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RESEARCH ARTICLE

Selective attention in peacocks during assessment of rival males

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ABSTRACT

Males in many species compete intensely for access to females. In order to minimize costly interactions, they can assess their rivals' competitive abilities by evaluating traits and behaviors. We know little about how males selectively direct their attention to make these assessments. Using Indian peafowl (*Pavo cristatus*) as a model system, we examined how males visually assess their competitors by continuously tracking the gaze of freely moving peacocks during the mating season. When assessing rivals, peacocks selectively gazed toward the lower display regions of their rivals, including the lower eyespot and fishtail feathers, dense feathers, body and wings. Their attention was modified based on the rivals' behavior such that they spent more time looking at rivals when rivals were shaking their wings and moving. The results indicate that peacocks selectively allocate their attention during rival assessment. The gaze patterns of males assessing rivals were largely similar to those of females evaluating mates, suggesting that some male traits serve a dual function in both intra- and intersexual selection. However, males spent more time than females looking at the upper eyespots and this could indicate that the upper eyespots function more in close-up rival assessment than mate choice.

KEY WORDS: Attention, Communication, *Pavo cristatus*, Sexual selection, Vision

INTRODUCTION

Sexual selection operates through both female mate choice (intersexual selection) and male–male competition (intrasexual selection; Darwin, 1871; Andersson, 1994). Both rival males and female mates may be interested in gaining similar information about a male. Therefore, in many species, the same male trait is used by both sexes (Borgia, 1979; Loffredo and Borgia, 1986; Zahavi, 1991; Berglund et al., 1996). For example, horns in mountain sheep (Geist, 1971), spurs in pheasants (von Schantz et al., 1989) and wing patches in dragonflies (Moore, 1990) are used in both male–male aggressive interactions and female choice. In species where a male trait is only evaluated by one of the sexes, it is often the males that are assessing the trait, suggesting that male traits often evolve initially in the context of male–male competition, and subsequently, in female choice (Berglund et al., 1996; Borgia and Coleman, 2000).

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In order to make these assessments, males and females must selectively direct their attention toward male traits. Because of constraints in sensory processing, animals cannot simultaneously attend to all aspects of their environment (Dukas, 2002); indeed, behavioral performance on a peripheral task declines when animals are focused on a central task, especially when the central task is difficult (Vreven and Blough, 1998; Dukas and Kamil, 2000). Because of this limited attention, animals need to direct their attention to extract the exact information they require (O'Brian and Showalter, 1993; Yorzinski et al., 2013; Yorzinski and Platt, 2014). We know little about how animals selectively direct their attention during mate and rival assessment (Dukas, 2002; Rosenthal, 2007). Previous work has shown that female peafowl shift their gaze between potential mates and their environment, potentially scanning for predators and other conspecifics while assessing mates. And, when evaluating a mate, peahens selectively direct their attention toward specific display regions of peacocks (Yorzinski et al., 2013). In contrast, we do not know how males selectively alter their attention when assessing other males.

We therefore investigated how males direct their attention when they assess potential rivals, using peacocks as a model system. Indian peafowl (*Pavo cristatus*) are a lekking species in which males establish display territories and females visit the males to select their mates (Petrie et al., 1991). Competition among peacocks is intense as mating success is highly skewed toward a small proportion of successful males. Males compete with each other by displaying their erect trains or walking parallel to other males. If aggression escalates, they chase each other and engage in fights that consist of them jumping and using their spurs (Petrie et al., 1991; Loyau et al., 2005). Males with longer trains and tarsi establish territories in central locations within leks and engage in more agonistic behaviors with other males. In contrast, males with shorter trains are less likely to establish display territories (Loyau et al., 2005). We monitored the gaze of freely moving peacocks as they evaluated the displays of other males to determine how they allocate their attention during rival assessment and whether their attention was influenced by the behavior of their rivals. We also compared their gaze patterns during rival assessment with the gaze patterns of females during mate evaluation.

MATERIALS AND METHODS

We analyzed the gaze behavior of 14 adult peacocks (*Pavo cristatus* Linnaeus 1753) during the mating season (April and May of 2012 and 2013) in Durham, NC, USA (36.01°N, 79.02°W). The males were housed in an enclosure (92 m perimeter) that was ∼400 m from the enclosure (46 m perimeter) in which the females were regularly housed; the males and females therefore did not physically interact with each other (with the exception of experiments conducted in Yorzinski et al., 2013). For each trial, a focal male was outfitted with a telemetric eye-tracker (Yorzinski et al., 2013; Yorzinski et al., 2015). The eye-tracker consisted of a transmitter (Iscan, Woburn, MA, USA; 345 g) connected to a headpiece (designed by Positive Science, LLC, New York, NY, USA; 25 g) that had two cameras that recorded the bird's eye and the scene in front of the bird (see Yorzinski et al., 2013 for further details on the eye-tracker).

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The transmitter sent both video images (30 frames s^{-1}) to a nearby 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. The eye-tracker does not prevent birds from looking at elevated targets or holding their heads upright; birds exhibit natural mating behavior while wearing the eye-tracker (Yorzinski et al., 2013). Because the eye-tracker recorded the eye movements of only one of the bird's eyes, a patch was placed on the bird's other eye to ensure that we were monitoring all the visual information that the bird was using to assess their rivals. Birds were trained wearing the patch along with the headgear and exhibited normal behaviors even when one eye was covered. The males were habituated to wearing the eye-tracker in daily sessions of about 60 min for several weeks prior to the trial. After the eye-tracker was calibrated using an oculometric approach based on corneal reflections (<5 deg error; Yorzinski et al., 2013), the focal male was put inside a testing enclosure (27 m perimeter) that contained another peacock ('rival') and two peahens (there were therefore 4 birds in the testing enclosure during each trial). The peahens were transported from the female enclosure to a holding enclosure (20 m perimeter) beside the testing enclosure at least 1 day before the trials began so that the females could habituate to the new area (they were not able to see males when they were in the holding enclosure); they were then relocated to the testing enclosure immediately before a trial. The focal peacock was allowed to move freely within the testing enclosure for 1–1.5 h. The behavior of the birds was continuously recorded using external camcorders (Sony SR47) placed in the corners of the testing enclosure. Each of the 14 focal peacocks was tested in one to four different trials (mean: 2.0±0.21 trials) for a total of 28 trials (20 trials recorded the left eye and 8 trials recorded the right eye of the birds). The experiments in this study were approved by Duke University (IACUC: A169-11-07).

