godin, 1996; Li, Jackson, & Lim, 2003). Our results suggest that humans could selectively avoid prey that are difficult to capture: Hunters who rapidly identified prey that had detected them could potentially use that information to abort attacks (Coss, 2017). Predators in other species also incorporate information about prey orientation in their hunting decisions. Cichlid and spider predators are less likely to attack prey that are oriented toward them versus away from them (Krause & Godin, 1996; Li et al., 2003). In a similar manner, primates emit alarm calls indicating that they detected a predator and these calls can deter that predator (Zuberbühler, Jenny, & Bshary, 1999).

Alternatively, it is possible that humans' rapid detection of forward-facing prey is a nonadaptive carry-over effect from their ability to rapidly detect forward-facing predators (our study) and people (Aya, 2012). They may actually be less efficient at hunting prey if their attention is drawn toward forward-facing prey that are more difficult to capture rather than focusing on prey that are facing away from them and easier to capture. A future study could examine predator hunting success for prey oriented away from them when those prey are within groups that vary in the percentage

of prey oriented toward versus away from the predator. Similarly, humans' rapid detection of forward-facing predators could be a carry-over effect from their ability to rapidly detect forward-facing people (Aya, 2012). In this case, as discussed earlier, it is still likely beneficial that humans focus on forward-facing predators.

Even though participants were faster to detect forward-facing predators and prey, they were faster at detecting forward-facing predators than forward-facing prey. These results are consistent with previous work showing that humans detect predators faster than prey (Penkunas & Coss, 2013a, 2013b; Yorzinski et al., 2014). Because failing to detect predators can have immediate survival consequences (Lima & Dill, 1990), it is beneficial for humans to rapidly detect predators.

Human participants were slower to detect predators and prey facing away from them because they spent more time looking at the forward-facing distractor animals and looked at more of those distractors. These results support the enhanced dwell-time hypothesis, which posits that dangerous animals are effective at maintaining attention or delaying disengagement (Fox et al., 2002; Yorzinski et al., 2014), as participants were slow to disengage their attention from the forward-facing predators and prey. Furthermore, these results also support the pop-out hypothesis, which posits that dangerous animals exogenously attract attention through low-level features (such as edges and shapes; Simons, 2000; Treisman, 1988), as participants looked at a larger number of forward-facing distractor predators and prey. This indicated that the forward-facing predators and prey drew attention despite the participants being instructed to search for predators and prey that were facing away from them. Future experiments in which participants are not instructed to search for specific targets (and are therefore able to freely view the images) could lend additional support for this hypothesis. However, we found that other low-level features (luminance and spatial frequency) did not impact the quicker detection of forward-facing predators or prey.

Many species, including humans, experience strong sources of natural selection that shape their antipredator behaviors (Coss & Ramakrishnan, 2000; Hart & Sussman, 2005; Isbell, 2006; Lima & Dill, 1990; Stanford, 2002). These antipredator behaviors include attentional processes that guide the rapid detection and evaluation of threats (Öhman, Flykt, & Esteves, 2001; Penkunas & Coss, 2013a, b; Yorzinski et al., 2014). Additional experiments that investigate how variation in risk levels impact attention across species would be informative.

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