

Corrigendum

## **Through their eyes: selective attention in peahens during courtship**

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The authors inadvertently omitted to declare a competing interest for one of the authors. The correct Competing Interests statement is given below.

J.S.B. owns the company (Positive Science) that manufactured the eye-tracking headpiece and designed the eye-tracking software, which were used in the experiments described within this manuscript.

The authors apologise for any inconvenience that this error may have caused, but assure readers that it does not affect the results or conclusions of the paper.

## RESEARCH ARTICLE

### Through their eyes: selective attention in peahens during courtship

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#### SUMMARY

**Conspicuous, multicomponent ornamentation in male animals can be favored by female mate choice but we know little about the cognitive processes females use to evaluate these traits. Sexual selection may favor attention mechanisms allowing the choosing females to selectively and efficiently acquire relevant information from complex male display traits and, in turn, may favor male display traits that effectively capture and hold female attention. Using a miniaturized telemetric gaze-tracker, we show that peahens (*Pavo cristatus*) selectively attend to specific components of peacock courtship displays and virtually ignore other, highly conspicuous components. Females gazed at the lower train but largely ignored the head, crest and upper train. When the lower train was obscured, however, females spent more time gazing at the upper train and approached the upper train from a distance. Our results suggest that peahens mainly evaluate the lower train during close-up courtship but use the upper train as a long-distance attraction signal. Furthermore, we found that behavioral display components (train rattling and wing shaking) captured and maintained female attention, indicating that interactions between display components may promote the evolution of multicomponent displays. Taken together, these findings suggest that selective attention plays a crucial role in sexual selection and likely influences the evolution of male display traits.**

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/216/16/3035/DC1>

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#### INTRODUCTION

Charles Darwin (Darwin, 1871) introduced the concept of sexual selection to explain seemingly ornamental display traits in animals, such as the elaborate trains of peacocks. It is now well established that sexual selection can operate through female choice when females choose their mates based upon these displays (Andersson, 1994; Bradbury and Vehrencamp, 2011). However, the cognitive and sensory processes that females use to assess male displays and choose their mates remain mysterious (Jones and Ratterman, 2009). This is particularly true in species where males have complex displays with multiple components, which could contribute to female choice, competition among males, or both (Hebets and Papaj, 2005). Selection may favor attention mechanisms, which may have originally evolved in response to natural selection (Basolo, 1990; Ryan, 1998), allowing females to selectively and efficiently acquire information relevant to mating decisions (Dukas, 2002). These female attention mechanisms may in turn influence the evolution of male courtship displays, favoring males with traits that effectively capture and hold female attention (Fleishman, 1988; Hebets and Papaj, 2005; Rosenthal, 2007). A promising tool to examine the role of attention mechanisms in mate choice is eye-tracking, which has found strong links between visual orienting and choice behavior in human and non-human primates (Land and Tatler, 2009; Shimojo et al., 2003). Despite a growing literature on visual attention, we still know little about how animals evaluate aspects of their environment that are crucial to their reproduction (Rupp and Wallen, 2007; Yorzinski and Platt, 2010).

In order to examine the relationship between attention and reproduction, we tracked the gaze of freely moving peahens (*Pavo cristatus* L.) to examine how they direct their attention during courtship. In the breeding season, peacocks aggregate on leks where they display to visiting peahens, which visit leks mainly to obtain fertilizations. A female approaches the side or back of a displaying male while the male intermittently shakes his primary wings up and down (backside display); as the female moves toward the front of the male, the male turns directly toward her and periodically rattles his feathers (shimmering his iridescent feathers and producing a rattle-like sound; frontal display) and then the male turns away from the female (backside display; this courtship sequence has also been observed in feral populations in California and wild populations in India; J.L.Y., personal observation). Females appear to assess these displays and choose to mate with one or several different males (Petrie et al., 1992). The number of eyespots on males' trains, the length of the longest 'fishtail' feather (the outermost feathers that end in a fishtail-like shape) (Manning, 1987) and male courtship behavior have been related to male mating success in some populations (Petrie and Halliday, 1994; Yasmin and Yahya, 1996; Takahashi et al., 2008; Dakin and Montgomerie, 2011).

We trained captive peahens to wear a wireless eye-tracker that continuously recorded monocular gaze (the other eye was covered; Fig. 1A) by dark pupil and corneal reflection. The equipment closely tracked their area centralis, an area of high retinal ganglion cell density with the highest visual acuity that is similar to the human

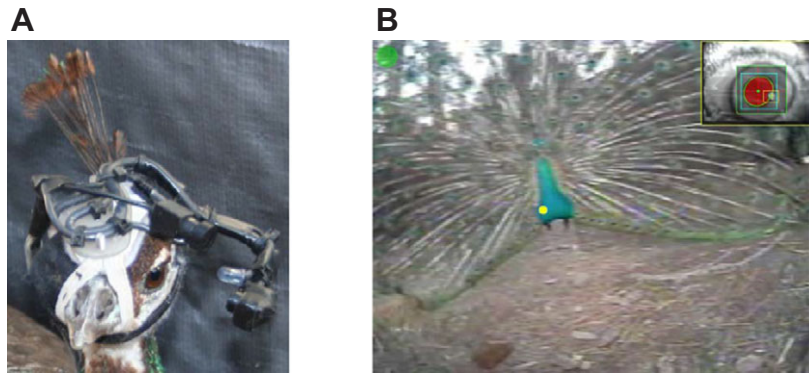


Fig. 1. (A) A peahen wearing the eye-tracking headpiece with a patch covering the unrecorded eye. (B) A sample frame from a display clip showing a female looking at a displaying peacock; the yellow dot indicates that the female is looking at the male's body. The eye-tracker records her eye position (upper right of image) and the field of view of her eye.

fovea (Hart, 2002). Because many birds, including peafowl, make eye movements (Martin et al., 2008; Wallman and Letelier, 1993), it was necessary to track gaze rather than only head movements. We tested whether peahens selectively direct their attention toward particular male traits (such as eyespot and fishtail feathers), and if so, whether the behavior of the male or female influences this attention. Furthermore, we examined the distance at which male display components influence female attention.

## MATERIALS AND METHODS

### Study site and animal subjects

We used a head-mounted, telemetric, infrared eye-tracker to study how peahens evaluate courting males in Durham, NC, USA (36.01°N, 79.02°W) from March to May 2010. The birds were housed in outdoor enclosures within a wooded area. The 'male enclosure' (92 m perimeter) housed the males and the 'female enclosure' (46 m perimeter) housed the females; the two enclosures were ~400 m apart so that the males and females could not physically interact with or see each other. The 'testing enclosure' (27 m perimeter) and 'holding enclosure' (20 m perimeter) were adjacent to the male enclosure. All of the enclosures were completely surrounded by black plastic to prevent birds in the different enclosures from seeing one another.

The birds were purchased between 2008 and 2010 from peafowl breeders across the country or were caught from free-ranging populations in Florida and California. The females in the female enclosure originated from five different sources. The birds were raised by their mothers and were sexually mature. In captivity, the birds were given food and water *ad libitum*. The females had a white plastic leg band on one leg and a metal leg band on their other leg; the males had a metal leg band on one of their legs.

### Eye-tracker and calibration technique

The eye-tracker consisted of a battery pack and transmitter (Iscan, Woburn, MA, USA) connected to a headpiece (designed by Positive Science, LLC, New York, NY, USA). The mass of the battery pack and transmitter was 345 g and the mass of the headpiece was 25 g (the mean mass  $\pm$  s.e.m. of the peahens was 3.68 $\pm$ 0.13 kg; range 3.0–4.3 kg). The headpiece had two cameras: one camera recorded the scene in front of the bird while the other, infrared camera recorded the eye of the bird. The headpiece was attached to a thermoplastic (Patterson Medical Products, Bolingbrook, IL, USA) helmet that was custom molded to fit onto the head of the females (Fig. 1A). The transmitter sent both video images (30 frames  $s^{-1}$ ) to a receiver. The receiver was connected to a DVD recorder (Toshiba D-R410) that recorded the video signals and then passed the signals to a computer (Dell Dimension 2300). The computer processed the video signals with custom eye-tracking software (Iscan) and

displayed the videos. A crosshair continuously marked the center of the pupil in real-time (Fig. 1B).

We calibrated the eye-tracker using an oculometric approach based on corneal reflections (Fantz, 1958; Hamada, 1984). The eye is similar to a convex spherical mirror such that light will reflect off the cornea with an angle of reflection that equals the angle of incidence. This light creates a corneal reflection (also known as glint, first Purkinje image or corneal reflex), which is 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 (Hamada, 1984)]. The optic axis is offset from the visual axis by less than 5 deg in humans (Nagamatsu et al., 2008) and pigeons (McFadden and Reymond, 1985). This method has been successfully used to calibrate human eye-trackers (Hamada, 1984; Smith et al., 2005).

We employed this oculometric approach in peahens by shining a 3 mm infrared LED light toward the eye of a peahen when she was wearing the eye-tracker (supplementary material Fig. S1A,B). This light created a corneal reflection on her eye. We then moved the light so that its corneal reflection was aligned with the crosshair marking her pupil center on the video. When she naturally moved her eye to a different position, we moved the infrared light so that it was again aligned with her pupil center. We repeated this process for ~5 min so that we had multiple points during which the optic axis of the female was aligned with the light source. We then immediately released the female and conducted the experiment (see 'Training and experimental design').

After the experiment ended, the videos were calibrated offline using the information collected above. 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). These were analyzed with custom-designed eye-tracking software (Yabus, Positive Science, LLC) that used at least three points, which were based on the LED corneal reflections, to calibrate the system. After the system was calibrated in this way, we ran the entire video through this software and a crosshair tracked the estimated point of gaze of the bird in the scene camera in front of her. After the system was calibrated, data from experimental trials consisted of videos of the scene camera with a dot that indicated where the females were looking at each frame (Fig. 1B).

We quantified the error associated with our calibration method by throwing pieces of food or other objects (such as a ping pong ball or water bottle cap) toward the ground near the females as they were wearing the eye-tracker (recording from the left eye of the birds; see Appendix, 'Video coding') and measuring the distance between the bird and stimuli (supplementary material Movie 1). We employed this relatively unconstrained method to check our

calibration accuracy because of difficulty in training peahens to orient to objects on command (as is typically done with monkeys in the laboratory). We performed these calibration tests at different distances (distance between the female and the objects was  $116.1 \pm 8.8$  cm, range 28–200 cm, 52 trials,  $N=14$ ). When the females immediately oriented toward these objects when they landed on the ground, we assumed that they were fixating on the objects. We then measured the distance between the estimated point of gaze (as determined by the eye-tracking software and then adjusted to correct for parallax errors; see Appendix, ‘Video coding’) and the actual object as well as the distance between the female and the actual object. These measurements allowed us to calculate the error in degrees. This overall error rate included error associated with imprecision in the calibration and error caused by the offset between the visual and optic axis.