Gaze and behavioral extraction

We isolated clips (N=230) from the trial recordings in which the focal male was directing his gaze toward the displaying male rival. Because the focal males did not often display (likely because they were wearing the eye-tracker), we only selected clips in which the focal male was not displaying. A clip began when the focal male directed his gaze toward a displaying rival male and ended when he looked away from the rival male for at least 10 s. A single clip could therefore include sequences when the focal male directed his gaze toward the rival male, then looked at the environment, females, or himself for less than 10 s, and then returned to looking at the rival male (mean±s.e.m. clip length: 40.5±2.7 s). The videos (30 frames s^{-1}) were deinterlaced to generate 60 fields s^{-1} (Turbo.264, Elgato Systems, San Francisco, CA, USA). The gaze data were adjusted for parallax errors (Maurer, 1975; Yorzinski and Platt, 2014), which exist because the scene camera cannot be perfectly aligned with the eye of the bird without physically blocking the bird's vision. Out of these clips, the rival male was directly displaying toward a female ('directed') in 65% of the clips; in the remaining 35% of clips, the rival male was displaying but the display was not directed toward a female ('non-directed'). In the directed clips, a female was within ∼3 m of the rival male and the rival male was tracking the female by shifting his display relative to her movement by keeping his train perpendicular to her body; in the non-directed clips, a female was not within ∼3 m of the rival male and the rival male was not adjusting his display relative to the movement of the female.

All of the clips were analyzed field-by-field using custom MATLAB scripts to assign each gaze coordinate to a target. The targets included whether the gaze was directed toward the rival male, one of the females, the focal male, or the environment. If the target was the rival male or the females, the gaze coordinate was assigned to a region-of-interest (ROI; see Results for ROI demarcations). We used the same ROI designations from our previous work (Yorzinski et al., 2013) such that there were 9 ROIs in the rivals' frontal display (body, head/crest, scale feathers, legs, dense feathers, lower eyespots, lower fishtails, upper eyespots, upper fishtails) and 10 ROIs in the rivals' backside display (black feathers, white feathers, wings, tail, legs, dense feathers, lower eyespots, lower fishtails, upper eyespots, and upper fishtails). We designated 6 ROIs in the female (head/crest, neck, chest, wings/body, tail, and legs).

In addition, the behavior of the males and females during the clips was analyzed. The videos from the external camcorders were imported into video editing software (Final Cut Express, Apple, Cupertino, CA, USA) and synchronized with the eye-tracking videos. We synchronized them by aligning frames in which birds made distinct movements that were visible in both videos. The behaviors analyzed were wing shaking (vertical movement of the wings), movement (walking or stepping) and train rattling (shaking the iridescent feathers and producing a rattle-like sound) of the rival male, movement of the focal male and females (walking, running or stepping), as well as the distance between the focal male and rival male. We estimated the distance between the focal and rival male by measuring the width of the rival 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 the males. Because the focal male and rival male were within 4 m of each other in 93% of the clips, the distance was categorized as <2 m and 2–4 m. For each of the behaviors, we assessed whether or not the behavior was occurring in each field of the video clip. Train rattling only occurred during clips when the rival male was performing a directed display. Train shivering (Dakin et al., 2016) only occurred in four of the non-directed display clips and we did not therefore analyze this behavior. Because focal males only looked at females in 9% of the non-directed display clips, we only analyzed female movement during directed clips, in which males looked at females in 62% of the clips.

Morphological features

In order to investigate the relationship among morphological features of peacocks, we obtained photographs (N=30) of peacocks directly facing the camera and displaying from online sources and our study birds. We measured the width and height of the train in pixels (Adobe Photoshop 7.0, San Jose, CA, USA) and then converted these values to mm (the average width of the peacock's blue body is 155 mm, which was used as a conversion factor). We also counted the number of lower eyespot feathers (eyespot feathers below a horizontal line directly above the scale feathers) and upper eyespot feathers (eyespot feathers above a horizontal line directly above the scale feathers; see Results for further details on these morphological measurements).

Statistical analysis

We performed repeated-measures mixed linear models (PROC mixed) to compare whether the percentage of time that focal males directed their attention toward different targets varied based on whether the rival male was performing a directed or non-directed

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display. We analyzed overall gaze patterns with respect to ROIs using a generalized linear mixed model (GLMM) for the rival males' frontal display and backside display as well as the female analyses (the model was similar to that used in eqn 1 in Yorzinski et al., 2013). For each analysis, we modeled the number of counts in each ROI as drawn from an over-dispersed Poisson distribution and used a log link function. The ROIs were categorical regressors, focal male and rival male identity were zero-mean random effects, and the logarithm of total clip duration and the logarithm of total ROI size (as a fraction of total average male size) were constant offsets. By including the size of the ROIs within the model, we accounted for variation in the surface area of different ROIs. We excluded one ROI (black feathers) from the backside display model because it had zero gaze counts in all recorded trials. We also re-ran this analysis using the rival male as the sampling unit rather than focal male. To investigate whether the eye that was being monitored by the eye-tracker influenced the results, we re-ran these models separately for the left and right eye. In addition, we re-ran the models separately for whether the rival male was performing a directed or non-directed display; because of insufficient data, it was not possible to perform the analyses on non-directed display clips for the backside and female analyses. 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/bykau/peacock.

We performed mixed linear models (PROC mixed) to compare whether males (this study) and females (previous study; Yorzinski et al., 2013) differed in the percentage of time they spent viewing ROIs in the frontal and backside displays; the dependent variable was the percentage of time that males or females spent gazing at each ROI; the independent variables were the sex of the focal bird, ROI and their interaction (the ID of the focal bird was a random variable). It is possible that males spent more time looking at the upper eyespots compared with females (see Results) because males are taller than females (~100 mm taller) and their area centralis may project slightly higher than that of females. In order to test for this possibility, we re-ran this analysis a second time but modified the upper eyespot ROI such that it excluded the lower part of the upper eyespots (the horizontal line that forms the lower boundary of the upper eyespot ROI was shifted upwards by 100 mm).

We performed mixed linear models (PROC mixed) to assess whether behaviors impact the focal males' gaze. The dependent variable was the percentage of time that the focal males spent gazing at the rival males (compared with gazing at the environment, themselves or females). The independent variables were whether the behavior was occurring or not, the identity of the focal male and rival male, the clip type (directed or non-directed) and the interaction between behavior and clip type. The behaviors were wing shaking, movement and train rattling of the rival male, movement of the focal male and females, as well as the distance between the focal male and rival male. Linear regressions were performed to assess morphological relationships (train width versus train height and lower eyespots versus upper eyespots). The linear mixed models and regressions were performed using SAS (Cary, NC, USA); means±s.e.m. are reported.

