

Selective attention in peacocks during predator detection

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Received: 26 July 2013 / Revised: 4 November 2013 / Accepted: 7 November 2013
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Abstract Predation can exert strong selective pressure on the evolution of behavioral and morphological traits in birds. Because predator avoidance is key to survival and birds rely heavily on visual perception, predation may have shaped avian visual systems as well. To address this question, we examined the role of visual attention in antipredator behavior in peacocks (*Pavo cristatus*). Peacocks were exposed to a model predator while their gaze was continuously recorded with a telemetric eye-tracker. We found that peacocks spent more time looking at and made more fixations on the predator compared to the same spatial location before the predator was revealed. The duration of fixations they directed toward conspecifics and environmental features decreased after the predator was revealed, indicating that the peacocks were rapidly scanning their environment with their eyes. Maximum eye movement amplitudes and amplitudes of consecutive saccades were similar before and after the predator was revealed. In cases where conspecifics detected the predator first, peacocks appeared to learn that danger was present by observing conspecifics' antipredator behavior. Peacocks were faster to detect the predator when they were fixating closer to the area where the predator would eventually appear. In addition, pupil size increased after predator

exposure, consistent with increased physiological arousal. These findings demonstrate that peacocks selectively direct their attention toward predatory threats and suggest that predation has influenced the evolution of visual orienting systems.

Keywords Attention · Eye movements · Eye-tracking · Peafowl · Predation · Pupil dilation

Introduction

Predators have exerted strong selective pressures that have influenced many avian traits (Caro 2005). Birds often adjust their behavioral strategies in different contexts, including foraging and reproduction, to minimize predation (Lima and Dill 1990). They can even tailor these adjustments based on the perceived level of predation risk (Schneider 1984; Newman and Caraco 1987). Some species also have morphological adaptations that reduce predation. Birds that are under increased predation pressures, such as parents incubating their eggs, have camouflaged plumage (Martin and Badyaev 1996). Because predator detection is essential to survival (Caro 2005) and most birds are highly visual (Zeigler and Bischof 1993), predation pressure may have also shaped avian visual systems (Martin 1986).

Avian visual systems have many specializations that could aid birds in detecting and responding to predators (Zeigler and Bischof 1993). Many species have wide visual fields that could enable them to detect threats from many different angles (Martin 1986; Guillemain et al. 2002). Retinal specializations, such as visual streaks (Meyer 1977), can help birds respond to predators by enabling some species to simultaneously forage and remain vigilant (Lima

Electronic supplementary material The online version of this article (doi:10.1007/s10071-013-0708-x) contains supplementary material, which is available to authorized users.

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and Bednekoff 1999; Moore et al. 2012). Photoreceptor densities may have been shaped by predation pressures as well. Birds living in closed-habitats have a higher density of photoreceptor cells directed toward the ground, whereas birds living in open-habitats have a higher density of photoreceptor cells directed toward the sky; the location of these photoreceptor cells aligns with the direction from which predators would most likely appear in the different habitat types and may maximize birds' abilities to detect predators (Hart 2001). In addition, birds with greater visual acuity (the ability to resolve objects) may be able to detect predators at a distance faster than those with lower acuity (Kiltie 2000; Tisdale and Fernández-Juricic 2009).

Behavioral experiments suggest that birds use these acute visual capabilities to rapidly orient and respond to potential danger (Kaby and Lind 2003; Devereux et al. 2006). Birds can detect predators within seconds of a predator's appearance but many factors can influence detection time (Whittingham et al. 2004; Devereux et al. 2006). When birds are located in visually obscured habitats, they are slower to detect predators (Whittingham et al. 2004). Birds that are oriented with their heads down or facing away from the predator are slower to locate a predator (Kaby and Lind 2003; Tisdale and Fernández-Juricic 2009). Conspecifics can also influence a bird's ability to find a predator. Birds that are foraging in larger groups are faster to respond to predators than those in smaller groups (Pulliam 1973; Roberts 1996). Despite our knowledge of avian antipredator behavior, we know relatively little about how visual ecology and attention directly influence it.

The goal of this study was to investigate the visual mechanisms guiding antipredator behavior in peacocks (*Pavo cristatus*). Peacocks are an appropriate avian species to explore this topic because they are subject to predation and exhibit antipredator behavior (Kannan and James 1998; Yorzinski and Platt 2012). Peacocks have an area of high retinal ganglion cell density (area centralis) with the highest visual acuity, which is analogous to the human fovea (Hart 2002). We tested whether peacocks selectively direct their attention toward a potential predator and whether conspecifics' behavior influences this attention. We also examined pupil size to determine whether predator exposure affected physiological arousal responses.

