ORIGINAL PAPER

Peacocks orient their courtship displays towards the sun

Roslyn Dakin · Robert Montgomerie

Abstract We studied two courtship displays of male peafowl (*Pavo cristatus*), focusing particularly on male orientation relative to the position of the sun. During the "wing-shaking" display, females were generally behind the displaying male, and male orientation with respect to the position of the sun was not significantly different from random. However, during the pre-copulatory "train-rattling" display, males were on average directed at about 45° to the right of the sun azimuth with the female positioned directly in front, suggesting that this behaviour is involved in the communication of a visual signal. A model presentation experiment confirmed that courting peacocks were more likely to perform the train-rattling display when the female was on the sunny side of their erect train, but more likely to perform wing-shaking behaviour when the female was on the shaded side of the male. This study underscores the importance of visual signalling in peafowl courtship, and we suggest that an angle of about 45° relative to the sun may allow males to enhance the appearance of their iridescent eyespot feathers.

R. Dakin (✉) · R. Montgomerie
Department of Biology, Queen's University,
Kingston, ON K7L 3N6, Canada
e-mail: 2rd@queensu.ca

Introduction

In many species, both the location and timing of courtship displays appear to be selected for signal efficacy. For example, it has been suggested that the almost ubiquitous dawn chorus of birds is timed to minimize interference from wind and other noise (Henwood and Fabrick 1979) and thus maximize signal transmission distance and quality. Similarly, several neotropical lekking birds (*Rupicola rupicola*, *Corapipo gutturalis*, *Lepidothrix serena*) perform courtship displays at times when the contrast of male plumage against the visual background is maximized (Endler and Théry 1996), and the vertical placement of display arenas in several lekking manakins corresponds with the locations predicted to maximize male plumage contrast against the background (Heindl and Winkler 2003). Moreover, the courtship and territorial dive displays made by male Anna's hummingbirds (*Calypte anna*) are "oriented in the general direction of the sun" such that the "reflecting value" of the iridescent, rose-coloured gorget plumage is maximized towards the target female or male (Hamilton 1965). To the best of our knowledge, this is the only example of both the location and orientation of a display influencing the efficacy of a signal.

In the present study, we examine the courtship displays of free-ranging peacocks (*Pavo cristatus*) in relation to both the light environment and the relative positions of females being courted. Peahens visit a number of males during each breeding episode before copulating with one or (at most) two of the males that they visited previously (Petrie et al. 1991, 1992). Most studies to date indicate that peahens base their mate choices on some visible aspect of the elaborate and colourful male upper-tail feathers (or "train"; Petrie et al. 1991; Petrie and Halliday 1994; Loyau et al. 2005, 2007a), as Darwin (1871) surmised. Interestingly, however,
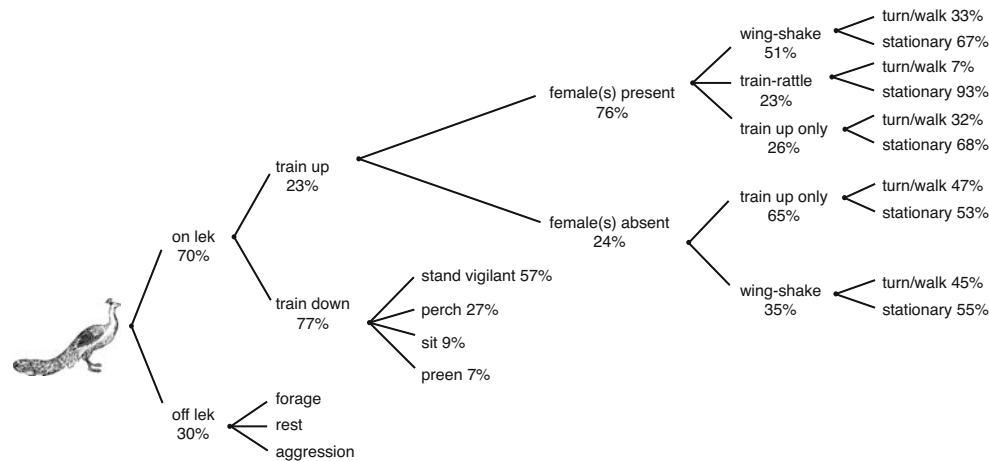
Fig. 1 Daily time budget for peacocks showing the average percent of time males devoted to each activity at each level in the hierarchy. Percentages during "train up" are averages calculated from the longest display bouts recorded for each of 11 males at LAA and APZ in 2008 between 07:00 and 19:00 local times. Percentages during all other activities (including "train up" versus "train down") are averages calculated from observations over a single day at LAA where we sampled each of 17 males once per hour for 12 h (07:00–19:00)