RESULTS

During our sample clips, focal males spent 27.9% of their time gazing at the displaying rivals. They spent 43.4% of their time gazing at the environment, as well as 3.1% and 0.5% of their time looking at females and themselves, respectively. Because of errors with the eye-tracking system (e.g. transmission problems and battery failure), 25.1% of gaze data could not be analyzed. Based on the data that could be analyzed, focal males allocated their attention toward targets differently depending on whether the rivals' display was directed or non-directed (Fig. 1A,B). Focal males spent more time gazing at the rival males' frontal display ($F_{1,13}$=29.77, P=0.0001) and less time looking at the females ($F_{1,13}$=31.12, P<0.0001) and environment ($F_{1,13}$=19.18, P=0.0007) during non-directed displays compared with directed displays. The amount of time they spent looking at the rival males' backside display ($F_{1,13}$=0.54, P=0.47) and themselves ($F_{1,13}$=2.28, P=0.15) was not affected by the type of display (Fig. 1C).

When focal males directed their attention toward their rivals, their gaze was directed toward specific display areas (Table S1; Fig. 2). During the rivals' frontal display, the focal males spent more time than random expectation (based on the surface area of the ROIs) looking at the dense feathers, lower eyespots, lower fishtails, legs and body, and less time looking at the upper eyespots and upper fishtails; the amount of time they gazed toward the head, crest, and scales was not different than expected (Table 1, Frontal; Fig. 3A). During the rivals' backside display, the focal males spent more time than random expectation gazing at the lower eyespots, lower fishtails and wings, and less time gazing at the black feathers and tail; the amount of time they gazed at the other backside display regions (upper eyespots, upper fishtails, white feathers, dense feathers and legs) was not different than expected (Table 1,

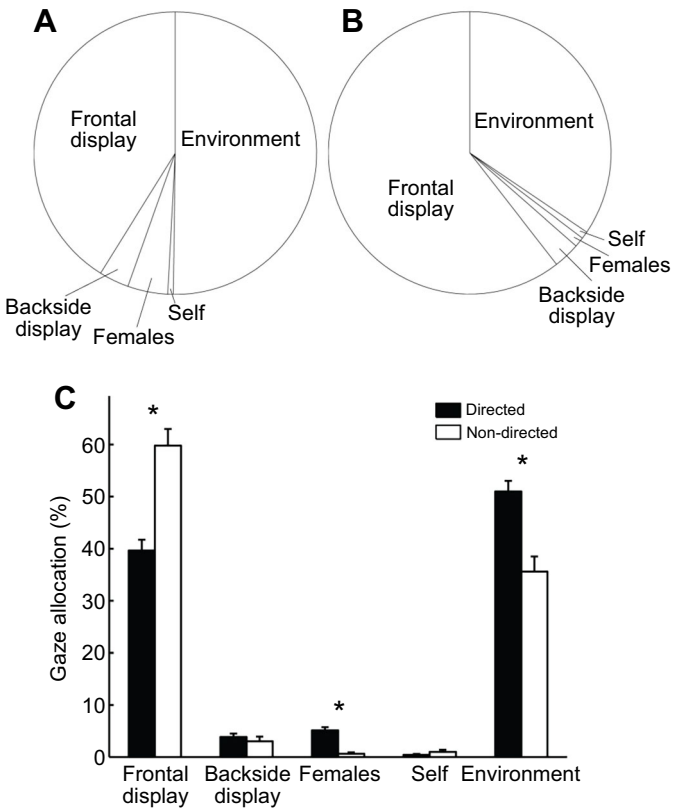

Fig. 1. Peacocks allocate their attention toward targets differently depending on whether a rival's display is directed or non-directed. (A,B) Fraction of time allocated to various targets during (A) directed or (B) non-directed rival displays. (C) Bar graph of percentage of time allocated to targets during directed and non-directed rival displays. Peacocks spend more time looking at rival males during frontal displays and less time looking at females and the environment when the rival displays are directed compared with non-directed. Values are means+s.e.m; *P<0.05.

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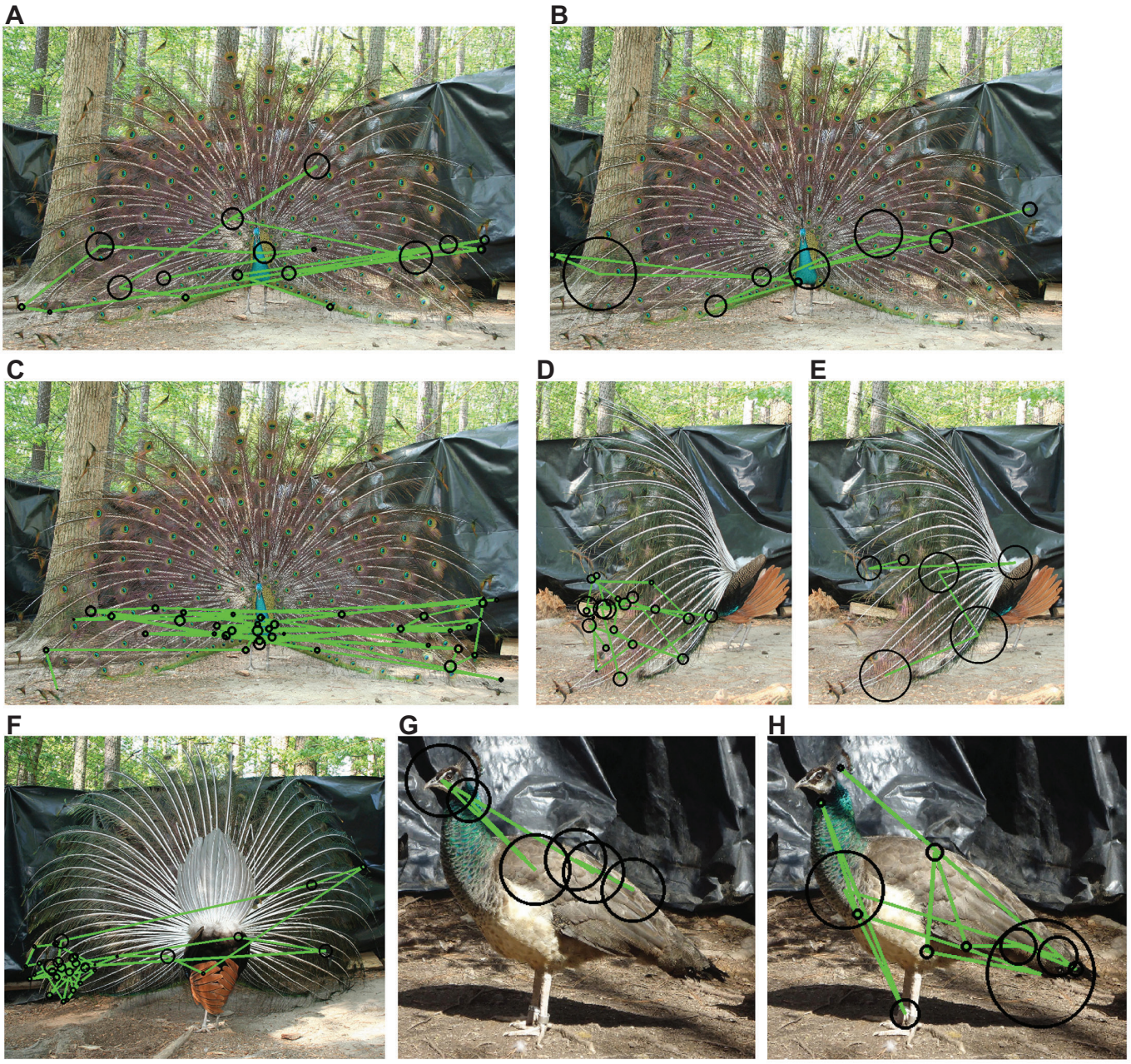