Methods

Animals and housing

We used a head-mounted, telemetric, infrared eye-tracker (Fig. 1a) to investigate how peacocks respond to predators

in Durham, NC, USA (36.01°N, 79.02°W) in April 2013 between 8:00 and 13:00 as well as 16:00–18:00. The males and females were housed in separate enclosures within wooded areas (male enclosure 92 m perimeter; female enclosure 46 m perimeter). The birds were therefore familiar with individuals of their own sex but had limited interactions with individuals of the opposite sex before the trials began (with the exception of male–female interactions during a previous study; Yorzinski et al. 2013). The experiment was performed in a large outdoor cage (27 m perimeter) that was adjacent to the males' enclosure (Fig. 1b). This testing cage was within the wooded area (and was therefore partially shaded in sections) but was completely open (with the exception of one tree—0.48 m diameter at 1 m high—that was positioned in a corner). The birds had limited experience within this testing cage, as they were only inside of it during these trials and another study (Yorzinski et al. 2013). The enclosures were completely surrounded by black plastic to prevent birds in the different enclosures from seeing one another. With the exception of one female (which was purchased from a breeder but had been free-ranging up until a year before the breeder captured her), all of the birds were caught from free-ranging populations in Florida, North Carolina, and California between 2008 and 2012. Since the birds were captured as adults, they each had at least 3 years of experience in natural environments, with likely exposure to native predators (such as foxes, raccoons, and coyotes). Yorzinski et al. (2013) describe further details of this population.

Eye-tracker and experimental design

Males were habituated to wearing a telemetric eye-tracker. The eye-tracker has a headpiece (25 g; Positive Science, LLC, New York, USA) that is attached to a transmitter and battery pack (345 g; Iscan, Woburn, MA, USA). The headpiece has one camera that records the eye of the bird and another camera that records the scene in front of the bird. The males were habituated to wearing the eye-tracker by gradually training them in daily sessions of approximately 60 min for several weeks. We outfitted males with components of a facsimile eye-tracker (first getting them accustomed to the backpack, then the backpack with mass, and finally the headpiece) until they were comfortable wearing the full eye-tracking gear. We considered a male habituated to the eye-tracker when he freely walked around the enclosure while wearing the gear. In a previous study, we found that the eye-tracker did not interfere with natural behaviors of the birds (Yorzinski et al. 2013). The video signals were transmitted wirelessly to a nearby computer (Dell Dimension 2300) and saved onto a DVR (Toshiba D-R410).

Fig. 1 **a** Close-up of a peacock wearing the telemetric eye-tracker. **b** The testing cage during a trial, with two females, a focal male with the eye-tracker, and a displaying non-focal male



We calibrated the videos using an oculometric approach based on corneal reflections (Fantz 1958; Hamada 1984; Yorzinski et al. 2013). Light reflects off the cornea with an angle of reflection that equals the angle of incidence and this creates a corneal reflection (a virtual image of the light source created by the cornea; Maurer 1975). When the corneal reflection from a light source is in the center of the pupil, the optic axis is aligned with that light source (see Fig. 1 in Hamada (1984)). The optic axis is offset from the visual axis by less than 5° in humans (Nagamatsu et al. 2008) and pigeons (McFadden and Reymond 1985). We employed this oculometric approach in peacocks by shining a 3 mm infrared LED light toward the eye of a peacock when he was wearing the eye-tracker and this light created a corneal reflection. We moved the light so that its corneal reflection was aligned with the pupil center. When the bird naturally moved his eye to a different position, we moved

the infrared light so that it was again aligned with the pupil center. We repeated this process for approximately 5 min so that we had multiple points during which the optic axis of the male was aligned with the light source. The error associated with this calibration technique is approximately 5° (Yorzinski et al. 2013). The videos (originally 30 frames s^{-1} or 60 interlaced fields) were deinterlaced to generate 60 fields s^{-1} (Turbo.264, Elgato Systems, San Francisco, CA, USA). The offline calibration was performed using custom-designed eye-tracking software (Yarbus, Positive Science, LLC).

For each trial, a focal male was outfitted with the eye-tracker and the eye-tracker was calibrated. Conspecifics (a second male and two females) were released into the testing cage. The focal male was then released into the testing cage and his gaze was continuously recorded. After a minimum of 25 min, the researcher (JLY) revealed a

taxidermy fox (*Vulpes vulpes*) by silently lifting up the cloth wall of the cage and sliding the fox through (the researcher was never visible). The fox remained stationary for 5 min and was then pulled back behind the wall. Camcorders (Sony SR47) recorded the testing cage. Each focal male was tested one time while wearing the eye-tracker and different females were used in each trial. Due to limitations in the number of males, the focal males also served as non-focal males in different trials one or two times (at least 48 h lapsed between trials using a given male; the use of a male as a focal and non-focal was randomized). Eleven trials were performed while recording from the left eye of the peacock and three trials were performed while recording from the right eye. We put a black cloth over the eye that was not being recorded (because we were only able to record from one eye at a time) so that the males were only obtaining visual information monocularly from the eye we were monitoring.