### Training and experimental design

We trained females in the female enclosure to wear the eye-tracking equipment. They were trained in daily sessions that lasted ~60 min. We first outfitted the females with empty backpacks (MBLDesigns, Benton, AR, USA). After they became habituated to wearing the backpacks, we gradually added weight to the backpacks until the total mass was the same as the actual eye-tracking battery and transmitter. We next habituated the females to wearing headpieces using facsimile eye-tracker headpieces so that multiple females could be trained simultaneously and to avoid damage to the real equipment. We put thermoplastic helmets on the females and gradually added components until they were wearing the entire headpiece. Lastly, we put a black cloth over the eye that was not being recorded with the eye camera so that the female was only obtaining visual information monocularly. By the end of their training, peahens engaged in normal behavior (such as walking, eating and copulating) while wearing the eye-tracker.

We transported peahens from the female enclosure to the holding enclosure at least 1 day before the trials began so that females could habituate to the new area. Two males were transported from the male enclosure to the testing enclosure. For each trial, a female was outfitted with the eye-tracker and the eye-tracker was calibrated. She was then released into the testing enclosure. She was allowed to freely move within this arena for ~1–1.5 h and her gaze was continuously recorded. After this time, the female was removed from the testing enclosure, the eye-tracking equipment was removed, and she was transported back to the holding enclosure. A female was only tested once within a given day. Overall, the trials were conducted during different times, days and weather conditions. Four camcorders (Sony SR47) were positioned in the corners of the testing enclosure to continuously record the behavior of the males and female. The video from these camcorders was imported into video editing software (Final Cut Express, Apple) and synchronized with the eye-tracking videos. Video clips were coded and checked for inter-observer reliability (see Appendix). We tested 16 females on two to five different days each for a total of 39 trials. Seventeen trials recorded eye movements of the left eye and 22 trials recorded eye movements of the right eye. We used multiple males ( $N=4$ ) as our stimuli. Because of limitations in animal numbers and logistics, we were unable to test each female with novel pairs of males. Statistical tests account for multiple testing on each individual by including male and female identity as random effects (see Eqn 1 below); but because of this small sample, further studies are needed to determine whether female responses to these males are typical of responses to the population of males.

### Measurements and statistical analyses

We quantified overall gaze patterns using a generalized linear mixed model (GLMM). We examined nine regions of interest (ROI; Fig. 2) in the frontal display analysis (body, head and crest, scale feathers, dense feathers, lower eyespots, upper eyespots, lower fishtails, upper fishtails, and legs) and 10 ROIs in the backside display analysis (dense feathers, lower eyespots, upper eyespots, lower fishtails, upper fishtails, legs, black feathers, white feathers, wings, and tail). We modeled the number of counts in each ROI as drawn from an over-dispersed Poisson distribution. That is, the number of fixations in each clip was assumed to depend on the total number of frames in the clip, the size of the ROI and the intrinsic relative attractiveness of each ROI, with fixations arriving independently and identically as a function of time. The rate of the process was given by a linear model with a log link function (as rates must be positive), using ROI as a categorical regressor, male and female identity as zero-mean random effects, and the logarithm of total clip time (in frames) and the logarithm of total ROI size (as a fraction of total average male size) as constant offsets. The last two terms compensate for our expectation that count totals should be proportional to both total available looking time and the size of a given ROI. As a result, the ROI coefficients represent a time- and area-independent measure of ROI attractiveness. Lastly, we excluded two ROIs (head/crest and black feathers from the frontal and backside display models, respectively) that had zero gaze counts in all recorded trials. While it is possible to assign a posterior estimate to these parameters, doing so slowed convergence of the estimation algorithms and skewed the estimation of effect sizes. To control for the possibility that male identity leads to an additional non-independence in trials not captured by the random effects in our GLMM, we also reran this analysis using male as the sampling unit rather than female, using the average of female responses to each male, to confirm that these results are robust to different methods of addressing multiple tests with the same stimuli (supplementary material Table S1).

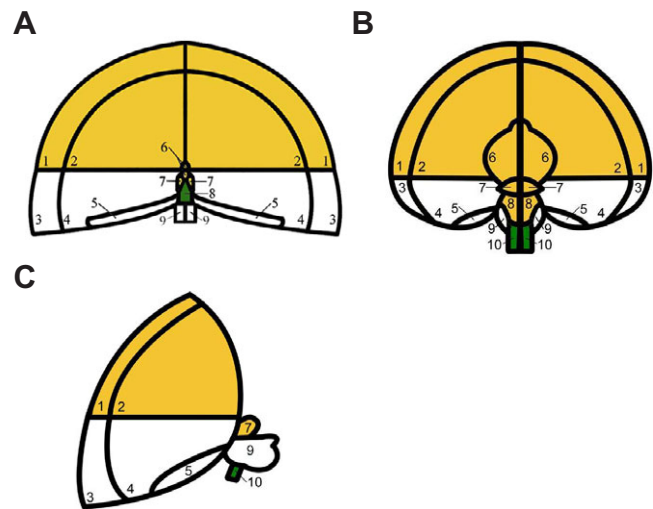


Fig. 2. The probability that peahens gazed at specific regions of interest (ROIs) in the male's frontal (A) and backside (B,C) display: white, yellow and green shading indicates areas viewed at levels greater than expected by chance, less than expected by chance and not different from chance, respectively. 1, upper fishtails; 2, upper eyespots; 3, lower fishtails; 4, lower eyespots; and 5, dense feathers. In A: 6, head crest and head; 7, scale feathers; 8, body; and 9, legs; in B and C: 6, tail; 7, white feathers; 8, black feathers; 9, wings; and 10, legs.

More specifically, we modeled frame counts as being drawn from an over-dispersed Poisson distribution:

$$n_i \sim \text{Poisson}(\lambda_i)$$

$$\log(\lambda_i) = \beta_i + \log(N) + \log(a_i / A) + \text{male} + \text{female} + \varepsilon, \quad (1)$$

where  $n$  is the number of frames in which the peahen looked at the given ROI (out of a total of  $N$ ),  $a_i$  is the size of the ROI (in pixels),  $A$  is the total average size of the ROI across males,  $\varepsilon$  is the overdispersion noise, and  $\beta_i$  is a (fitted) attractiveness for each region. The areas and total counts terms are constant offsets and not fitted parameters.

The two log terms compensate for the fact that longer clip times and larger areas should lead to higher counts. Thus,  $\beta$  measures an ROI-intrinsic attractiveness. Male and female are zero-mean Gaussian-distributed random effects. Finally, to investigate effects of visual laterality, we fitted an additional Poisson mixed model with separate regressors for each ROI for each eye (an eye $\times$ ROI effect). All other aspects of the model specification were as above. Model fits were performed using Markov Chain Monte Carlo methods in JAGS *via* the rjags package in R. Data, model files and additional plots are available at <https://github.com/jmpearson/peafowl>.

We examined whether behaviors (train rattling, male movement, female movement, distance between the female and male, and wing shaking) influenced female gaze. For each behavior, we isolated fields (deinterlaced frames; see above) in which the behavior was occurring and compared these fields with those in which the behavior was not occurring. We categorized the distance between females and males as close if the individuals were 1–2 m apart and far if they were 2–3 m apart; females were within 1–3 m of the males in 90% of display clips (median 1.9 m, mean  $2.03 \pm 0.001$  m) so we split this distance into two for analysis purposes. We used generalized linear models (PROC MIXED) to examine whether females differed in the amount of time they spent looking at the male display (compared with the environment) with respect to the presence or absence of these behaviors:

$$T = \text{male} + \text{female} + \text{clip} + \text{treatment} + \varepsilon, \quad (2)$$

where  $T$  is the amount of time that females spent looking at male displays (compared with the environment), male and female are fixed effects, clip is the display clip (coded as a zero-mean Gaussian-distributed random effect), treatment is a categorical variable coding whether the behavior was occurring or not, and  $\varepsilon$  is Gaussian noise.

Because we found that females spent more time looking at frontal male displays when males were rattling their feathers and at backside male displays when males were shaking their wings and moving (see Results), we conducted a follow-up test to further examine this effect. We calculated the amount of time females spent looking at the male display immediately before, during and after rattling or shaking moments using contrasts within our generalized linear models. The pre- and post-rattle/shake sample periods were of the same duration as the rattling/shaking with which they were associated. For example, if the rattling lasted 30 s, then the pre- and post-rattle sample periods were 30 s each. If the post-rattling moment of one rattling bout overlapped with the pre-rattling moment of a second rattling bout, the amount of time was equally divided between them to create mutually exclusive time periods. The results were similar for the pre- and during rattle/shake comparison when the pre-rattle/shake periods only included the one frame immediately before the male began rattling his feathers or

shaking his wings. We used generalized linear models (PROC MIXED) to examine whether females differed in the amount of time they spent looking at the male display with respect to the pre-, during and post-rattle/shake periods; the model was the same as Eqn 2 except that clip is the particular bout within a display clip and treatment is a categorical variable coding the time period (pre, during and post).

Because only some of the peahens copulated, we were unable to analyze female gaze patterns with respect to final mating decisions. All statistics were performed with SAS (SAS Institute), Minitab or R; means  $\pm$  s.e.m. are reported. When our data did not meet the assumptions underlying parametric statistics, we performed non-parametric tests instead.