Fig. 2. Peacocks direct their attention toward specific rival display areas and specific areas of peahens. Representative scan paths of different focal males showing visual assessment of their rival's frontal (A–C) and backside (D–F) display as well as a female (G,H). B and F are scanpaths from the same male; the other scanpaths are each from different males. The size of the black circles indicates the relative amount of time males spent looking at each location.

Backside; Fig. 3B,C). These frontal and backside display results were similar regardless of whether the rivals' displays were directed or non-directed (Table S2) and when the analysis was re-run using the rival male as the sample unit (Table S3). Compared with female gaze patterns (data from Yorzinski et al., 2013), males spent a larger percentage of time looking at the upper eyespots and less time looking at the dense feathers in the frontal display and less time looking at the dense feathers in the backside display (Table 2). Even when accounting for males being taller than females, males still tended to spend more time looking at the upper eyespots compared with females (t=2.40, d.f.=342, P=0.017). When males directed their gaze toward females, the amount of time they spent looking at different regions on the female did not differ from random expectation (Table 1, Female; Fig. 3D).

Based on measurements taken from photographs of displaying peacocks facing directly toward the camera (N=30), the width of peacocks' trains was positively correlated with the height of peacocks' trains ($F_{1,28}$=44.55, R^2=61%, P<0.0001; Fig. 4A). Furthermore, the number of lower eyespots was negatively correlated with the number of upper eyespots ($F_{1,28}$=13.39, R^2=32.4%, P=0.001; Fig. 4B). Variation among peacocks in the total number of lower and upper eyespots was relatively small (mean: 154±1.5 feathers; range: 130–169 feathers; first quartile: 148 feathers; third quartile: 160 feathers) and similar to the total reported in previous studies (reviewed in Dakin and Montgomerie, 2011).

We found that males' gaze behavior was impacted by the behavior of their potential rivals (Table S4; Fig. 5). Focal males spent more time gazing at their rivals (compared with the

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Table 1. Model coefficients and confidence intervals for focal male gaze with respect to rival male (frontal and backside display) and female regions of interest (ROIs)

	Both eyes			Left eye			Right eye		
ROI	*B* (median)	2.5%	97.5%	*B* (median)	2.5%	97.5%	*B* (median)	2.5%	97.5%
Frontal									
Body	1.51	0.65	2.41	1.46	0.37	2.38	2.62	0.88	4.41
Head/crest	0.10	−0.90	1.11	0.80	−0.36	1.84	−2.00	−4.61	0.18
Scale feathers	−0.14	−1.10	0.86	0.41	−0.73	1.52	−1.90	−4.24	−0.09
Legs	1.20	0.29	1.97	0.82	−0.16	1.96	1.96	0.22	3.55
Dense feathers	1.21	0.36	2.07	1.10	−0.03	2.18	1.53	−0.19	3.25
Lower eyespots	1.20	0.41	2.11	1.16	0.21	2.18	1.75	0.11	3.47
Lower fishtails	1.04	0.15	1.92	0.96	0.05	1.89	1.59	−0.02	3.28
Upper eyespots	−2.37	−3.25	−1.61	−2.77	−3.78	−1.76	−1.69	−3.38	0.12
Upper fishtails	−3.75	−4.64	−2.89	−3.91	−4.97	−2.84	−3.80	−5.54	−2.06
Backside									
Black feathers	–	–	–	–	–	–	–	–	–
White feathers	−0.78	−2.59	0.92	−1.87	−4.15	−0.02	1.37	−1.99	4.38
Wings	3.33	2.08	4.81	3.28	1.83	4.85	2.28	−0.76	5.35
Tail	−3.65	−5.81	−1.67	−3.96	−6.28	−1.98	−2.30	−5.93	1.29
Legs	−1.47	−3.67	0.29	−1.87	−3.99	0.12	−0.94	−5.47	2.71
Dense feathers	0.09	−1.60	1.69	0.94	−0.66	2.50	−0.72	−4.88	2.62
Lower eyespots	2.55	1.15	3.94	2.87	1.49	4.32	2.12	−0.61	4.96
Lower fishtails	2.61	1.11	4.13	2.97	1.48	4.55	2.81	0.01	5.60
Upper eyespots	−1.37	−2.91	0.09	−1.36	−2.93	0.36	−2.41	−5.88	1.01
Upper fishtails	−1.29	−2.85	0.25	−0.92	−2.62	0.63	−1.77	−5.54	1.25
Female									
Head/crest	−0.73	−1.63	0.16	−0.88	−2.17	0.29	−0.58	−2.34	0.93
Neck	−0.16	−0.97	0.65	−0.21	−1.36	0.96	−0.61	−2.09	0.95
Chest	0.27	−0.56	1.06	0.38	−0.67	1.56	0.24	−1.19	1.79
Wings/body	0.40	−0.40	1.20	0.28	−0.87	1.42	0.93	−0.43	2.42
Tail	0.36	−0.45	1.24	0.57	−0.57	1.71	0.02	−1.49	1.46
Legs	−0.10	−0.87	0.69	−0.12	−1.23	0.98	0.01	−1.52	1.51

environment, themselves or females) when their rivals were shaking their wings and moving. The focal males also spent more time looking at their rivals when the focal males were stationary rather than moving and when the females were moving. In contrast, the amount of time that focal males spent looking at their rivals did not vary depending on the distance between the males or whether the rival male was train rattling. These results were qualitatively similar when analyzed with non-parametric methods (Wilcoxon signed-rank test) except that focal males did not spend significantly more time looking at rival males when the focal males were stationary. The amount of time that focal males gazed at rivals varied depending on the specific focal male and rival during the wing shaking, train rattling, female movement and distance analyses. In most cases, focal males gazed at male rivals more during non-directed clips versus directed clips.