Gaze analysis

We analyzed a 5-min period before the fox was revealed (pre-predator) and a 5-min period while the fox was visible (post-predator). We chose to compare gaze behavior after the predator was revealed to the period immediately before the predator was revealed to control for short-term biases in gaze behavior. In two trials, these periods were shorter because of equipment problems (one trial 4.15 min pre-predator; another trial 3.02 min pre-predator and 2.33 min post-predator). The gaze data were adjusted for parallax errors (Maurer 1975; Yorzinski et al. 2013). Parallax errors exist because the scene camera cannot be perfectly aligned with the eye of the bird without physically blocking the bird's vision. The scene camera was approximately 30 mm above the eye and either 15 mm to the right of the eye (when recording from the left eye) or 15 mm to the left of the eye (when recording from the right eye). The approximate distance between focal males and the target of their gaze was estimated to the nearest 1/3 m by pinpointing the location of the focal male and target onto a schematic grid of the cage. A parallax correction was then calculated based on the scene camera offset and the distance between the focal male and the targets of his gaze (Yorzinski et al. 2013).

The videos were analyzed field-by-field to determine the target of gaze during fixations. First, gaze data were preliminarily classified into fixations or saccades using a custom Matlab script. The script classified fixations as eye coordinates that fell within a specified range of movement and lasted at least 100 ms. The specified range was calculated by subtracting the pixel difference between the eye coordinates of one field and the next and then dividing by the pixel size of the eye; if this value was less than 2 %

(and there was therefore little change in eye position), the coordinate was classified as a fixation. Due to imprecision in the eye-tracking software, the eye coordinates sometimes changed slightly even though the eye was not actually moving; therefore, the 2 % allowance minimized this error.

Second, the videos were analyzed field-by-field to identify the target of gaze during fixations. Because of error associated with the eye-tracker ($\sim 5^\circ$; Yorzinski et al. 2013) and errors associated with estimating parallax errors using the schematic grid system, we conservatively created a 10° radius around each point of gaze. For each fixation, we determined whether a given target fell within this 10° radius. There were three targets: conspecific (females and non-focal male), predator (or area where the predator would be located in the pre-predator periods), and environment. The environmental target was identified when none of the other targets were within the radius (environmental features were visible within the radius in nearly all fields). The target sometimes included both a conspecific and the predator (or control region; conspecific + predator). If the target only fell within the gaze radius for part of a given fixation (occurred when the target moved), the target was still scored as being fixated. We also made any necessary corrections to the preliminary automatic fixation/saccade classification; such corrections were necessary, for example, when transmission was poor such that the researcher could see that the bird's eye did not move (and was therefore still part of a given fixation) but the automatic classification scored the gaze point as a saccade because the eye-tracking software did a poor job of tracking the noisy video signal. We ensured that two fixations were scored in cases where the eye did not move but the bird blinked.

Measurements and statistical analysis

We compared the percentage of time that peacocks spent looking at targets (conspecifics, predator (or control region), and environment) using a repeated-measures mixed linear model with a variance components covariance structure. For each male, we summed the amount of time he looked at each of the targets before ("pre") and after ("post") the predator was revealed. In instances when the target was conspecific + predator, we added the fixation time to both the conspecific and predator target times. We then divided by the total fixation time for the pre- or post-period, respectively. It was necessary to divide by the total fixation time because the total fixation time was never exactly 5 min in each period due to time spent making saccades, blinks, or equipment problems (e.g., poor transmission). We created a priori contrasts to compare the percentage of time peacocks looked at the predator,

conspecifics, and the environment before versus after the predator was revealed (e.g., conspecific during “pre” period and conspecific during “post” period). We performed this analysis a second time using number of fixations (we applied a square-root transformation on this variable to normalize it). Because peacocks spent similar amounts of time looking at (before $t = 2.13$, $p = 0.053$; after $t = 0.35$, $p = 0.72$; $n = 14$) and made a similar number of fixations on (before $t = 1.94$, $p = 0.075$; after $t = 0.31$, $p = 0.76$; $n = 14$) the non-focal male compared to the female conspecific targets, we pooled across the sex of the conspecific. We compared the overall number of fixations by dividing the number of fixations by the amount of time that peacocks spent making fixations within the before and after periods for each male.