### Upper train experiments

We also tested the hypothesis that the upper train of peacocks serves as an attraction signal in obscured environments. Because dense vegetation can obscure the lower train of a peacock in the bird's native habitat (J.L.Y., personal observation) (Yorzinski and Anoop, 2013) (supplementary material Fig. S2B), we performed trials in which we obscured the lower part of male trains and therefore mimicked the natural situation in which peahens would only be able to see the upper train from a distance. In these trials, we placed the females close to the stimuli so that we could obtain accurate gaze measurements and we recorded their gaze (recording from the left eye of the birds and correcting for parallax errors by measuring the distance between the bird and stimuli) in March 2012. Peahens were presented with the lateral train (i.e. the right half of a peacock train; supplementary material Fig. S2C), the lateral branches of a tree (i.e. the right half of a tree; supplementary material Fig. S2D), the lateral upper train (i.e. the right upper region of a peacock train; supplementary material Fig. S2E), and the lateral upper branches of a tree (i.e. the right upper region of a tree; supplementary material Fig. S2F). We only presented the right side of the peacock train (as opposed to presenting both sides of the train as we did in the behavioral tests of the upper train experiments; see below) so that we did not also need to present an artificial peacock body during the presentations where the lower train was visible. The artificial train was constructed by gluing together a column of seven eyespot feathers and a fishtail feather and then seven of these feather columns were arranged in a semicircle. An eighth feather column was added to the bottom of the semicircle that consisted of a fishtail feather along with dense feathers. These feathers were attached to a tripod so that the height of the longest fishtail feather was 1.5 m from the ground; this feather arrangement mimicked the appearance of a peacock's right half of a train and included a similar number of feathers to that found in a real male's train. The feathers were all in good condition (i.e. their shafts and vanes were undamaged). The branches were constructed by horizontally attaching four branches (~1.3 m long) to a PVC pipe; two of the branches were in the region where a lower train would be located (25–40 cm high) and the other two branches were in the region where an upper train would be located (100–120 cm high). During trials in which only the upper region of the stimuli was presented, a black sheet (0.80 m tall and 2.6 m wide) obscured the lower region of the stimuli. Two different peacock trains and two different branches were used as stimuli.

For each upper train eye-tracking trial, a peahen was placed 2.1 m in front of one of the stimuli (randomly selected) in a testing cage (5.7 $\times$ 4 m), allowed to view the stimulus for 3 min, and then temporarily removed from the enclosure; this process was repeated four times until the peahen was exposed to all four stimuli. We determined the amount of time each female spent looking within

5 deg of the upper train, lower train, upper branches and lower branches (upper regions were defined as areas above 0.8 m and lower regions were defined as areas below 0.8 m) for the first minute of each stimulus presentation [peahens spent about 1 min ( $45.9 \pm 4.9$  s, range 0.1–401.5 s) assessing natural peacock frontal displays when they were wearing the eye-tracker]. We tested *a priori* predictions to evaluate the amount of time females spent looking at the upper and lower regions of the train/branches and performed hypothesis tests to examine whether females spent more or less time looking at the designated regions. In particular, we compared the amount of time peahens spent looking at (1) the upper regions of the lateral upper train and the lateral upper branches, (2) the upper regions of the lateral upper train and the lateral full train, and (3) the lower regions of the lateral full train and the lateral full branches. We ran two linear models (PROC MIXED), similar to Eqn 2, with female as a fixed effect and treatment as the type of stimuli presented (lateral train, lateral upper train, lateral branches and lateral upper branches), and clip as the particular version of the stimuli that was presented; the dependent variable was the amount of time females spent looking at the upper portion of the stimuli or the lower portion of the stimuli.

In addition, we examined the role of the upper train by analyzing the behavior of the females in February 2012. Peahens were presented with an artificial upper train of a peacock (treatment; supplementary material Fig. S2G) or branches (control; supplementary material Fig. S2H). We did not use eye-trackers in these trials because the eye-tracking errors would have been too large (given the distance between the females and the stimuli) to make accurate gaze measurements. The artificial trains were constructed in a similar manner to those used in the eye-tracking tests of upper train experiments (see above). The artificial upper trains were constructed by gluing together a column of six eyespot feathers and a fishtail feather; 11 of these feather columns were then arranged in a semicircle. These feathers were attached to a tripod so that the height of the longest fishtail feather was 1.5 m from the ground; this feather arrangement mimicked the appearance of a peacock's upper train. The branches were constructed by attaching two branches to the tripod so that the tops of the branches were 1.5 m from the ground. Two different peacock trains and two different branches were used as stimuli. The tripod was placed on the ground and obscured behind a black sheet (0.80 m tall and 2.6 m wide). For each trial, a peahen was released into the middle of an enclosure (15 × 4.2 m) that contained the upper train or the branches (randomized across trials), which were located on either the right or left end of the enclosure (randomized across trials). The peahens were allowed to move within the enclosure for 10 min. Based on video recordings of the trials, we calculated the latency to approach to within 1 m, the number of times females approached to within 1 m, and the amount of time females spent within 1 m of the stimuli. We ran three linear models (PROC MIXED), similar to Eqn 2, with treatment as the type of stimuli presented (upper train or upper branches) and clip as the particular version of the stimuli that was presented; the dependent variables were latency to approach to within 1 m, the number of times females approached to within 1 m, and the amount of time females spent within 1 m of the stimuli.

## RESULTS AND DISCUSSION

### Validation

We found that females deploy their overt attention to specific types of stimuli that are relevant to the current behavioral context. Peahens oriented their gaze directly toward stimuli (such as food and small objects that were thrown in front of them) in non-mating contexts with minimal error (mean  $\pm$  s.e.m.  $3.90 \pm 0.39$  deg, range

1.75–5.87 deg,  $N=14$ ; supplementary material Fig. S1C, Movie 1) and these errors in our eye-tracking system are similar to those in human eye-trackers (Duchowski, 2003). The females made corrective saccades (a second saccade that moves the gaze closer to the target) (Becker and Fuchs, 1969) during 15.4% of these error tests and were therefore adjusting their gaze to orient directly toward the stimuli. Furthermore, peahens specifically directed their gaze toward a potential predator (taxidermy raccoon; supplementary material Fig. S2A) that was elevated above the ground (supplementary material Movie 2). They gazed toward the predator in all trials and spent more time looking at the predator and made more fixations on the predator (Table 1A) than they did toward the same area before the predator was revealed (supplementary material Fig. S1D). Based on this evidence that females look at food items and predator models, we take the female's gaze as an indication of the behavioral relevance of the visual features to which she orients.

Six females copulated with males, seven females avoided copulation attempts, and the remainder of the females displayed neither of these behaviors because the males did not attempt copulations. These results suggest that the eye-tracker does not prevent the females from engaging in natural breeding activities. For all 39 trials, we isolated all display clips in which males displayed with their trains erect while directly facing the females (frontal display). We then isolated clips immediately before and after these frontal display clips when the males displayed while facing away from the female (backside display). We identified 105 frontal display clips (Fig. 1B) and 114 backside display clips that involved four males and 12 females, and we used this set of clips in all analyses. Tests with a larger sample of males with more variable display traits may help to determine how females discriminate among potential mates based on variation in their display traits. Male peacocks on leks in their native habitat are often dispersed across a large area in tall vegetation (J.L.Y., personal observation) and females may therefore commonly assess males individually or in small groups, which is similar to our experimental set-up. Because a displaying male covers a wide area (approximate height and width of a displaying male, 1.7 and 2.7 m, respectively) and the females were usually within 1–3 m of the displaying males, the eye-tracking error (see above) did not likely systematically bias our results.

### Selective attention

When males were performing the frontal display (Fig. 3), peahens spent 27.5% of the time looking at the displaying male and 63.6% of the time looking at the environment (including the other male in the lek, who was performing the frontal display to the female in only one of the 105 frontal display clips). Only a small portion of their gaze records (8.9%) could not be analyzed as a result of sun glare, poor transmission or other technical problems. When males were performing the backside display, peahens spent 21.3% of the time looking at the displaying male and 63.4% of the time looking at the environment. Given that females spent less than one-third of their time gazing at the displaying male, it is not surprising that females often appear to human observers as coy and uninterested in males (Darwin, 1871).

When females were gazing at the male display (frontal and backside), however, they actively directed their attention to specific male traits (Figs 2, 4; supplementary material Movie 3). Compared with chance expectation when females were viewing the frontal display, peahens spent significantly more time looking at the lower eyespots, lower fishtails, dense feathers and legs. They spent less time looking at the scale feathers, upper eyespots, upper fishtails and head and crest than expected by chance; the

Table 1. Summary of experiments and statistical tests performed

Behavioral test	Statistical test	Test statistic	N	Num. d.f.	Den. d.f.	P	Figure
A Predator presentation experiment							
Time looking at predator	Wilcoxon signed rank	36.0	8	–	–	0.014*	S1D
Number of fixations	Wilcoxon signed rank	36.0	8	–	–	0.014*	S1D
B Eye-tracker effects experiment							
Head height	Mann–Whitney	142.0	24	–	–	0.66	S1E
Head tilt	Wilcoxon signed rank	9.0	7	–	–	0.79	
Locomotion	Mann–Whitney	123.0	24	–	–	0.13	
C Male movement experiment							
Frontal display	Generalized linear model: F test	46.75	12	1	105	<0.0001*	
Backside display	Generalized linear model: F test	3.53	11	1	76	0.064	
D Upper train: gaze response experiment							
Lower train gaze	Generalized linear model: F test	8.21	17	3	46	0.0002*	
Train vs control	Generalized linear model: Contrast: F test	4.88	17	1	46	0.032*	S3A
Upper train gaze	Generalized linear model: F test	11.43	17	3	46	<0.0001*	
Lower train visible vs lower train obscured	Generalized linear model: Contrast: F test	13.03	17	1	46	0.0008*	S3B
Lower train obscured vs control	Generalized linear model: contrast: F test	25.00	17	1	46	<0.0001*	S3B
E Upper train: behavioral response experiment							
Latency to approach	Generalized linear model: F test	9.87	22	1	18	0.0056*	S3C
Visits to train	Generalized linear model: F test	3.50	22	1	18	0.078	S3D
Time near train	Generalized linear model: F test	11.35	22	1	18	0.0034*	S3C
F Gazing at male experiment							
Frontal display							
Train rattling	Generalized linear model: F test	27.76	12	1	94	<0.0001*	
Male movement	Generalized linear model: F test	0.29	12	1	75	0.59	
Female movement	Generalized linear model: F test	0.24	12	1	83	0.63	
Distance	Generalized linear model: F test	7.76	12	1	22	0.011*	
Backside display							
Wing shaking	Generalized linear model: F test	21.97	11	1	59	<0.0001*	
Train rattling	Generalized linear model: F test	1.32	11	1	17	0.27	
Male movement	Generalized linear model: F test	4.08	11	1	105	0.046*	
Female movement	Generalized linear model: F test	0.71	11	1	94	0.40	
Distance	Generalized linear model: F test	2.52	10	1	9	0.15	
G Timing experiment							
Overall							
Train rattling	Generalized linear model: F test	54.89	12	2	1752	<0.0001*	
Wing shaking	Generalized linear model: F test	5.88	11	2	89	0.004*	
Male movement	Generalized linear model: F test	1.33	11	2	724	0.27	
Before vs during							
Train rattling	Generalized linear model: contrast: F test	107.50	12	1	1752	<0.0001*	5A
Wing shaking	Generalized linear model: contrast: F test	9.75	11	1	89	0.002*	5B
During vs after							
Train rattling	Generalized linear model: contrast: F test	40.65	12	1	1752	<0.0001*	5A
Wing shaking	Generalized linear model: contrast: F test	0.33	11	1	89	0.57	5B
Before vs after							
Train rattling	Generalized linear model: contrast: F test	15.54	12	1	1752	<0.0001*	5A
Wing shaking	Generalized linear model: contrast: F test	4.69	11	1	89	0.033	5B

An asterisk indicates that the result is significant, adjusting for false discovery rates if necessary.