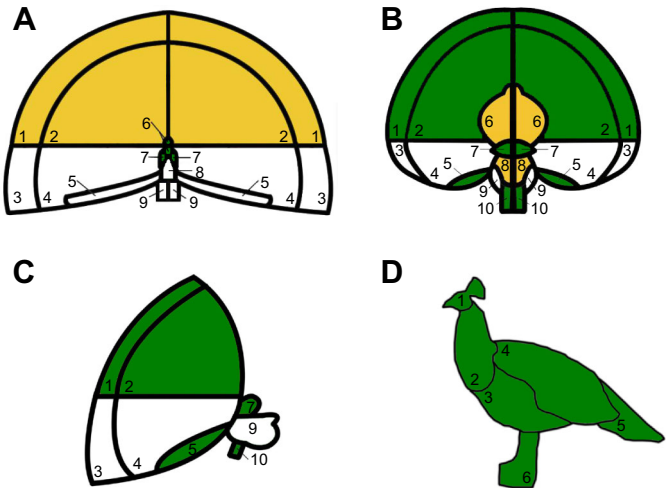

Fig. 3. Distribution of peacock gaze toward displaying rivals and peahens. The probability that focal peacocks gazed at specific regions of interest (ROIs) in the rival male's frontal (A) and backside (B,C) display as well as the female (D). White, yellow and green shading indicates areas viewed at levels 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; 5, dense feathers. In A: 6, head and crest; 7, scale feathers; 8, body; 9, legs. In B and C: 6, tail; 7, white feathers; 8, black feathers; 9, wings; 10, legs. In D: 1, head and crest; 2, neck; 3, chest; 4, wings and upper body; 5, tail; 6, legs.

DISCUSSION

Peacocks selectively shifted their gaze toward specific display regions of their displaying rivals. They focused on the lower display feathers (eyespots and fishtails), dense feathers, body and wings. They also directed more attention toward their rivals when the rivals were shaking their wings and moving but not when they were train rattling. During our observation periods, peacocks spent over a third of their time gazing at their displaying rivals, allowing them to monitor their rivals' traits and behaviors. Because our sample periods began when focal males gazed at displaying rivals (and continued until focal males looked elsewhere for >10 s), this percentage may be higher than if we had recorded focal male gaze during the total time rivals were displaying. However, it is clear from these sample periods that males spend a significant fraction of their time monitoring their rivals.

Rival traits and behavior

Peacocks focused their attention on specific traits of their rivals. They directed most of their gaze toward the lower eyespot feathers,

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Table 2. Comparison between male (this study) and female (previous study by Yorzinski et al., 2013) gaze patterns as they evaluate a displaying male rival or mate for the frontal and backside display

ROI	Males	Females	*t*	*P*-value
Frontal				
Body	5.7 (1.1)	3.2 (1.6)	1.36	0.18
Head/crest	1.0 (1.1)	0.0 (1.6)	0.52	0.60
Scale feathers	1.9 (1.1)	0.6 (1.6)	0.69	0.49
Legs	5.3 (1.1)	4.7 (1.6)	0.32	0.75
Dense feathers	8.4 (1.1)	14.6 (1.6)	3.31	0.001*
Lower eyespots	46.7 (1.1)	49.9 (1.6)	1.72	0.09
Lower fishtails	19.1 (1.1)	22.3 (1.6)	1.69	0.09
Upper eyespots	9.3 (1.1)	2.7 (1.6)	3.45	0.0006*
Upper fishtails	2.7 (1.1)	2.0 (1.6)	0.38	0.70
Backside				
Black feathers	0.0 (2.1)	0.0 (1.8)	0.00	1.00
White feathers	1.5 (2.1)	0.5 (1.8)	0.35	0.72
Wings	14.6 (2.1)	11.9 (1.8)	0.99	0.32
Tail	0.6 (2.1)	0.3 (1.8)	0.12	0.90
Legs	2.3 (2.1)	2.6 (1.8)	0.13	0.89
Dense feathers	2.6 (2.1)	16.5 (1.8)	4.95	<0.0001*
Lower eyespots	39.8 (2.1)	41.0 (1.8)	0.41	0.68
Lower fishtails	28.4 (2.1)	21.3 (1.8)	2.54	0.012
Upper eyespots	6.3 (2.1)	4.8 (1.8)	0.53	0.59
Upper fishtails	3.8 (2.1)	1.2 (1.8)	0.95	0.34

Least squares means of the percentage of time (and standard error) are displayed for each ROI of males and females as well as the *t* statistics and *P*-values comparing the sexes (d.f.=304 for frontal analysis and d.f.=297 for backside analysis). Asterisks indicate significant difference (using a Bonferroni correction) in the percentage of time that males versus females spend looking at a particular ROI of a displaying male.