We analyzed the duration of fixations that peacocks made on targets using a repeated-measures mixed linear model with a variance components covariance structure. We calculated the duration of each fixation made on conspecifics, the predator (or control region), the environment, and conspecific + predator. Then, we examined whether fixation duration differed with respect to these targets. We made a priori comparisons of fixation duration between each target before and after the predator was revealed. Because we did not know whether peacocks were fixating on the conspecific or predator in the conspecific + predator target category, we only directly compared fixation durations among the conspecific, predator, and environmental targets.

We investigated the relationship between the latency to discover the predator and the distance between the predator and where the bird was looking as the predator was revealed. We performed a regression and natural log transformed the latency to discover the predator in order to meet the assumption of normality. A first-order Markov chain analysis was performed to assess whether peacocks shifted their gaze in non-random sequences (we omitted the predator + conspecific target because we did not know which of these two targets the peacocks were directing their gaze toward). We tested whether gaze was more likely to shift between conspecifics and the predator/control region by calculating the Pearson’s chi-square test statistic. We also recorded the time at which peafowl first emitted loud antipredator calls (“bu” and “pe”); it was not possible to accurately record latency to emit quiet antipredator calls (“khok”; Takahashi and Hasegawa 2008).

We compared the maximum eye movement amplitude before and after the predator was revealed for each target. For each target in the before and after treatment, we used custom Matlab scripts to determine the maximum distance (in pixels) between any two gaze coordinates on the scene camera and converted this distance into angular degrees. For the environmental target, we used the raw gaze coordinates (rather than the parallax-corrected values) because

it was not possible to make a parallax correction since we did not know where the peacocks were gazing within the environment. We controlled for the amount of time peacocks gazed at different targets within the treatments because peacocks vary in the amount of time they gaze at different targets (see “Results”). The average maximum eye movement amplitude was calculated by taking the mean of the maximum eye movement amplitude across treatments and targets for each bird. The magnitude of consecutive saccades was examined by calculating the mean angular difference between consecutive saccades for each bird before and after the predator was revealed. Lastly, we compared the pupil size of peacocks 1 min before and 1 min after the predator was revealed; we only examined 1-min periods to minimize any longer term consequences of changing illumination (see “Discussion”). Because eye size on the videos varied across trials (due to different distances between the eye camera and the eye), we standardized pupil sizes by multiplying the pupil diameter (pixels) by the width of a peacock’s eye (approximately 10 mm) and dividing by the number of pixels the width of the peacock’s eye occupied in the videos. All analyses were performed in SAS (version 9.3).

Results

Peacocks varied the amount of time they fixated and the number of fixations they made on targets before and after the predator was revealed (Table 1; Fig. 2; Movie S1). They spent more time looking at and made more fixations on the predator after it was introduced compared to the same spatial location before the predator was visible (Table 1). They spent similar amounts of time looking at and making fixations on the environment (Table 1) and conspecifics (Table 1) before and after the predator was revealed. Overall, peacocks made more fixations after compared to before the predator was revealed (before 1.1 fixations/s; after 1.4 fixations/s; Wilcoxon signed rank test $W = 85.0$, $p = 0.045$). Peacocks also altered the duration of their fixations on targets before and after the predator was revealed (Table 1; Fig. 3). Fixation durations on the environment (Table 1) and conspecifics (Table 1) were shorter after the predator was presented compared to before it was presented. Fixation duration on the predator after it was introduced did not differ from the same area before the predator was presented (Table 1).

In most trials, peacocks detected the predator without first seeing a conspecific respond to the predator ($N = 9$). Similar to the focal bird, conspecifics responded to the predator by exhibiting alert postures (neck outstretched and head up), moving freely around the cage, emitting anti-predator calls, and ending courtship behavior (the non-

Table 1 The effect of target, treatment, and target \times treatment on the amount of time looking, the number of fixations, and the duration of fixations

		1.1		Amount of time	1.2		Number of	1.3		Duration of
		DF	DF		DF	DF	fixations	DF	DF	fixations
		(Num)	(Den)		(Num)	(Den)		(Num)	(Den)	
<i>Overall model</i>										
A	Target	2	26	113.05 (<0.0001)*	2	26	160.47 (<0.0001)*	3	38	31.54 (<0.0001)*
B	Treatment	1	13	0.36 (0.56)	1	13	4.28 (0.059)	1	13	43.50 (<0.0001)*
C	Target \times Treatment	2	26	5.75 (0.009)*	2	26	8.42 (0.0015)*	3	23	14.14 (<0.0001)*
<i>Contrasts</i>										
D	Before control versus after predator	1	26	9.70 (0.0045)*	1	26	19.82 (0.0001)*	1	23	0.82 (0.37)
E	Before environment versus after environment	1	26	0.99 (0.33)	1	26	1.24 (0.28)	1	23	84.6 (<0.0001)*
F	Before conspecific versus after conspecific	1	26	1.18 (0.29)	1	26	0.06 (0.81)	1	23	158.42 (<0.0001)*