Num., numerator; Dom., denominator.

amount of time they spent looking at the body was not different from that expected by chance (Fig. 2A, Table 2). When females were viewing the backside display, they spent significantly more time looking at the wings, lower eyespots, lower fishtails and

dense feathers, and significantly less time looking at the upper eyespots, upper fishtails, black feathers, white feathers and tail; the amount of time they spent looking at the legs was similar to that expected by chance (Fig. 2B,C, Table 2). The results were



Fig. 3. Peahens wearing the eye-tracker exhibit natural mating behavior by evaluating displaying males.

similar when this analysis was rerun using male as the statistical unit (supplementary material Table S1).

Females were surprisingly consistent in the amount of time they viewed different male traits (supplementary material Table S2). Variation among females was much smaller than the effect of ROIs in the frontal (median standard deviation 0.45, 95% confidence

interval 0.03–1.03) and backside (median standard deviation 0.32, 95% confidence interval 0.01–0.99) displays. Compared with variation among females, the variation among males was roughly twice as large in the frontal (median standard deviation 0.92, 95% confidence interval 0.17–2.91) and backside (median standard deviation 0.71, 95% confidence interval 0.13–3.22) displays. This suggests that variability in female gaze patterns was driven more by male identity than by variation in females' gaze behavior. Females also viewed males similarly regardless of which eye was assessing the male (Table 2; only one eye could be recorded because of equipment limitations), which was unexpected given that other galliformes exhibit eye laterality during courtship (Rogers et al., 1985).

Because females spent less than 5% of their time gazing at the upper eyespots (Table 2), it seems unlikely that accurate assessment of the total number of eyespots was a priority but brief glances at the upper eyespots may have been sufficient for females to detect large deficiencies in eyespot number and thus avoid mating with males that did not meet minimum requirements (Dakin and Montgomerie, 2011). Alternatively, the number of eyespots in the lower train may be correlated with the overall number of eyespots and females may therefore not need to assess eyespots in the upper regions. Because peahens that were viewing the frontal display gazed

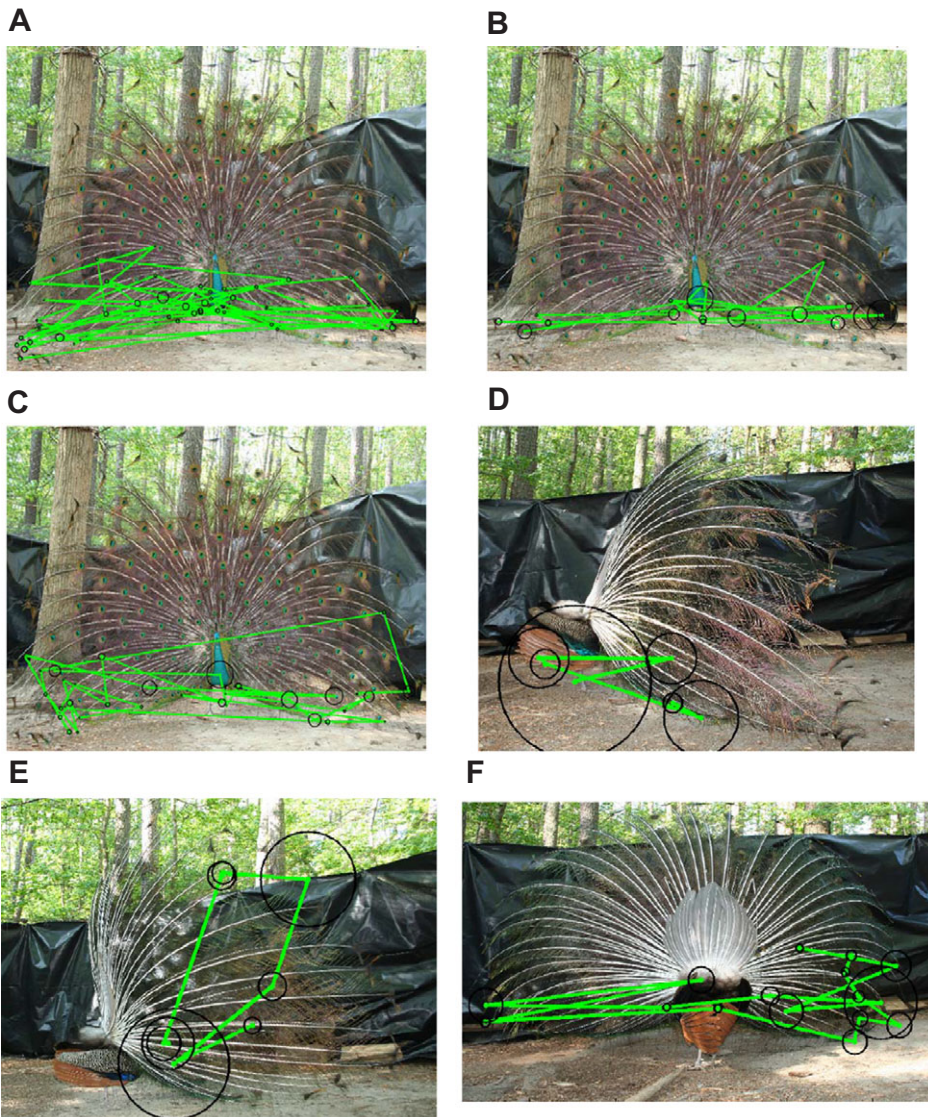


Fig. 4. Scanpaths of three different females showing visual assessment of the male's frontal (A–C) and backside (D–F) display; the size of the black circles indicates the amount of time females spent looking at each location.



Table 2. Model coefficients and confidence intervals for the generalized linear mixed model (Eqn 1)

ROI	Both eyes			Left eye			Right eye		
	B coefficient (median)	2.50%	97.50%	B coefficient (median)	2.50%	97.50%	B coefficient (median)	2.50%	97.50%
Frontal									
Body	0.13	-0.55	0.81	0.67	-0.70	2.01	0.45	-0.75	1.58
Head/crest	–	–	–	–	–	–	–	–	–
Scale feathers	-1.90	-2.86	-1.02	-0.35	-1.89	1.04	-2.82	-4.97	-1.27
Legs	1.19	0.46	1.84	1.96	0.67	3.21	1.11	0.00	2.21
Dense feathers	3.00	1.85	3.73	3.34	2.13	4.50	2.76	1.79	3.74
Lower eyespots	3.51	3.04	4.35	3.54	2.47	4.75	3.63	2.73	4.59
Lower fishtails	3.16	2.68	3.62	3.65	2.50	4.81	2.96	1.96	3.90
Upper eyespots	-3.67	-4.43	-2.92	-5.52	-7.07	-4.00	-2.41	-3.53	-1.35
Upper fishtails	-5.42	-6.39	-4.50	-8.78	-11.69	-6.45	-4.00	-5.13	-2.82
Backside									
Black feathers	–	–	–	–	–	–	–	–	–
White feathers	-2.00	-3.23	-0.97	-1.86	-4.48	0.43	-1.45	-3.13	0.11
Wings	2.19	1.21	2.90	1.71	0.00	3.40	2.89	1.69	4.24
Tail	-6.45	-9.22	-4.36	-11.86	-20.87	-5.19	-5.32	-8.28	-3.02
Legs	-0.64	-1.68	0.43	-1.11	-3.62	1.38	0.00	-1.58	1.56
Dense feathers	4.06	3.28	4.87	5.06	3.63	6.58	4.12	2.85	5.34
Lower eyespots	5.10	4.34	6.16	4.99	3.63	6.40	5.93	4.78	7.14
Lower fishtails	4.17	3.45	5.13	5.42	3.95	6.79	4.33	3.10	5.57
Upper eyespots	-2.60	-3.59	-1.60	-3.11	-5.50	-1.07	-1.58	-2.89	-0.24
Upper fishtails	-3.73	-5.03	-2.59	-4.63	-7.33	-2.00	-2.97	-4.71	-1.45

Coefficients are contributions of each ROI to log fixation rate, controlled for ROI area and total looking duration. Values reported are medians, and 2.5% and 97.5% quantiles of the posterior distribution of each coefficient. Values are reported separately for models that estimated unique looking rates for each eye. Positive coefficient estimates represent increases in fixation rate (above that predicted by the overall mean rate, adjusted for surface area); negative rates represent decreases. We omitted head/crest and black feather ROIs from our frontal and backside display models, respectively, because peahens never looked to these regions.

back and forth between the lower portions of the male trains (supplementary material Movie 3), they may have been assessing the total width or symmetry of the trains (Hewig et al., 2008). Because train length increases with male age (Manning, 1989), at least until maturity (Petrie, 1993), females could evaluate male age by assessing train width and ensure they only mate with mature males. Furthermore, the width of the peacocks' train may be correlated with the length of the train, a trait that is correlated with mating success in some populations (Yasmin and Yahya, 1996). Future experiments that manipulate the width and symmetry of male trains will reveal whether these traits are important to female mate choice.