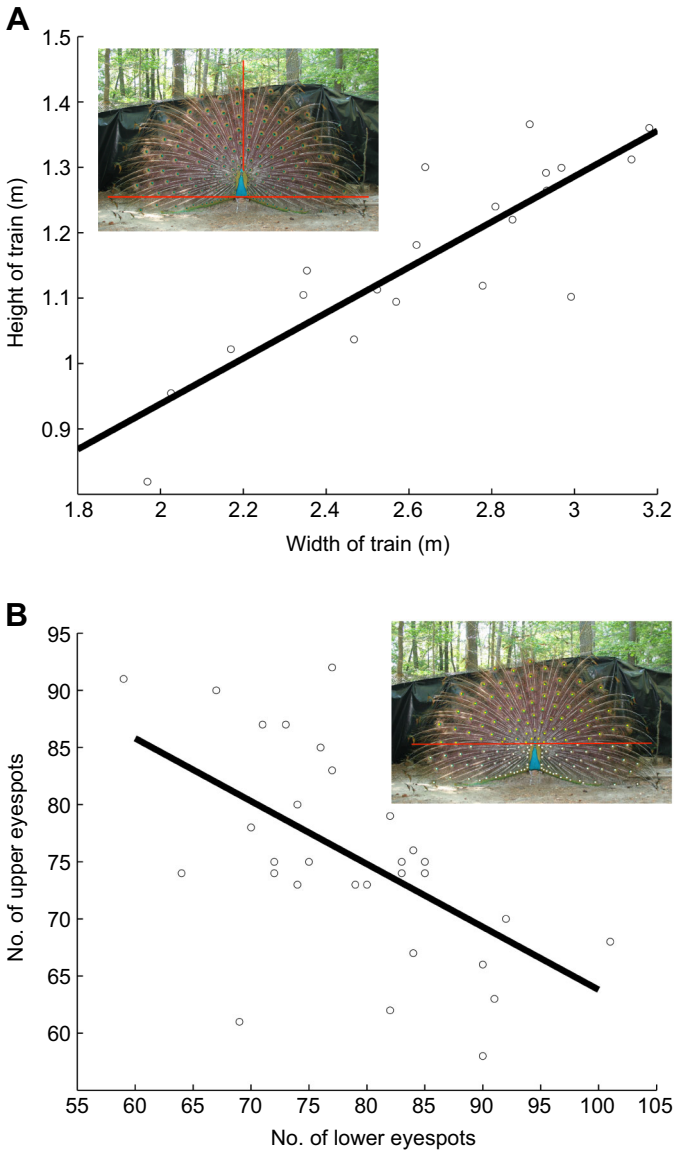

Fig. 4. Morphological features of peacock trains. (A) The width of peacock trains (horizontal red line in insert) is positively correlated with the height of peacock trains (vertical red line). (B) The number of lower eyespots (dots below horizontal red line in insert) is negatively correlated with the number of upper eyespots (dots above red line).

lower fishtail feathers, dense feathers and legs. Interestingly, previous work found that train and tarsi length in peacocks were important traits during intrasexual selection. Males with longer trains and tarsi established territories in central locations within leks and engaged in more agonistic behaviors with other males (Loyau et al., 2005). Given that peacocks were gazing along the bottom portions of their rivals' displays and their rivals' legs, they could have been assessing the width of the trains (which is positively correlated with the length of the train) and length of the tarsi. In addition, we found a negative relationship between the number of eyespots in the lower and upper train. It would be interesting to determine whether peacocks that invest in more eyespots in the lower train versus the upper train are more successful in deterring rivals given that male gaze is directed toward the lower display regions and the total number of eyespot feathers is fairly similar across males (this study; Dakin and Montgomerie, 2011). Peacocks also often gazed toward the body of their rivals. By directing their attention toward the bodies as well as the legs, peacocks could have been monitoring their rivals for aggressive movements.

Peacocks' attention toward their rivals also varied depending on their rivals' behavior. Peacocks spent more time looking at their rivals when the rivals were moving and shaking their wings. Because movement could potentially lead to aggressive behavior (such as a chase), it is likely to be important for peacocks to monitor any movement so that they can respond quickly and appropriately. The wing shaking behavior could be an indicator of a rival's physical abilities if the speed and frequency of wing shaking indicates male quality. Physical performance, including strength, endurance and agility, can impact the outcome of contests among males in some species (McCullough and Simmons, 2016). If the wing shaking behavior reflects a rival's physical abilities, then attention toward this trait could provide males with an assessment of their rivals without needing to engage in costlier contests. Further research is needed to investigate whether wing shaking is related to male condition or fighting ability. Interestingly, males did not direct more attention toward their rivals when their rivals were train rattling, suggesting that train rattling is not under intrasexual selection.

Female and self assessment

While assessing their competitors, peacocks did not spend very much time looking at females. In fact, they allocated less than 5% of their time during our sample periods gazing at females. It is possible that focal males did not often attend to females because these males were outfitted with the eye-tracking equipment. Males wearing the eye-tracker rarely displayed or attempted to copulate with females. Further research will be necessary to determine whether displaying males exhibit similar gaze patterns as non-displaying males. However, non-displaying males may also need to stay highly

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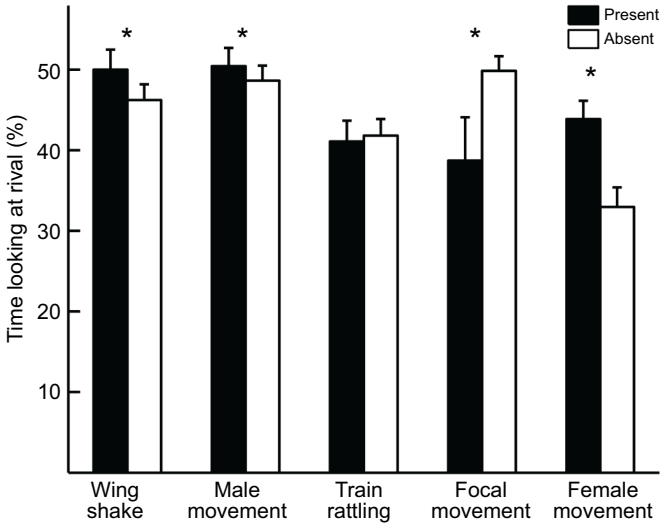

Fig. 5. Time peacocks spend looking at rivals depending on the behavior of rivals, females and themselves. Focal males spend more time looking at their rivals when the rivals are shaking their wings and moving but not when they are rattling their feathers. They also spend more time looking at their rivals when the focal males are stationary and the females are moving. Values are means+s.e.m; *P<0.05.

focused on their rivals to avoid possible injury; they may only direct attention toward females when they are directly engaged in courtship displays. Further experiments will be necessary to determine how much time males allocate to monitoring females while they are courting them. We found that when males directed their gaze toward females, they evenly distributed their gaze among different female regions. While the females are mostly brown and white, they have iridescent feathers on their neck and crest. Because males were not preferentially gazing at these iridescent feathers, they may not use these traits when assessing female mating partners. These iridescent feathers may instead be targets of selection among females or a by-product of selection on iridescence in males.