Takahashi et al. (2008) present data to suggest that male train ornamentation, in general, and eyespots, in particular, do not influence female choice and may be relics of past selection. The findings of Takahashi et al. (2008) have recently been interpreted in the science press as indicating "that Darwin's theory of sexual selection might not work in the case of the peacock's colourful tail" (Anonymous 2008; see also Morell 2008).

Peacocks strut around with trains erect in both the presence and absence of females (Fig. 1; see also Video 1 in the Electronic Supplementary Material (ESM)). When their trains are erect, males occasionally perform a "wing-shaking display" whether or not females are present, shaking their wings up and down vigorously behind the erect train, sometimes for 5–10 min at a time. In the presence of females, males also perform a "train-rattling display" for up to 6 min at a time, rapidly vibrating the rectrices that support their train feathers in the upright position, such that those feathers make a noise audible from several metres away (also called shivering in Petrie et al. (1992) and Takahashi et al. (2008)). The wing-shaking display often precedes the train-rattling display when females are present, and the train-rattling display always precedes copulation, though the sequence of events during courtship can be somewhat variable (Fig. 2).

Given the complexity of peacock displays and the observation that peacocks do not necessarily orient their erect trains towards a target female, our aims in this study were twofold. First, we sought to describe the directionality of peacock display behaviour and quantify the relative positions of both the male and the target female being courted during a courtship sequence. Second, we asked whether the direction that a male faces during train displays is related to the position of the sun, as one might expect if

male behaviour functions to display the iridescent colours of the train plumage (see Loyau et al. 2007a) effectively to prospective mates.

We addressed these questions by observing males courting females over the normal course of the breeding season and by conducting an experiment involving the presentation of a model female. The experiment allowed us
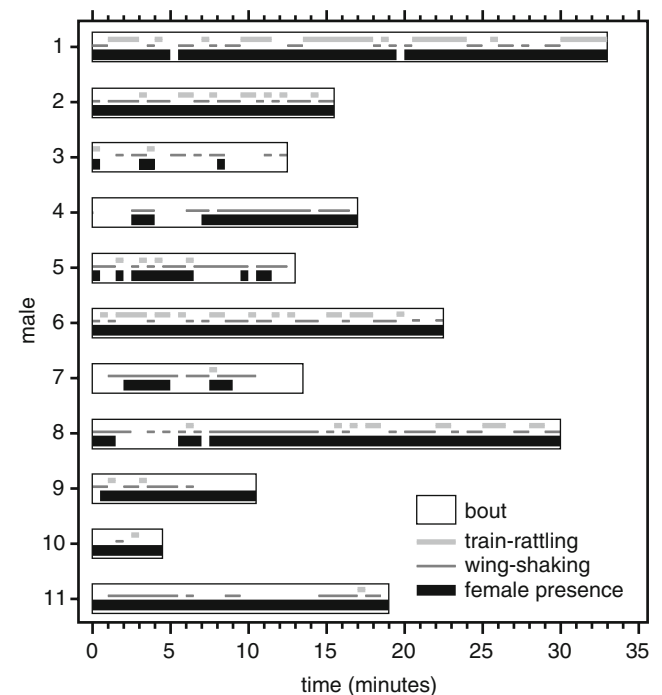
Fig. 2 Sequence of events over the longest bout recorded from each of 11 different males, based on point samples taken at 30-s intervals. Note that wing-shaking and train-rattling displays sometimes stopped briefly between point samples, even though they are illustrated here as continuous

to control for the potential effect of female movement on male orientation and to determine how the patterns of male display behaviour observed under normal conditions were influenced by the positions of both the sun and the target female.

Materials and methods

Study species

Peafowl are native to the Indian subcontinent but began to be introduced to other parts of the world at least 12 centuries ago (Kannan and James 1998) and are now found in both captive and feral populations in parks, farms, zoos and estates worldwide. Almost all that is known about peafowl comes from studies conducted in these populations away from the ancestral habitats of these birds, but these 'captive' birds do exhibit behaviours similar to those of free-ranging birds in their natural habitats (Hillgarth 1984).