#### Possible confounds

One explanation for the observed gaze bias toward the lower regions of the male displays is that the mass of the eye-tracker prevented the birds from looking at higher regions. This is unlikely, however, because peahens could easily look at objects that were thrown on the roof of their enclosure (175.7±7.2 cm between the ground and object on which they were fixating, 32.5±1.5 deg of gaze elevation,  $N=7$ ). In addition, females that were wearing the eye-tracker and females that were not wearing the eye-tracker held their heads at similar heights when evaluating displaying males (Table 1B, Fig. 3; supplementary material Fig. S1E). Furthermore, females that were wearing the eye-tracker did not tilt their heads under the weight of the eye-tracker (test of the null hypothesis that the slope of a line tangent to the head was equal to zero,  $0.0072±0.014$ , Table 1B). Lastly, peahens wearing the eye-tracker exhibited similar locomotory behavior: peahens wearing the eye-tracker and peahens that were not wearing the eye-tracker spent a similar amount of time walking while examining a peacock's frontal display (eye-tracker  $18.6±5.16%$ , no eye-tracker  $31.75±5.83%$ , Table 1B). Thus, gaze

bias in females is unlikely to result from the weight of the eye-tracker headpiece.

Furthermore, females were not looking at the lower train regions simply because males were moving their feet: females looked at the lower train region less often when males were moving ( $52.11±4.7%$ ) compared with when they were not moving ( $86.1±2.0%$ ) in the frontal display (Table 1C) and looked at the lower train region for similar amounts of time in the backside display when males were moving ( $87.6±3.0%$ ) compared with when they were not moving ( $79.9±2.8%$ ; Table 1C). Females were actively directing their gaze toward the lower train and spent more time looking at the lower train (supplementary material Fig. S2C) compared with the lower region of a similarly sized control (Table 1D; supplementary material Fig. S2D, Fig. S3A), demonstrating that females were selectively directing their attention toward relevant stimuli. It remains possible, however, that females could have processed other areas of the male display through peripheral vision, covert attention or retinal specializations. The relationship between visual perception and retinal specializations for high acuity vision has been most extensively studied in humans. Humans are capable of perceiving visual stimuli outside of the center of gaze but they tend to direct their gaze toward objects relevant to their choices (Land and Tatler, 2009; Shimojo et al., 2003). Presently, there is no precise information regarding specializations across the peafowl retina. Peafowl have a weak horizontal streak but do not have multiple areas of high ganglion density (they have only one area of high retinal ganglion cell density in the central retina) (Hart, 2002). We therefore assume that females direct their gaze toward the lower male display during courtship in order to preferentially process those visual features (future studies could reveal whether they also use information gathered from covert or peripheral attention mechanisms during courtship). This assumption is supported by our calibration

procedure in which females oriented directly toward novel objects or food with minimal offset (supplementary material Movie 1) and by our predator trials in which females directed their gaze directly toward the threat (supplementary material Movie 2).

### Role of the upper train

Even though we found that the peahens were primarily assessing the lower train, the upper train of the peacock may play an important role in courtship as a long-distance attraction signal in dense vegetation (supplementary material Fig. S2B). Peahens spent more time looking at the upper region of an artificial train when the lower train was obscured (supplementary material Fig. S2E) (which can occur in the birds' natural habitat by thick vegetation; J.L.Y., personal observation; Fig. S2B) compared with when the lower train was visible (Table 1D; supplementary material Fig. S2C, Fig. S3B). When the lower train was obscured (supplementary material Fig. S2E), peahens also spent more time looking at the upper train compared with a control of the upper region of similarly sized branches (supplementary material Fig. S2F, Fig. S3B; Table 1D). Most importantly, when the lower train of a peacock was obscured (supplementary material Fig. S2G) and the peahens were relatively far away from the artificial train, peahens approached the upper train with a shorter latency, tended to make more visits to the upper train, and spent more time near the upper train (Table 1E) compared with a control of similarly sized branches (supplementary material Fig. S2H, Fig. S3C,D). These results suggest that when the lower train of the peacock is not visible, peahens direct more attention toward the upper train and use it as a long-distance attraction signal to help locate mates for close inspection.

### Gaze in relation to behavior

Female gaze is influenced by certain male and female behavior (Table 1F). We found that female gaze depends upon train rattling and wing shaking (the only auditory components of these displays) as well as male movement, suggesting an interaction between behavioral and physical components of the male visual display. Females spent more time gazing at frontal displays ( $51.2 \pm 2.4\%$ ) when the males were train rattling (occurring during 28.3% of the displays) compared with when they were not train rattling ( $37.4 \pm 2.2\%$ ; Table 1F). Similarly, females spent more time gazing at backside displays ( $33.16 \pm 2.8\%$ ) when the males were shaking their wings (occurring during 64.4% of the displays) compared with when they were not shaking their wings ( $15.0 \pm 2.3\%$ ; Table 1F); they spent more time gazing at backside displays ( $31.3 \pm 3.2\%$ ) when the males were moving (occurring during 24.2% of the displays) compared with when they were not moving ( $25.6 \pm 2.1\%$ ; Table 1F). Females also spent more time gazing at frontal displays when the males were located closer to the females ( $45.5 \pm 2.2\%$ ) compared with when they were farther away ( $35.3 \pm 3.6\%$ ; Table 1F); males may therefore be able to attract attention by minimizing the distance between themselves and the females. To determine whether females spent more time looking at male displays because males rattled, shook their feathers, or moved more when females were already looking at them or females looked at male displays more because the males were rattling, shaking their feathers or moving, we examined female gaze patterns directly before, during and after males rattled, shook their feathers and moved (there was only an effect for train rattling and wing shaking; Table 1G). Directly before males rattled their feathers, females spent less time looking at the frontal display compared with when the males were rattling their feathers

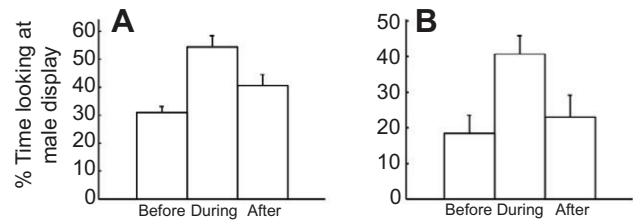


Fig. 5. (A) The mean (and s.e.m.) amount of time females ( $N=11$ ) gazed at the male frontal display before, during and after train rattling. (B) The mean amount of time females ( $N=9$ ) gazed at the male backside display before, during and after wing shaking.

(Table 1G, Fig. 5A); directly before males shook their wings, females spent less time looking at the backside display compared with when the males were shaking their feathers (Table 1F, Fig. 2A). These differences in attention suggest that females directed their attention toward male displays (both frontal and backside) because the males were rattling their feathers and shaking their wings.

Directly after males rattled their feathers, females spent less time looking at frontal displays than when the males were rattling their feathers (Table 1G); directly after males shook their wings, females spent similar amounts of time looking at backside male displays than when the males were shaking their wings (Table 1G). Females also looked at the displays more often after the males rattled their feathers (Table 1G, Fig. 5A) and tended to look at the displays more often after the males shook their wings (Table 1G, Fig. 5B) compared with before they rattled their feathers or shook their wings, indicating that train rattling and wing shaking helped maintain the attention of females even after the rattling or wing shaking ended. Overall, these findings demonstrate that the train-rattling and wing-shaking components of male displays serve to both attract and maintain the attention of females.

### CONCLUSIONS

The evolution of complex, multicomponent sexual traits has been controversial, but recent evidence suggests that they may evolve to capitalize on female sensory and cognitive processes (Hebets and Papaj, 2005). Assessing potential mates on leks, peahens are faced with one of the most famously elaborate displays in the natural world, as competing males fan and shimmer their trains. Surprisingly, we found that peahens selectively attend to only a fraction of this display, mainly gazing at the lower portions of the male train and only rarely at the upper portions, head or crest. However, the females appear to use the upper train as a long-distance attraction signal. Therefore, elaboration of the peacock's train may reflect a complex and multi-stage process of mate choice, with different components of the train acting at different stages. In addition, we found that males can attract and maintain female attention by rattling their trains and shaking their wings. Taken together, these results suggest that the evolution of complex, multicomponent displays may be favored both by multiple functions for different display components and by interactions between display components (Fleishman, 1988; Hebets and Papaj, 2005; Rosenthal, 2007). These findings, based on the first measurements of eye movements in any freely moving bird, support the hypothesis that female cognitive processes, including selective attention, play a crucial role in sexual selection (Dukas, 2002). Furthermore, they highlight the potential of eye-tracking technology to understand the evolution of animal signals by looking at these signals through the

eyes of the animals (Rupp and Wallen, 2007; Shepherd and Platt, 2008; Yorzinski and Platt, 2010).

## APPENDIX

### Validation experiments

To confirm that the peahens were able to look upwards (and were therefore not inhibited by the weight of the eye-tracker from doing so), we conducted trials in 2010–2011 in which we threw salient objects (such as a large stick or a ball of tinfoil) on the roof of their enclosure (approximately 1.8 m tall) and recorded their gaze as they responded. Furthermore, to demonstrate that females with the eye-trackers were adopting normal head orientations (and not drooping their heads under the weight of the equipment), we compared the height of their heads with that of females that were not wearing the eye-tracker. To do so, we randomly selected video clips in which females were evaluating male displays while wearing the eye-tracker (videos were taken from this study) and not wearing the eye-tracker (videos were taken from online sources or private collections). At 5 s intervals, we obtained the screen coordinates of the top of the bird's head, the top of the bird's shoulder and the ground. The distance between the top of the head and the shoulders was divided by the distance between the shoulders and the ground (this proportion ensured that the values were consistent irrespective of the distance between the birds and the video camera). The mean value of this ratio was taken for each video clip. In addition, we addressed whether peahens with the eye-tracker tilted their heads toward one side under the weight of the eye-tracker. We examined video images of females with the eye-tracker while they were looking directly at an external camcorder and assessed whether they were tilting their heads. We obtained the screen coordinates of both sides of the birds' heads and then calculated the slope (a slope of zero indicates that the head was not tilted). We took the mean of two different measurements from each bird. Lastly, we examined whether peahens spent a similar amount of time walking while examining a peacock's frontal display by comparing the amount of time females spent walking when they were or were not wearing the eye-tracker. We also compared the percentage of time that females looked at the lower train region (lower eye-spots, lower fishtails, lower dense feathers and legs) with respect to whether males were moving to assess whether females were looking at the lower train regions (see Results and discussion) simply because males were moving their feet.