A priori contrasts were performed to compare specific target groups

F values are displayed; *p* values are indicated in parentheses; * statistically significant results

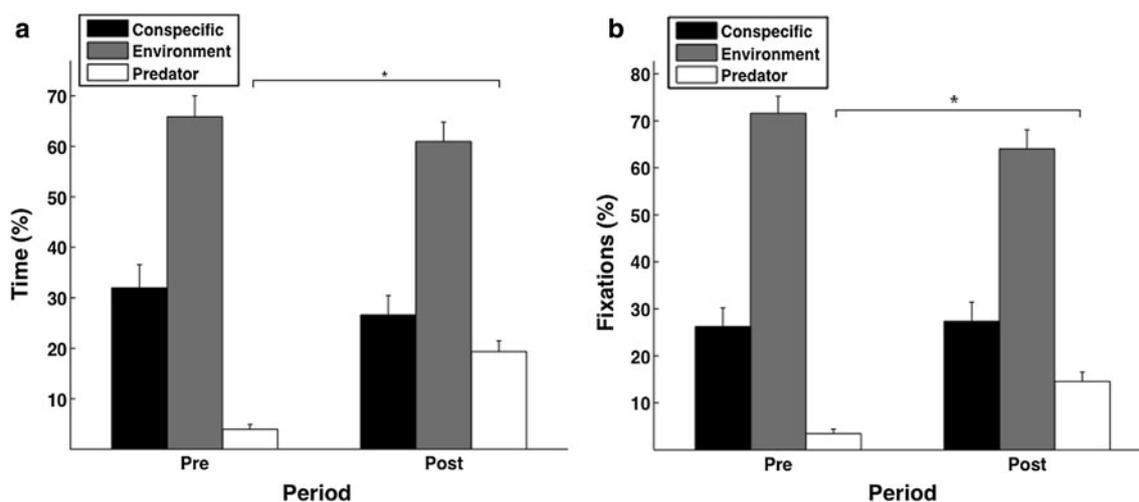


Fig. 2 Peacocks **a** spent more time looking at and **b** made more fixations on the predator after the predator was revealed (post) compared to a control region before the predator was revealed (pre).

A priori comparisons were made within targets across both periods. Asterisks indicate significant results

focal males were displaying in 9 trials before the predator was revealed and put their trains down in 7 of these trials as soon as the predator was revealed). In two trials, peacocks fixated conspecifics that were responding to the predator (but the peacocks did not fixate on the predator until more than four fixations afterward) and exhibited antipredator behavior before fixating the predator themselves. In another three trials, it is possible that peacocks detected conspecifics' antipredator behavior peripherally. In two of these trials, the conspecific's head/eyes were within 20° of

the focal peacock's point of gaze (movie S1) and the focal peacocks looked from near the conspecific to the predator within two fixations; in one trial, the peacock was looking at a displaying male (from the side) that froze upon seeing the predator but it was unclear whether the focal male would have been able to see this other male's head/eyes because the train was erect. Except in one of these three trials, the latency to detect the predator (2.20, 1.62 and 0.17 s) was not among the fastest detection times (median 2.0 s; range 0.17–23.5 s). The latency to discover the

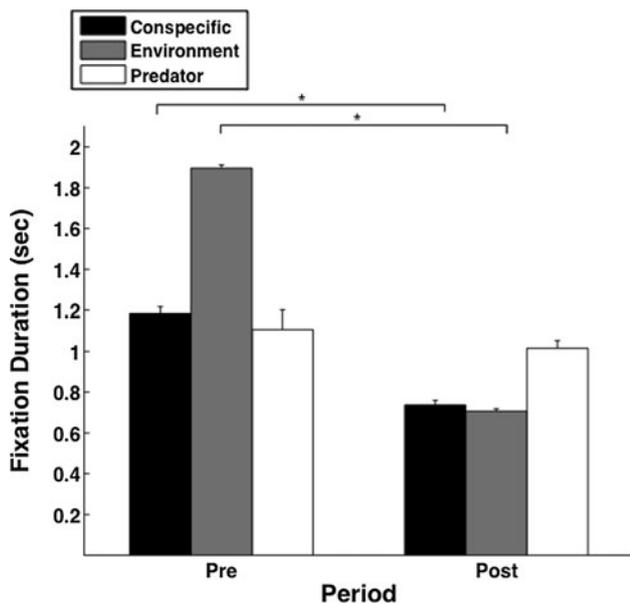


Fig. 3 Peacocks made shorter fixations on conspecifics and the environment when the predator was present (post) compared to when it was not present (pre). A priori comparisons were made within targets across both periods

predator, however, was faster when the focal peacock was fixating closer to the area where the predator would be located immediately before the predator was revealed [$F(1,12) = 6.10, R^2 = 33.7\%, p = 0.03$; Fig. 4].