During the breeding season, sexually mature males gather at leks comprising one to 11 males, with individual males generally using the same display court throughout the breeding season (Yasmin and Yahya 1996; R. Dakin, personal observation). At our study sites, one to six males occupied the leks we sampled, with a median lek size of four males. Males displayed on their leks each day, mostly from 08:00 to 10:00 and 16:00–18:00 local times (see also Petrie et al. 1991). On a lek, each male occupied and defended a 2–3-m^2 display court where almost all displays and copulations occurred. Courts within a lek were 5–20 m apart, and all males on a lek could easily see one another.

In the presence of females, peacocks perform an elaborate courtship ritual involving calls and the presentation of the visual train ornament (Video 1 in the ESM), comprised of about 150 highly elongated upper-tail coverts, each with a single multi-coloured, iridescent eyespot. Darwin (1871) described the males "strutting about, with expanded and quivering tail-feathers" and mentioned that they also "rattle their quills together". Petrie et al. (1992) provided a more detailed description of the sequence of events during courtship: "when a female approaches a displaying male, he turns away [from her]… showing the rear surface of his train and his orange primaries which are moved vigorously up and down… if the female follows the male's turning movement, so that she appears in front of him, he turns to face her head-on and shivers his train." This sequence may be repeated a number of times, after which the male will usually attempt to mount the female (Petrie et al. 1992; R. Dakin, personal observations; Video 1 in ESM). The male is generally stationary during the train-rattling display but may take a few steps towards the target female.

Field sites

We observed peafowl at the Assiniboine Park Zoo (Manitoba, Canada; APZ, 50 ha) in May 2007, at the Los Angeles Arboretum (California, USA; LAA, 50 ha) in March–April 2008 and at the Bronx Zoo (New York, USA; BZ, 100 ha) in May 2008. APZ has a population of approximately 60 peafowl that range freely over the zoo's parklands from April to October and are kept in large indoor enclosures during the winter months. LAA and BZ are each inhabited by feral populations of >100 peafowl that range throughout the park grounds and surrounding habitats year-round. Birds at all sites were observed on their display courts during their respective peak lekking seasons: March at LAA; May–June at APZ and BZ.

Male display orientation

We studied the behaviour of 11 displaying peacocks during the morning (07:00–12:00 local times) and late afternoon (15:00–19:00) at both APZ (five males in two leks) and LAA (six males in four leks) on days when the sky was clear enough for shadows to be visible on the ground and thus when the position of the sun could be clearly discerned. For many of the display bouts observed, however, male display courts were in full shade such that the sun was not directly visible and no shadows were cast (see "Results" for details).

We identified males mainly by numbered leg bands or unique morphological features, but in a few cases by the location of a display court maintained by a particular male—peacocks almost always maintain a single display court throughout the breeding season (unpublished data). We observed individual males from 5–10 m away, as this appeared not to interfere in any way with their behaviour.

We observed display bouts by walking between lek sites and sampling any males that were displaying their erect trains. For each bout, we recorded the time and the identity of the male, as well as the following variables at 30-s intervals: display behaviour with train erect (none, wing-shake, train-rattle), any movement (walking forwards, backwards, to the left or right, turning), whether there were any females in sight and the location of any target female to whom the male was clearly displaying. The location of a target female was recorded as being in one of the six 60° sectors around the male (Fig. 3a). At each 30-s interval, we also measured the bearing (to the nearest 10°) of the displaying male as the compass bearing (relative to true north) of the axis through the male's body perpendicular to the horizontal axis of the erect train (Fig. 3b). All compass bearings taken in the field were corrected for magnetic declination (National Geophysical Data Center 2008).