To demonstrate that peahens orient their gaze toward behaviorally relevant stimuli, we presented females with a taxidermy raccoon (*Procyon lotor*) in an outdoor enclosure (3.4×5.7 m) while recording the gaze of the peahens [recording from the left eye of the birds and correcting for parallax errors (see 'Video coding' below) by measuring the distance between the bird and stimuli] in January–February 2012. The taxidermy raccoon was mounted on a skateboard (supplementary material Fig. S2A) and hidden underneath a large container that had a cloth covering one of the sides. A researcher revealed the raccoon by pulling on a fishing line that was attached to the front of the skateboard and pulled the raccoon out of the container (approximately 0.21 m s<sup>-1</sup>) through the side with the cloth (Yorzinski and Platt, 2012). The raccoon moved along a track (5 m long) that was elevated 0.85 m off the ground. It was pulled halfway across the track (2.5 m), remained stationary for 90 s, and was then pulled through the remainder of the track and removed from the enclosure. We determined the amount of time each female spent looking within 5 deg of the area where the raccoon would be located (halfway across the track) for 90 s before the raccoon was revealed ('pre-trial'). We compared this pre-trial time to the amount of time each female spent looking within 5 deg of

the raccoon while the raccoon was stationary (90 s; 'during-trial') using a Wilcoxon signed rank test to determine whether the pre-trial and during-trial values were different from zero. We also compared the number of fixations peahens made within 5 deg of the predator (while the predator was stationary) and of where the predator would be located during the pre-trial period using a Wilcoxon signed rank test. The peahens were always within several meters of the stationary raccoon (mean ± s.e.m. 2.01±0.21 m, range 1.26–3.84 m).

### Video coding

We isolated all video clips in which a male displayed to a female with his train erect and while directly facing her. This display clip began when the females first directed their gaze toward the displaying male. The clip ended when the females looked away from the male and did not look at him again during that particular display; if the females continued gazing at the male after the display ended (which occurred when the male turned away from the female), then the clip ended as soon as the male turned away. We refer to the displays during these clips as frontal displays. We also isolated all video clips that were 15 s before and 15 s after the frontal display clips; we refer to the displays during these clips as backside displays. We analyzed fewer backside display clips than frontal display clips because we excluded backside display clips in which the females never looked at the displaying male. We used custom-written Matlab scripts to analyze these clips field-by-field. For each clip, the gaze point on the first field was categorized into three mutually exclusive and exhaustive categories: directed at the displaying male, directed at environmental features (including the other male in the lek) or indeterminate. The gaze was classified as environmental even if the female was looking at the other male because the females rarely compared the displays of males simultaneously (in fact, only one female ever gazed back and forth between the frontal displays of the two males she was viewing). The gaze was classified as indeterminate when the software did not accurately track the gaze of the bird, such as when sunlight obscured the videos, radio frequency transmission was poor or when the bird was blinking. If the gaze was categorized as being directed at the displaying male, then the relative location of the gaze on the displaying male in the video was mapped on to a still image of that particular male. For example, if the female was looking at a particular eyespot of the male in the video, then the corresponding eyespot of the male in the still image was marked. This process was repeated for all fields in the clip and generated a list of *x*-*y* coordinates for each field that indicated where the female was looking.

The gaze coordinates were adjusted to eliminate parallax errors (Maurer, 1975). Parallax errors exist because the scene camera cannot be perfectly aligned with the eye of the bird without physically occluding the bird's vision. The errors occur when the distance between the eye of the bird and the target differ from the distance between the eye of the bird and the calibration plane. The scene camera was approximately 20 mm above the eye and either 10 mm to the right of the eye (when recording from the left eye) or 10 mm to the left of the eye (when recording from the right eye). Given that the calibration plane was 200 mm from the eye, the gaze coordinates needed to be shifted upwards by 5.71 deg [ $\arctan(20/200)$ ] and to the left by 2.86 deg [ $\arctan(10/200)$ ; when we recorded from the right eye] or to the right by 2.86 deg (when we recorded from the left eye) (Li, 2006). For example, if the female was fixating a male that was 1000 mm away with her left eye, the gaze was shifted upwards by 80 mm [ $1000-200\tan(5.71)$ ] and to the right by 40 mm [ $1000-200\tan(2.86)$ ]. We estimated the distance

between the displaying male and female by measuring the width of the male's body (in pixels) in the eye-tracker scene camera. We determined the width of a similarly sized object at known distances and then used this conversion to estimate the distance between males and females.

We used additional custom-written Matlab scripts to process the data. We identified 16 ROIs on each still image of the frontal male display (Fig. 2A) and 20 ROIs of each still image of the backside male display (Fig. 2B,C). The frontal display regions included exact outlines of different areas of the display: body, head and crest, left scale feathers (green feathers that are directly behind the body of the displaying males), right scale feathers, left dense feathers (a row of feathers along the bottom of the train that contain curved feathers and eyespot feathers), right dense feathers, left lower eyespots (feathers that end in ocelli and go as high as the height of the male's head), right lower eyespots, left upper eyespots, right upper eyespots (feathers that end in ocelli and are higher than the height of the male's head), left lower fishtails (the longest feathers that border the top and side of the train and are lower than the height of the male's head), right lower fishtails, left upper fishtails (the longest feathers that border the top and side of the train and are higher than the height of the male's head), right upper fishtails, left leg, and right leg. The backside display male regions included exact outlines of different areas of the display: right upper eyespots, left upper eyespots, right upper fishtails, left upper fishtails, right lower eyespots, left lower eyespots, right lower fishtails, left lower fishtails, right dense feathers, left dense feathers, right tail, left tail, right white feathers, left white feathers, right black feathers, left black feathers, right wings, left wings, right leg, and left leg.

For each field in each clip in which a female was gazing at the male, the scripts determined within which ROI the gaze coordinates fell. Given the existence of eye-tracker error, it is possible that gaze coordinates positioned near ROI boundaries fell within an adjacent ROI rather than the ROI within which the true gaze was directed; however, this error should be random with respect to our hypotheses, and given the large number of gaze points, this is unlikely to have significantly affected the results. We then determined the total number of fields a female spent looking at each ROI and the number of different ROIs a female looked at for each clip. We made these calculations for all of the clips. We only analyzed fixations and define fixations as looking at one or more gaze points within a 50 pixel diameter area that lasted at least 100 ms. There are infinite ways by which the male display could be demarcated into ROIs but we chose to divide the male display into sectors based on the observed scanpaths (Fig. 4). The scanpaths demonstrate that the females gaze at the lower sections of the train and we therefore divided the male display into ROIs that captured this clear division of attention. The conclusions presented in this manuscript are not dependent on our choice of ROIs: as clearly shown in Fig. 4, any reasonable ROI demarcations would support our main conclusions.

We also used the eye-tracker videos and the camcorder videos to analyze behavioral data. For each video clip, we recorded the fields during which the males were rattling their feathers, the males were shaking their primary wings (backside display only), the males were walking, or the females were walking. We used sound analysis software (Raven, Cornell Lab of Ornithology) to view the audio track of the DVD recordings and analyzed the times during which males rattled their feathers.

#### Inter-observer reliability

One research assistant coded the gaze of the peahens in all of the frontal display videos and another research assistant coded all of

the backside display videos; these data were used in the analyses. To ensure that coding was unbiased, we had the same set of frontal display videos scored again by a different research assistant. The gaze points were assigned to the same category (male display, environment or indeterminate gaze) in the majority of cases (mean  $\pm$  s.e.m. across all of the display clips  $88.4 \pm 0.73\%$ ). Furthermore, when the gaze was directed at the displaying male, we determined the difference in pixel locations between the  $x$ -coordinates and  $y$ -coordinates for both coders for each field and took the mean for each display clip; we then tested whether these differences were equal to zero. We found that the locations of the gaze that were mapped onto the still images were not significantly different between coders ( $x$ -coordinates:  $t=1.15$ ,  $N=135$ ,  $P=0.251$ ;  $y$ -coordinates:  $t=0.48$ ,  $N=135$ ,  $P=0.631$ ).

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#### AUTHOR CONTRIBUTIONS

J.L.Y. conceived the project and collected the data. J.S.B. and J.L.Y. engineered the peafowl eye-tracker. J.L.Y. and J.M.P. analyzed the results. J.L.Y., G.L.P. and M.L.P. designed the experiments and wrote the manuscript.

#### COMPETING INTERESTS

No competing interests declared.

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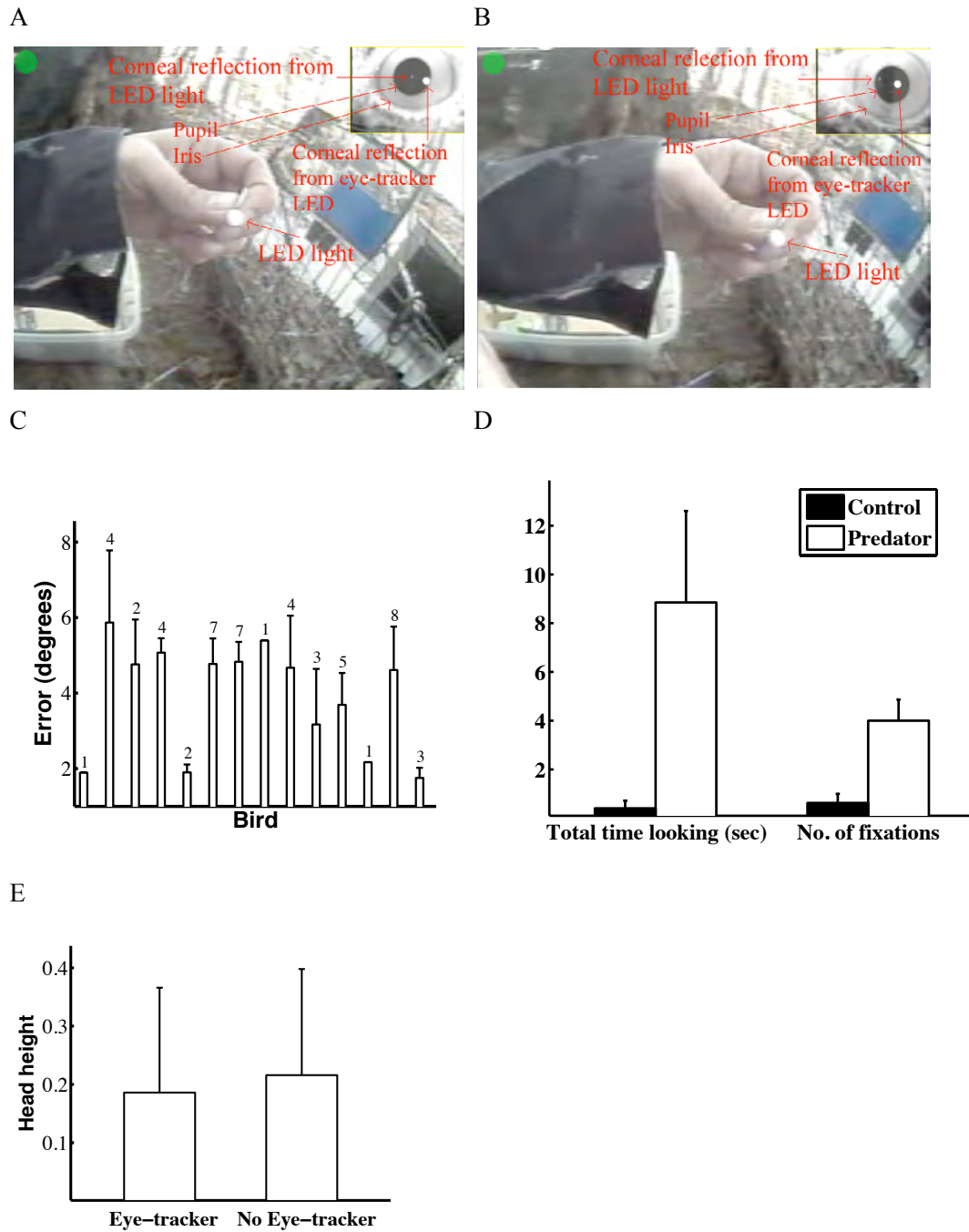
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#### REFERENCES

- Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Basolo, A. L. (1990). Female preference predates the evolution of the sword in swordtail fish. *Science* **250**, 808-810.
- Becker, W. and Fuchs, A. F. (1969). Further properties of the human saccadic system: eye movements and correction saccades with and without visual fixation points. *Vision Res.* **9**, 1247-1258.
- Bradbury, J. and Vehrencamp, S. (2011). *Principles of Animal Communication*, 2nd edn. Sunderland, MA: Sinauer Associates.
- Dakin, R. and Montgomerie, R. (2011). Peahens prefer peacocks displaying more eyespots, but rarely. *Anim. Behav.* **82**, 21-28.
- Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. London: Murray.
- Duchowski, A. (2003). *Eye Tracking Methodology: Theory and Practice*. London: Springer-Verlag.
- Dukas, R. (2002). Behavioural and ecological consequences of limited attention. *Philos. Trans. R. Soc. B* **357**, 1539-1547.
- Fantz, R. (1958). Pattern vision in young infants. *Psychol. Rec.* **8**, 43-47.
- Fleishman, L. J. (1988). Sensory influences on physical design of a visual display. *Anim. Behav.* **36**, 1420-1424.
- Hamada, T. (1984). A method for calibrating the gain of the electro-oculogram (EOG) using the optical properties of the eye. *J. Neurosci. Methods* **10**, 259-265.
- Hart, N. S. (2002). Vision in the peafowl (*Aves: Pavo cristatus*). *J. Exp. Biol.* **205**, 3925-3935.
- Hebets, E. A. and Papaj, D. R. (2005). Complex signal function: developing a framework of testable hypotheses. *Behav. Ecol. Sociobiol.* **57**, 197-214.
- Hewig, J., Trippe, R., Hecht, H., Straube, T. and Miltner, W. (2008). Gender differences for specific body regions when looking at men and women. *J. Nonverbal Behav.* **32**, 67-78.
- Jones, A. G. and Ratterman, N. L. (2009). Mate choice and sexual selection: what have we learned since Darwin? *Proc. Natl. Acad. Sci. USA* **106 Suppl. 1**, 10001-10008.

- Land, M. and Tatler, B.** (2009). *Looking and Acting: Vision and Eye Movements in Natural Behaviour*. New York, NY: Oxford University Press.
- Li, D.** (2006). Low-cost eye-tracking for human computer interaction. MSc thesis, Iowa State University.
- Manning, J. T.** (1987). The peacock's train and the age-dependency model of female choice. *J. World Pheasant Ass.* **12**, 44-56.
- Manning, J. T.** (1989). Age-advertisement and the evolution of the peacock's train. *J. Evol. Biol.* **2**, 379-384.
- Martin, G. R., White, C. R. and Butler, P. J.** (2008). Vision and the foraging technique of Great Cormorants *Phalacrocorax carbo*: pursuit or close-quarter foraging? *Ibis* **150**, 485-494.
- Maurer, D.** (1975). Infant visual perception: Methods of study. In *Infant perception: From Sensation to Cognition*, Vol. 1, *Basic Visual Processes* (ed. L. B. Cohen and P. Salapatek), pp. 1-76. New York, NY: Academic.
- McFadden, S. A. and Reymond, L.** (1985). A further look at the binocular visual field of the pigeon (*Columba livia*). *Vision Res.* **25**, 1741-1746.
- Nagamatsu, T., Kamahara, J., Iko, T. and Tanaka, N.** (2008). One-point calibration gaze tracking based on eyeball kinematics using stereo cameras. In *Proceedings of the 2008 Symposium on Eye Tracking Research Applications*, pp. 95-98. Savannah, GA: ACM.
- Petrie, M.** (1993). Do peacock's trains advertise age? *J. Evol. Biol.* **6**, 443-448.
- Petrie, M. and Halliday, T.** (1994). Experimental and natural changes in the peacock's (*Pavo cristatus*) train can affect mating success. *Behav. Ecol. Sociobiol.* **35**, 213-217.
- Petrie, M., Hall, M., Halliday, T., Budgley, H. and Pierpoint, C.** (1992). Multiple mating in a lekking bird: why do peahens mate with more than one male and with the same male more than once? *Behav. Ecol. Sociobiol.* **31**, 349-358.
- Rogers, L. J., Zappia, J. V. and Bullock, S. P.** (1985). Testosterone and eye-brain asymmetry for copulation in chickens. *Experientia* **41**, 1447-1449.
- Rosenthal, G. G.** (2007). Spatiotemporal dimensions of visual signals in animal communication. *Annu. Rev. Ecol. Evol. Syst.* **38**, 155-178.
- Rupp, H. A. and Wallen, K.** (2007). Sex differences in viewing sexual stimuli: an eye-tracking study in men and women. *Horm. Behav.* **51**, 524-533.
- Ryan, M. J.** (1998). Sexual selection, receiver biases, and the evolution of sex differences. *Science* **281**, 1999-2003.
- Shepherd, S. V. and Platt, M. L.** (2008). Spontaneous social orienting and gaze following in ringtailed lemurs (*Lemur catta*). *Anim. Cogn.* **11**, 13-20.
- Shimojo, S., Simion, C., Shimojo, E. and Scheier, C.** (2003). Gaze bias both reflects and influences preference. *Nat. Neurosci.* **6**, 1317-1322.
- Smith, J. D., Vertegaal, R. and Sohn, C.** (2005). ViewPointer: lightweight calibration-free eye tracking for ubiquitous handfree deixis. In *Proceedings of UIST 2005*, pp. 53-61.
- Takahashi, M., Arita, H., Hiraiwa-Hasegawa, M. and Hasegawa, T.** (2008). Peahens do not prefer peacocks with more elaborate trains. *Anim. Behav.* **75**, 1209-1219.
- Wallman, J. and Letelier, J.-C.** (1993). Eye movements, head movements, and gaze stabilization in birds. In *Vision, Brain and Behavior in Birds* (ed. H. Zeigler and H.-J. Bischof), pp. 245-263. Cambridge, MA: MIT Press.
- Yasmin, S. and Yahya, H.** (1996). Correlates of mating success in Indian peafowl. *Auk* **113**, 490-492.
- Yorzinski, J. L. and Anoop, K. R.** (2013). Peacock copulation calls attract distant females. *Behaviour* **150**, 61-74.
- Yorzinski, J. L. and Platt, M. L.** (2010). Same-sex gaze attraction influences mate-choice copying in humans. *PLoS ONE* **5**, e9115.
- Yorzinski, J. and Platt, M.** (2012). The difference between night and day: antipredator behavior in birds. *J. Ethol.* **30**, 211-218.

1 Fig. S1.



2

**Fig. S1.** (A,B) The eye-tracker was calibrated using an oculometric approach. An LED light (visible in the scene camera of the eye-tracker) was directed toward the bird's eye so that it created a corneal reflection (the eye camera of the eye-tracker is shown in the upper right of each image). When the corneal reflection (created by the LED light) was in the center of the pupil (A), the visual and optic axis were aligned and the peahen was looking at the LED light; when the corneal reflection (created by the LED light) was not in the center of the pupil (B), the visual and optic axis were not aligned and the peahen was not looking at the LED light. (C) Peahens ( $N=14$ ) oriented their gaze directly toward specific stimuli (such as small food objects) in non-mating contexts with minimal error (error bars represent standard errors). Numbers above error bars indicate the number of trials performed. (D) Peahens ( $N=8$ ) spent more time looking at the predator and made more fixations on the predator compared with the control region. (E) Peahens that were ( $N=12$ ) and were not ( $N=12$ ) wearing the eye-tracker held their heads up at similar heights when they were evaluating displaying males (see Materials and methods for explanation of head height metrics).