Peacocks did not randomly shift their gaze among targets before ($\chi^2 = 589.2, df = 4, p < 0.0001$) or after ($\chi^2 = 788.1, df = 4, p < 0.0001$) the predator was revealed (Table 2). Peacocks were more likely to gaze from a conspecific to the predator/control region after the predator was revealed compared to before it was revealed ($\chi^2 = 42.8, df = 1, p < 0.0001$). They were also more likely to gaze from the predator/control region to a conspecific after the predator was revealed compared to before it was revealed ($\chi^2 = 30.2, df = 1, p < 0.0001$).

In eight trials, one of the peafowl emitted a loud anti-predator call (“pe” or “bu”; Takahashi and Hasegawa 2008); one of the females emitted the call in 5 trials, the focal male emitted the call in 2 trials, and it was not possible to determine which individual produced the call in one trial. In seven of these eight trials, the call was emitted after the focal male had already fixated the predator. In the one trial during which a female emitted the call before the focal male fixated the predator, the male was making a saccade during the alarm call and fixated the predator immediately afterward. Although it was not possible to reliably analyze the khok calls because they could be too quiet for the microphone to record them reliably, in trials where we could hear them ($N = 7$), the calls were likewise emitted after the focal male detected the predator (with the exception of one trial).

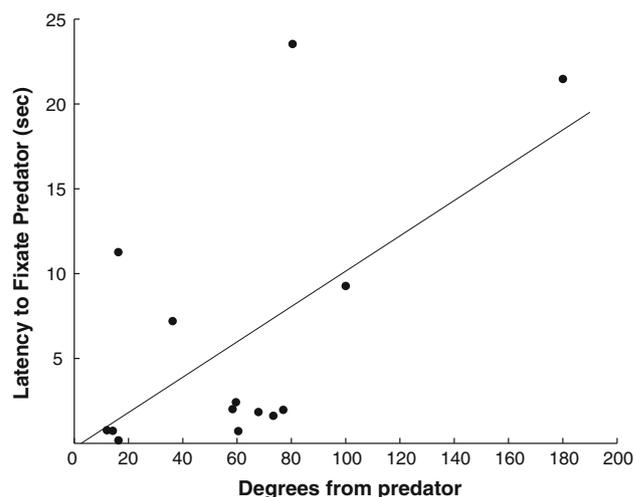


Fig. 4 Peacocks were faster to detect the predator when they were fixating closer to the area where the predator would be located immediately before the predator was revealed [$F(1,12) = 6.10, R^2 = 33.7\%, p = 0.03$]

Table 2 The number of times peacocks looked between targets (a) before and (b) after the predator was revealed

	First gaze		
	Environment	Conspecific	Predator
(a) Before			
Second gaze			
Environment	1,682	298	33
Conspecific	305	419	10
Predator	36	7	10
(b) After			
Second gaze			
Environment	1,935	283	150
Conspecific	298	337	63
Predator	138	71	123

For example, peacocks gazed from conspecifics to the predator 71 times after the predator was revealed

The maximum eye movement amplitude did not vary depending on whether the predator had been revealed or not [$F(1,13) = 0.47, p = 0.50$], the target of gaze [$F(3,38) = 1.38, p = 0.27$], or the interaction between the two variables [$F(3,22) = 0.43, p = 0.73$] when controlling for the amount of time peacocks spent gazing at each target within the treatments (Fig. 5). Not surprisingly, peacocks exhibited a larger maximum eye movement amplitude when the amount of time they spent gazing at the targets within treatments was longer [$F(1,72) = 6.83, p = 0.011$] and there was therefore a larger sample size of gaze coordinates. Peacocks had an average maximum eye movement amplitude of 54.3° (SE 4.66°). The magnitude of consecutive saccades was similar before and after the