Males allocated a small amount of time (less than 1%) toward looking at their own train (as well as their feet in one clip). Even though the focal peacocks were not displaying, it is probably still important for them to maintain the appearance and condition of their feathers. Birds with ornamental plumage spend more time maintaining their plumage than birds without ornamental plumage (Walther and Clayton, 2005). And, female budgerigars prefer males that maintain their plumage by preening (Griggio et al., 2010). Peacocks also devote a significant amount of their daily time budget to preening (Walther, 2003) and directing attention toward themselves could allow them to monitor the condition of their feathers.

Dual function of male traits

Male traits could function in intersexual selection, intrasexual selection, or both (Berglund et al., 1996). Females and males exhibited strikingly similar gaze paths when evaluating a displaying male. Similar to the results in this study on peacocks, peahens primarily gazed at the lower display regions of males: at their lower trains, body and legs (Yorzinski et al., 2013). These gaze results suggest that male traits are under selection by both rivals and potential mates. Males did spend more time looking at the upper eyespots and less time looking at the dense feathers in the frontal display compared with females, which could indicate that the upper eyespots play a larger role in rival assessment compared with mate choice and the dense feathers play a larger role in mate choice compared with rival assessment. Both peahens (Yorzinski et al., 2013) and peacocks allocated a similar amount of time toward looking at displaying males versus the environment (males: 27.9% of time looking at rival male; females: 27.5% of time looking at potential mate). They both spent over half of their time scanning the environment, which is important given that predation risk can be elevated during rival and mate assessment (Cooper, 1999; Hebets, 2005). We also found a key difference between the gaze patterns of males and females. Peahens spent more time looking at males when they were train rattling (Yorzinski et al., 2013) but males did not (this study), suggesting that train rattling functions in intersexual selection but not intrasexual selection.

Both males and females directed little attention toward the upper train of displaying males. Even though females do not spent much time looking at the upper train, we previously found that they are probably using the upper train to locate potential mates in environments with dense vegetation (Yorzinski et al., 2013). Future experiments will be necessary to assess whether the upper train functions similarly in male–male competition, with males using the upper train to locate rivals in complex environments.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization, J.L.Y.; Formal Analysis, J.L.Y. and S.B.; Funding Acquisition, J.L.Y., G.L.P. and M.L.P.; Investigation, J.L.Y.; Visualization, J.L.Y. and S.B.; Writing - Original Draft Preparation, J.L.Y.; Writing - Review & Editing, J.L.Y., S.B., G.L.P. and M.L.P.

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Data availability

Model files and additional plots are available at https://github.com/bykau/peacock.

Supplementary information

Supplementary information available online at http://jeb.biologists.org/lookup/doi/10.1242/jeb.150946.supplemental

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Table S1. Variation in focal male gaze patterns with respect to the rival male (frontal and backside) and female regions of interest (ROIs). Mean percentage of time that focal peacocks (n=14) gazed at the rival male and female ROIs are displayed.

	Bird ID	# clips	Body	Head/crest	Scale feathers	Legs	Dense feathers	Lower eyespots	Lower fishtails	Upper eyespots	Upper fishtails	
Frontal												
	42	20	7.81	1.96	3.59	2.95	12.19	53.74	16.30	1.47	0.00	
	44	7	0.00	0.00	0.00	16.30	7.10	47.70	28.90	0.00	0.00	
	46	7	12.42	0.00	4.88	3.45	8.90	49.68	20.67	0.00	0.00	
	47	8	5.86	0.00	0.00	3.49	4.70	48.66	11.93	16.42	8.95	
	49	16	6.41	0.24	0.59	5.61	3.99	55.85	18.75	6.91	1.65	
	50	16	5.56	1.83	0.21	6.60	6.15	48.92	16.09	14.31	0.32	
	51	18	5.24	0.00	3.31	3.17	6.02	52.02	25.95	2.72	1.58	
	52	14	1.23	0.73	5.94	9.50	3.59	47.04	21.46	6.64	3.87	
	53	14	5.16	0.00	0.00	5.87	3.55	48.13	28.79	8.04	0.46	
	59	6	0.00	0.00	0.00	8.93	15.05	52.43	12.99	4.32	6.29	
	60	24	3.66	1.76	0.69	6.38	13.90	38.48	16.46	15.25	3.42	

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	61	36	5.28	0.19	2.27	6.18	6.99	53.10	18.45	6.23	1.32	
	75	40	4.57	0.64	0.42	2.32	6.66	56.65	12.58	11.79	4.38	
	76	4	3.55	0.00	0.91	5.99	13.86	51.88	14.21	9.61	0.00	
Mean:			4.77	0.53	1.63	6.19	8.05	50.31	18.82	7.41	2.30	
Backside												
	Bird ID	# clips	Black feathers	White feathers	Wings	Tail	Legs	Dense feathers	Lower eyespots	Lower fishtails	Upper eyespots	Upper fishtails
	42	20	0.00	0.00	4.51	0.00	0.00	12.51	35.12	47.86	0.00	0.00
	44	7	0.00	0.00	0.00	0.00	0.00	0.00	68.67	31.33	0.00	0.00
	46	7	0.00	0.00	20.30	0.00	0.00	0.00	19.47	26.46	30.78	3.00
	47	8	0.00	0.00	34.78	0.00	0.00	0.00	0.00	0.00	45.65	19.57
	49	16	0.00	3.57	10.02	1.45	3.03	4.33	30.03	31.73	14.20	1.63
	50	16	0.00	0.00	22.55	0.00	0.00	0.00	54.07	0.00	12.80	10.59
	51	18	0.00	0.00	6.17	0.00	0.00	2.23	57.62	33.98	0.00	0.00
	52	14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	0.00
	53	14	0.00	2.17	14.61	0.00	4.41	1.93	59.78	12.68	2.96	1.45

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	59	6	0.00	0.00	17.14	0.00	0.00	0.00	20.00	62.86	0.00	0.00
	60	24	0.00	2.10	10.38	1.15	2.30	3.29	44.51	27.35	7.57	1.35
	61	36	0.00	0.00	6.04	0.00	0.00	3.34	49.42	36.36	2.70	2.13
	75	40	0.00	3.52	8.73	2.54	1.14	0.64	47.96	12.73	20.77	1.98
	76	4	0.00	0.00	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mean:			0.00	0.81	18.23	0.37	0.78	2.02	34.76	30.24	9.82	2.98
Female												
	Bird ID	# clips	Head/crest	Neck	Chest	Wings/Body	Tail	Legs				
	42	20	6.82	12.25	28.06	9.09	24.70	19.07				
	44	7	0.00	9.19	1.84	42.10	2.76	44.12				
	46	7	0.00	4.87	9.73	27.43	27.88	30.09				
	47	8	0.00	14.66	14.66	38.51	27.01	5.17				
	49	16	3.94	10.41	24.39	47.96	12.71	0.59				
	50	16	3.25	21.60	9.52	44.95	7.67	13.01				
	51	18	0.00	18.64	20.95	6.94	21.32	32.16				