1 Fig. S2.

A



B



C



D



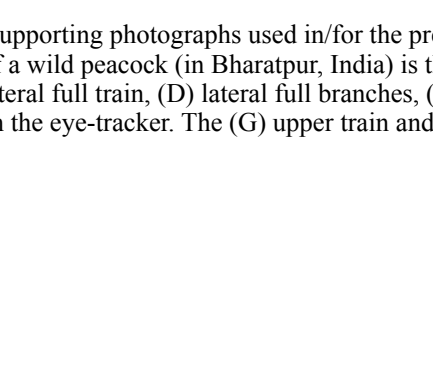
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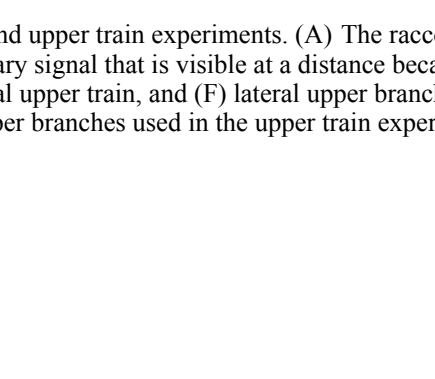
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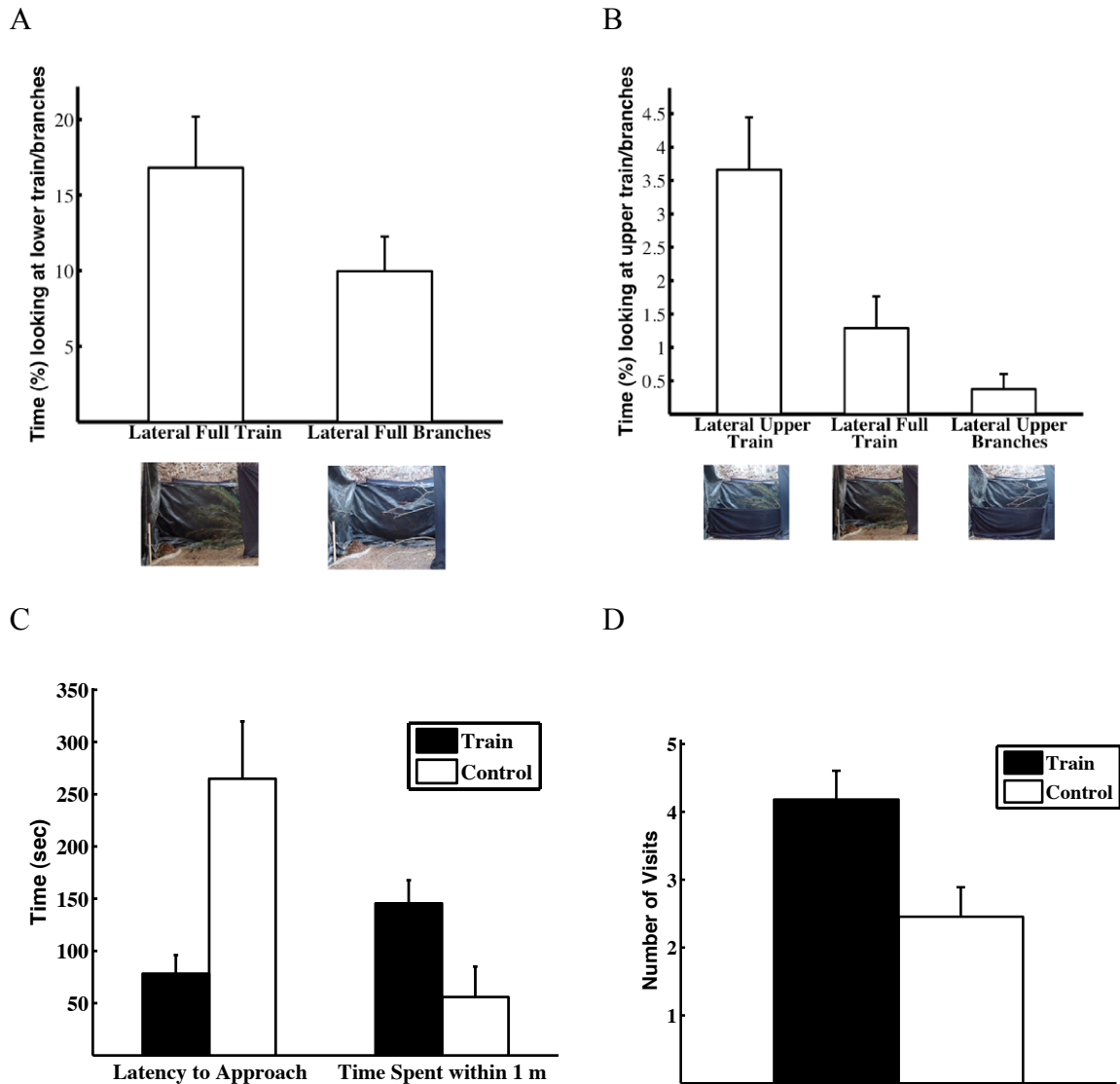


H



**Fig. S2.** Stimuli and supporting photographs used in/for the predator and upper train experiments. (A) The raccoon on a skateboard. (B) The upper train of a wild peacock (in Bharatpur, India) is the primary signal that is visible at a distance because of thick vegetation. The (C) lateral full train, (D) lateral full branches, (E) lateral upper train, and (F) lateral upper branches used in the upper train experiments with the eye-tracker. The (G) upper train and (H) upper branches used in the upper train experiments without the eye-tracker.

1 Fig. S3.



2

**Fig. S3.** (A) Peahens spent more time looking at the lower region of the lateral full train compared with the lower region of the lateral full branches and (B) spent more time looking at the lateral upper train compared with the upper region of the lateral full train; they also spent more time looking at the lateral upper train compared with the lateral upper branches ( $N=17$ ). (C) Peahens approached the upper train with a shorter latency and spent more time near the upper train, and (D) made more visits to the upper train compared with a control (upper train:  $N=11$ ; control:  $N=11$ ) when the peahens were initially relatively far from the artificial train.



1 Table S1. Model coefficients and confidence intervals for the generalized linear mixed  
 2 model using male as the sampling unit. Coefficients are contributions of each ROI to log  
 3 fixation rate, controlled for ROI area and total looking duration. Values reported are  
 4 median, 2.5%, and 97.5% quantiles of the posterior distribution of each coefficient.  
 5 Positive coefficient estimates represent increases in fixation rate (above that predicted by  
 6 the overall mean rate, adjusted for surface area); negative rates represent decreases. We  
 7 omitted head/crest and black feather ROIs from our frontal and backside display models,  
 8 respectively, because peahens never looked to these regions.

ROI		Both Eyes		
		B Coefficient (median)	2.50%	97.50%
Frontal				
	Body	1.59	0.93	2.36
	Head/crest	-	-	-
	Scale			
	feathers	0.16	-0.68	0.95
	Legs	1.74	1.02	2.47
	Dense			
	feathers	1.30	0.51	2.07
	Lower			
	eyespot	0.73	0.01	1.50
	Lower			
	fishtails	0.94	0.27	1.70
	Upper			
	eyespot	-2.83	-3.51	-2.09
	Upper			
	fishtails	-3.61	-4.44	-2.83
Backside				
	Black			
	feathers	-	-	-
	White			
	feathers	-0.59	-2.82	1.56
	Wings	1.75	-0.28	3.82
	Tail	-4.1	-7.24	-1.82
	Legs	-0.39	-2.69	1.95
	Dense			
	feathers	3.09	1.05	5.22
	Lower			
	eyespot	2.56	0.64	4.76
	Lower			
	fishtails	2.98	1.1	5.16
	Upper			
	eyespot	-2.05	-4.1	-0.01
	Upper			
	fishtails	-3.17	-5.68	-1.15

Table S2. Variation in female gaze patterns with respect to male display regions of interest (ROIs) during the frontal (n=12) and backside (n=11) male display. Mean percentage of time that peahens gazed at different male ROIs are displayed.

Bird ID	# clips	Body	Head/crest	Scale feathers	Legs	Dense feathers	Lower eyespots	Lower fishtails	Upper eyespots	Upper fishtails	
Frontal											
1	10	2.10	0.00	1.94	3.25	16.68	55.24	18.61	2.18	0.00	
3	2	0.00	0.00	0.00	9.38	48.74	21.81	20.10	0.00	0.00	
5	21	1.13	0.00	1.64	4.50	11.83	53.30	26.87	0.74	0.00	
6	10	1.68	0.00	0.00	6.46	35.93	32.32	23.42	0.00	0.20	
8	2	0.00	0.00	1.63	4.66	2.73	61.84	26.94	0.00	2.20	
26	12	10.96	0.00	0.00	1.55	10.13	54.31	8.36	6.49	8.19	
27	3	1.35	0.00	0.00	0.00	0.85	70.30	21.90	5.58	0.00	
28	2	0.00	0.00	0.00	0.00	3.61	84.40	12.00	0.00	0.00	
31	12	1.06	0.00	0.33	6.87	7.35	61.67	18.07	3.02	1.64	
32	5	2.82	0.00	0.00	0.54	16.42	60.80	17.67	1.79	0.00	
34	22	0.86	0.00	0.00	4.37	15.07	40.62	30.21	4.93	3.93	
35	4	22.50	0.00	0.00	17.50	6.74	27.50	25.40	0.42	0.00	

Bird ID	# clips	Black feathers	White feathers	Wings	Tail	Legs	Dense feathers	Lower eyespots	Lower fishtails	Upper eyespots	Upper fishtails	Black feathers
Backside												
1	8	0.00	0.82	20.22	0.00	0.77	13.40	32.00	31.90	0.93	0.00	0.00
5	21	0.00	0.73	13.46	0.00	0.00	17.02	35.56	26.54	4.00	2.70	0.00
6	8	0.00	0.00	1.34	0.00	4.38	34.50	34.80	25.01	0.00	0.00	0.00
8	1	0.00	0.00	42.73	0.00	0.00	0.00	57.27	0.00	0.00	0.00	0.00
26	14	0.00	0.38	6.46	0.00	7.15	25.04	51.27	8.46	1.24	0.00	0.00
27	4	0.00	0.69	3.82	0.00	0.00	8.02	60.80	26.70	0.00	0.00	0.00
28	3	0.00	0.00	0.00	0.00	36.20	2.61	34.20	14.50	6.36	6.14	0.00
31	9	0.00	0.00	19.50	0.00	4.35	30.90	24.30	20.95	0.00	0.00	0.00
32	2	0.00	0.00	13.40	0.00	0.00	13.40	68.90	4.26	0.00	0.00	0.00
34	38	0.00	0.67	14.29	0.83	0.31	8.21	41.55	22.02	10.66	1.46	0.00
35	6	0.00	0.00	0.39	0.00	0.00	22.30	56.00	18.21	2.85	0.29	0.00



**Movie 1.** A peahen orients her gaze toward a mealworm (at time 2;12–3;03) that a researcher throws in front of her. In the slow-speed (25%) version of the clip, the mealworm is highlighted with a red ellipse. The female's estimated gaze (yellow dot) is approximately 4 deg from the middle of the mealworm.



**Movie 2.** A peahen directs her gaze toward a taxidermy raccoon that is elevated above the ground.



**Movie 3.** A peahen evaluates the backside and frontal male courtship display. The yellow dot indicates where the female is looking. The upper right inset video shows a simultaneous close-up of the female's eye movements: a green dot tracks the center of her pupil, which is shaded in red, and a yellow crosshair tracks her corneal reflection (the three colored squares are used by the software to locate the pupil center and corneal reflection). The female momentarily looks at a passing squirrel during the frontal display.