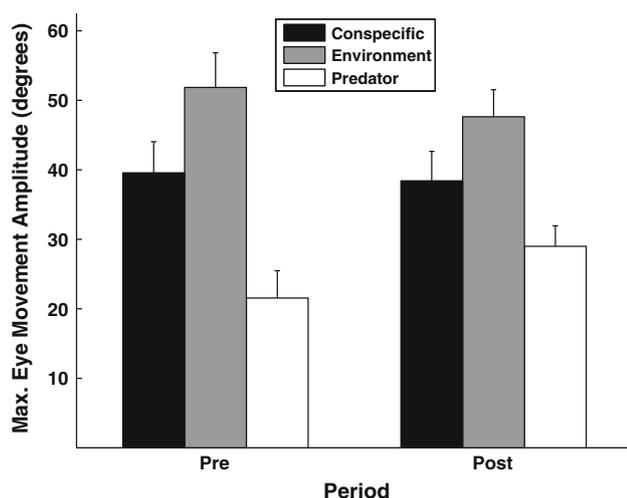


Fig. 5 The maximum eye movement amplitude of peacocks across targets before and after the predator was revealed

predator was revealed (before $10.0^\circ \pm 0.67^\circ$; after $11.1^\circ \pm 1.0^\circ$; $t = 0.97$, $N = 14$, $p = 0.35$).

Pupil size was larger after the predator was revealed compared to before it was introduced [before 3.45 mm; after 3.79 mm; $F(1,13) = 8.98$, $p = 0.01$]. Pupil size was not influenced by the particular target [$F(2,23) = 1.01$, $p = 0.38$] nor the interaction between the target and time period [$F(2,16) = 0.09$, $p = 0.92$; Fig. 6]. In all trials, pupil size was smaller before compared to after the predator was revealed. Saccades were always associated with head movements.

Discussion

Peacocks selectively directed their attention toward a potential predator. They spent more time looking at the predator and made more fixations on the predator compared to the same location before the predator was revealed. This is the first study to use eye-tracking to demonstrate that peacocks orient their gaze to predators, a much more accurate measure of overt attention than experimenter observation or peripheral video recording. These results are similar to the responses of peahens to predators, as they also direct more attention toward predators and make more fixations on predators compared to control areas (Yorzinski et al. 2013). It would be informative to compare peacocks' gaze behavior toward a predator to other novel stimuli to examine the specificity of their attentional responses. Similar to the findings reported here, humans selectively attend to potential threats by spending more time looking at dangerous animals compared to non-dangerous ones (Yorzinski et al. in review).

When peacocks fixated conspecifics or the environment, the duration of these fixations was shorter after the predator

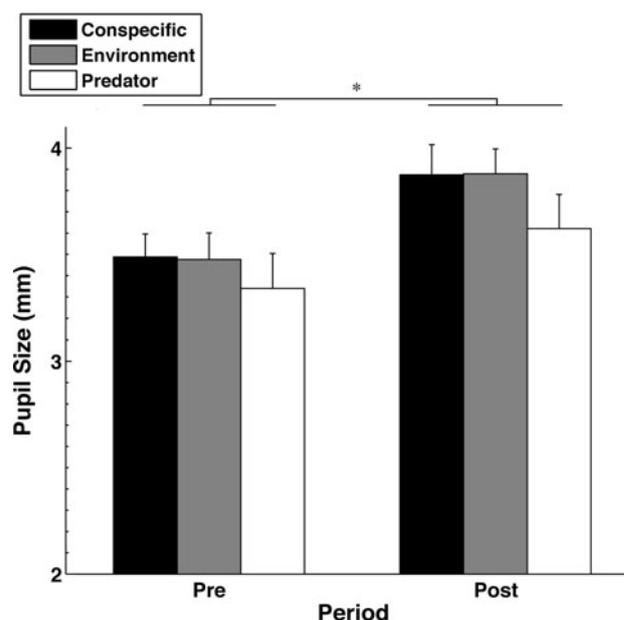


Fig. 6 Peacock's pupil size increased after the predator was presented

was revealed compared to before the predator was revealed. This suggests that peacocks were more alert after the predator was exposed, shifting their gaze rapidly rather than fixating targets for longer amounts of time. However, when peacocks fixated the predator, fixation duration was still relatively high. In order to appropriately respond to the threat, peacocks may still need longer fixations so they can extract critical information about the predator (Cresswell et al. 2008).

Peacocks largely detected the predator without the aid of conspecifics. However, in cases where peacocks saw conspecifics responding to the predator before they detected it themselves, the conspecifics may have influenced their own antipredator behavior. In some trials, the peacocks may have used their peripheral vision to detect conspecifics exhibiting antipredator behavior and then used this information to respond to danger. It would be interesting to determine experimentally whether peacocks spontaneously follow the gaze of conspecifics to potential threats in cases where the conspecifics detect the threat first (Hadjikhani et al. 2008). Peacocks shifted their gaze between the predator and conspecifics (and vice versa), suggesting they were monitoring conspecifics in relation to the predator. In addition, antipredator calls did not aid the peacocks in detecting the predator. Peacocks detected the predator before the first antipredator call was emitted in nearly all trials. The calls may have therefore functioned to dissuade the predator (Sherman 1977; Curio 1978) or served as tonic signals to indicate that the predator was still present (Schleidt 1973).