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	52	14	9.98	5.08	18.87	44.83	3.99	17.24				
	53	14	7.30	12.23	25.25	23.47	0.00	31.76				
	59	6	0.00	6.98	8.48	63.84	13.97	6.73				
	60	24	9.01	14.48	9.38	35.62	21.92	9.59				
	61	36	5.11	11.21	11.57	42.08	16.87	13.16				
	75	40	8.57	15.65	12.03	48.47	9.66	5.62				
	76	4	0.00	13.22	0.00	54.55	19.83	12.40				
Mean:			3.86	12.18	13.91	37.84	15.02	17.19				

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Table S2. Model coefficients and confidence intervals for focal male gaze (both eyes) with respect to rival male (frontal and backside display) and female regions of interest (ROIs) during directed and non-directed displays.

		Non-directed			Directed		
		B coefficient (median)	2.5%	97.5%	B coefficient (median)	2.5%	97.5%
	ROI						
Frontal							
	Body	1.31	-0.19	2.93	1.69	0.85	2.58
	Head/crest	-2.25	-4.74	-0.06	0.44	-0.59	1.34
	Scale feathers	0.49	-1.25	2.17	-1.08	-2.05	-0.17
	Legs	1.28	-0.41	2.72	1.25	0.36	2.17
	Dense feathers	1.58	0.06	3.07	1.59	0.72	2.43
	Lower eyespots	2.44	1.03	3.96	1.05	0.12	1.93
	Lower fishtails	1.99	0.60	3.58	1.07	0.28	1.92
	Upper eyespots	-1.72	-3.13	-0.25	-2.30	-3.26	-1.45
	Upper fishtails	-5.05	-7.06	-3.27	-3.70	-4.64	-2.83
Backside							
	Black feathers	-	-	-	-	-	-
	White feathers	-	-	-	-0.41	-2.66	1.55
	Wings	-	-	-	3.36	1.72	4.93
	Tail	-	-	-	-3.67	-6.11	-1.52
	Legs	-	-	-	-1.06	-3.42	0.85
	Dense feathers	-	-	-	0.44	-1.39	2.37
	Lower eyespots	-	-	-	2.56	1.01	4.18
	Lower fishtails	-	-	-	2.79	1.18	4.52
	Upper eyespots	-	-	-	-1.70	-3.52	0.05
	Upper fishtails	-	-	-	-2.15	-4.06	-0.33

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Female							
	Head/crest	-	-	-			
	Neck	-	-	-	-0.58	-1.42	0.17
	Chest	-	-	-	-0.07	-0.76	0.67
	Wings/body	-	-	-	-0.02	-0.75	0.73
	Tail	-	-	-	0.68	-0.11	1.38
	Legs	-	-	-	0.05	-0.69	0.76

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Table S3. Model coefficients and confidence intervals for focal male gaze (both eyes) using the rival male as the sampling unit.

		Both eyes		
		B coefficient (median)	2.5%	97.5%
	ROI			
Frontal				
	Body	1.53	0.60	2.39
	Head/crest	0.19	-0.85	1.06
	Scale feathers	-0.19	-1.13	0.76
	Legs	1.20	0.32	2.03
	Dense feathers	1.21	0.37	2.08
	Lower eyespots	1.22	0.34	2.06
	Lower fishtails	1.03	0.23	1.82
	Upper eyespots	-2.40	-3.30	-1.55
	Upper fishtails	-3.74	-4.71	-2.84
Backside				
	Black feathers	-	-	-
	White feathers	-0.73	-2.74	1.08
	Wings	3.25	1.53	4.69
	Tail	-3.42	-5.80	-1.41
	Legs	-1.26	-3.53	0.55
	Dense feathers	0.15	-1.75	1.92
	Lower eyespots	2.27	0.69	3.79
	Lower fishtails	2.38	0.71	4.08
	Upper eyespots	-1.29	-2.93	0.28
	Upper fishtails	-1.23	-2.98	0.62
Female				
	Head/crest	-0.69	-1.60	0.19
	Neck	-0.20	-0.97	0.68
	Chest	0.28	-0.52	1.04
	Wings/body	0.38	-0.53	1.15
	Tail	0.37	-0.46	1.18
	Legs	-0.12	-0.98	0.69

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Table S4. The impact of behavior and distance on the amount of time that focal males spend looking at rival males. The rivals' behavior includes wing shaking, movement and train rattling. The focals' behavior and females' behavior includes movement. F values (numerator degrees of freedom, denominator degrees of freedom) are displayed along with p-values.

	Rival Behavior			Focal Behavior	Female Behavior	Distance Between Focal and Rival Male
	Wing Shake	Movement	Train Rattling	Movement	Movement	
Behavior	12.16 (1,129) **0.0007**	16.31 (1,187) **<0.0001**	0.15 (1,127) 0.70	9.64 (1,54) **0.003**	14.44 (1,143) **0.0002**	0.30 (1,62) 0.58
Focal Male	1.92 (13,129) **0.034**	1.50 (13,187) 0.12	2.30 (11,127) **0.013**	1.61 (13,54) 0.11	3.27 (11,143) **0.0005**	3.02 (13,62) **0.0017**
Rival Male	2.43 (7,129) **0.023**	1.86 (7,187) 0.078	3.23 (4,127) **0.015**	2.13 (7,54) 0.056	2.68 (4,143) **0.034**	3.09 (7,62) **0.0073**
Clip Type	14.82 (1,129) **0.0002**	22.41 (1,187) **<0.0001**	-	3.46 (1,54) 0.068	-	14.05 (1,62) **0.0004**

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Behavior x Clip Type	3.58 (1,129) 0.061	2.44 (1,187) 0.12	-	2.07 (1,54) 0.16	-	0.27 (1,62) 0.61

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Movie S1. A peacock evaluates the frontal display of a potential rival that is directing his display toward a female and not directing his display toward a female. The yellow dot indicates where the peacock is looking. The upper right inset video shows a simultaneous close-up of the peacock's eye movements: a green dot tracks the center of his pupil, which is shaded in red, and a yellow crosshair tracks his corneal reflection.

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