(a)

(b)
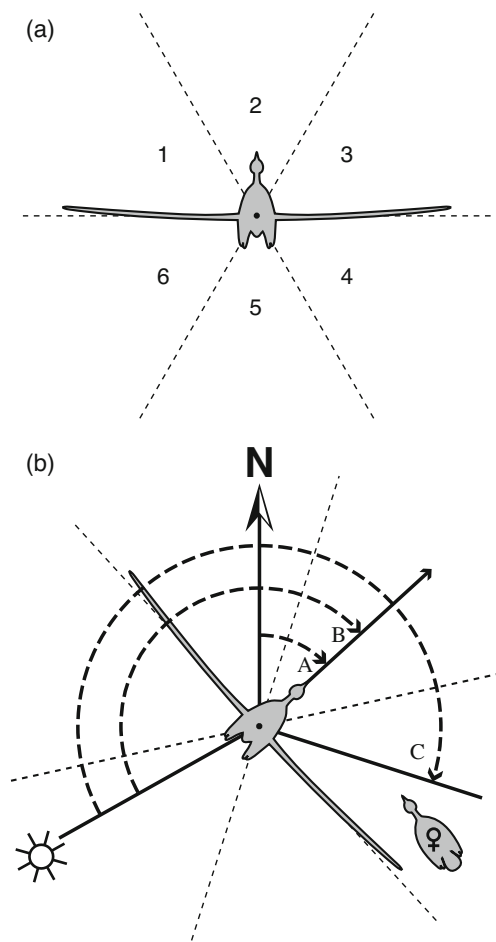
Fig. 3 **a** Diagram from above showing a displaying peacock with the 60° sectors used to identify the position of the female relative to the male. **b** Angles of interest: *A*=male bearing, *B*=sun–male angle, *C*= sun–female angle

At each 30-s interval during a display bout, we determined the local sun azimuth using a solar angle calculator that takes into account the date, time, latitude and longitude (Gronbeck 2005). Using the sun azimuth, the location of the target female and the bearing of the displaying male (angle A in Fig. 3b), we then calculated the following angles of interest for further analysis: (1) sun–male angle, as the clockwise angle between the sun's azimuth and the bearing of the displaying male (angle B in Fig. 3b) and (2) sun–female angle, as the clockwise angle between the sun's azimuth and the position of the female relative to the male (angle C in Fig. 3b), using the median angle for each of the six female position sectors (i.e. 300°, 0°, 60°, 120°, 180° or 240° for sectors 1–6, respectively, in Fig. 3a).

In total, we collected display data from 882 point samples (at 30-s intervals) for 58 display bouts of 11 males. On average, we measured 16 point samples (range 3–66) per display bout and five display bouts (range 2–10) per male. We analysed circular data according to Zar

(1999), where $\bar{a}$ is the mean angle and VL (vector length) is the length of the mean vector of a sample of angles. VL is a measure of angular dispersion that ranges from 0 (highly dispersed, adirectional sample) to 1 (highly directional such that all measured angles are the same). For each of the angles A, B and C in Fig. 3b, we calculated both a mean angle and a vector length using the following procedures to minimize pseudoreplication: first, we calculated $\bar{a}$ and mean VL for each bout using the procedure for first-order means (Zar 1999, pp 599–600). We then calculated $\bar{a}$ and mean VL for each individual male using a parametric second-order analysis (Zar 1999). Finally, we performed a grand mean analysis across males, using a further parametric second-order analysis on the mean male values and testing for directionality using the Hotelling procedure for second-order samples (Zar 1999, pp 638–639). This analysis tests whether the distribution of angles in the second-order sample differs significantly from uniform; if it does not differ from a uniform distribution, then the 95% confidence interval encompasses the circle and there is no mean angle, $\bar{a}$. We also used the two-sample Hotelling test to compare grand mean angles (Zar 1999, pp 641–642).

Model presentation experiment

To control for the effects of female movement on male orientation, we conducted experiments at LAA and BZ in 2008, presenting males with a taxidermically mounted peahen in four different contexts, varying both the time of day and the position of the model female. Trials were run in the morning or the afternoon (AM or PM) with the model female facing the male on either the EAST or WEST side of his body and thus on the sunny or shaded side of his erect train depending upon the time of day. Preliminary trials indicated that males did not respond to the model if their trains were not already erect. Thus, we selected males with erect trains as they were encountered and randomly chose the initial side (EAST or WEST) on which to place the model. Subsequent trials for each male were run at different time–side combinations, for a total of 33 trials with 17 different males (see ESM for details).

All model presentation trials were conducted with males that were displaying their erect trains (but not wing-shaking or train-rattling) with no live females in view. The model female was placed about 2 m from the displaying male, and we observed his response from 5–10 m to the north or south. Trials were started when the male began to display in a way that was clearly directed towards the model female (usually <30 s after the model was set up). Male courtship was considered to be directed towards the model when males began to perform either the wing-shaking or train-rattling display and moved towards the model. Each trial was run for 5 min.