Interestingly, peacocks were faster to detect the predator when they were fixating closer to the area where the

predator would be revealed immediately before the predator was visible. This suggests that peacocks can use their peripheral vision to detect danger and is consistent with the spotlight model of attention with constant velocity (Tsal 1983) and gradient model of attention (LaBerge and Brown 1989). These models of attention predict that reaction times are proportional to the distance between a target and where subjects are fixating before directing their gaze toward the target (reviewed in Turk-Browne and Pratt 2005). Previous studies have found that bird orientation affects predator detection time (Kaby and Lind 2003; Tisdale and Fernández-Juricic 2009) but had not yet been able to demonstrate that the specific location of a bird's gaze affects it. Birds that remain highly vigilant, by frequently moving their heads or eyes to scan their environment, are likely to detect predators faster and successfully avoid attacks compared to birds that are less vigilant (Pulliam et al. 1982; McNamara and Houston 1992; Cresswell et al. 2003).

Peacocks were obtaining visual information before and after the predator was revealed by using a combination of head and eye movements. They always moved their heads when making visual saccades. Small head movements may have served to stabilize the visual field (Wallman and Letelier 1993) while larger ones completely shifted the visual field. However, peacocks were not simply centering visual targets within their field of view. They actively moved their eyes to targets within the scene, with an average maximum eye movement amplitude of 55°. The maximum eye movement amplitude in other birds is reportedly smaller (e.g., 32° in starlings; Martin 1986) but this is likely because the eye movements were recorded while the birds were restrained (Collewijn 1977). Freely moving rabbits exhibit similar ranges of eye movements (50°; Collewijn 1977) compared to peacocks. The magnitude of consecutive saccades in peacocks was approximately 10° and they were therefore regularly shifting their eyes to examine the scene.

Lastly, the size of peacocks' pupils increased after the predator was revealed irrespective of the target they were fixating. The percentage change in the peacock's pupil diameter after the predator was revealed compared to before it was revealed (10 %) is similar to the percentage change in pupil diameter in humans during threatening situations (5–14 %; Nunnally et al. 1967; Bitsios et al. 1996) and slightly less compared to human (33–54 %; Whipple et al. 1992) and rat arousal situations (20–48 %; Szechtman et al. 1985). In humans, pupil dilation has been associated with processes implicated in antipredator behavior, such as arousal (Bradshaw 1967), alertness (Yoss et al. 1970), decision-making (Simpson and Hale 1969), surprise (Preuschoff et al. 2011), and fear (Charney et al. 1998). Because the appearance of the predator was unexpected and required defensive action, it was expected that

peacock pupil size would increase after predator exposure. Because our trials were conducted outdoors, luminance levels were not controlled and could have influenced pupil size (Bradley et al. 2008); however, it is unlikely that luminance levels changed dramatically and systematically during the brief period before and after the predator's appearance. Furthermore, pupil size increased after the predator was revealed in all trials even though the trials were conducted at different times of day and therefore under different lighting conditions. Even when light conditions are systematically varied, the percentage change in pupil diameter is small in domestic fowl (1–2 %; Barbur et al. 2002).

Birds and predators have co-evolved for millions of years and predation has therefore likely influenced avian antipredator behavior (Martin 1995; Briskie et al. 1999). Birds exhibit many antipredator responses, including emitting alarm calls, increasing vigilance levels, avoidance, and mobbing or attacking predators (Caro 2005). Birds, including peafowl, likely have higher survival probabilities by increasing their attention toward potential threats so they can respond appropriately (Cresswell et al. 2008). Future experiments can help us further understand the interplay between attention and predator avoidance.

Acknowledgments We thank Gail Patricelli for helpful discussion and Jason Babcock for assistance with the eye-tracker. Peter and Martha Klopfer allowed the birds to be housed on their farm. This research was funded by a National Science Foundation graduate research fellowship, an Animal Behaviour Society Student Research Grant, the Animal Behavior Graduate Group at UC Davis, the Chapman Memorial Fund, a grant-in-aid of research from the National Academy of Sciences (administered by Sigma-Xi, The Scientific Research Society), Gail Patricelli (through UC Davis), a Philanthropic Educational Organization Scholar Award, and a National Geographic Society/Waitt Foundation grant to J.L.Y. The Alfred P. Sloan Foundation and Duke Lemur Center provided funding to M.L.P.

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