During each model presentation trial, we recorded data at 30-s intervals as described above. Any trials where the male did not respond to the model within 2 min by wing-shaking or train-rattling were terminated and discarded. Trials were also terminated prematurely if males attempted to copulate with the model ($n=8$ trials), when male display behaviour was no longer directed towards the model due to the arrival of additional females ($n=5$ trials) or when males lost interest in the model and stopped displaying or moved away ($n=5$ trials). We have no reason to expect that the male behaviour prior to the premature termination of a trial was unusual in these cases, so we include all of these trials in our analyses.

We analysed male responses during model presentation trials in two ways. First, to quantify the type of display (wing-shaking or train-rattling) initially performed in response to the model, we used only the first point sample from each trial. In all cases where the male displayed continuously for the first 30 s of the trial, he performed only one of these two display behaviours, so this first point sample is a good measure of his initial, sustained response to the model. To avoid pseudoreplication in this analysis, we analysed data only from the first experimental trial performed with each individual male. Second, to examine the overall directionality of the display response, we calculated first-order mean angles for each trial and then calculated a parametric second-order mean if more than one trial type had been conducted with a given male in the same time period (AM or PM) or for the same model placement (EAST or WEST), and we used an additional parametric second-order analysis to test for directionality across individuals, as described above (Zar 1999).

Results

Peacock displays

Feral peacocks spend 10–15% of their daytime time budget displaying their erect trains during the breeding season (Fig. 1; see also Walther 2003), and most of this activity occurs during the morning and late afternoon (Petrie et al. 1991; Walther 2003; R. Dakin, personal observations). When females are present, the wing-shaking display often precedes the train-rattling display (Video 1 in the ESM), and the train-rattling display always precedes copulation, though the sequence of events during courtship can be somewhat variable (Fig. 2; contra Petrie et al. 1992).

Although we rarely recorded complete display bouts, this sampling method does not appear to have biassed our results, since male behaviours (e.g. Fig. 2) and female locations did not vary systematically during a display. For example, for the longest recorded bout from each male
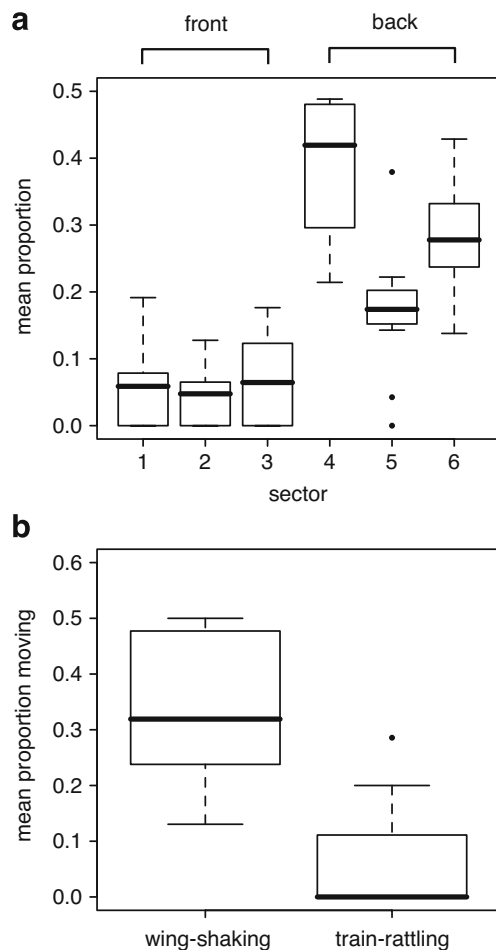
studied ($n=11$), the relation between bout length and the proportion of point samples with females present was not significant (Pearson correlation, $r=0.27$, $p=0.42$) nor was the relation between bout length and the proportion of samples where males were performing the wing-shaking display ($r=0.14$, $p=0.68$). There was a significant positive relation between bout length and the proportion of samples during which males were performing the train-rattling display ($r=0.63$, $p=0.04$), but this is not surprising given that this display is relatively infrequently performed. There was also no significant difference between the number of point samples of each display type observed in the first or second half of the observation period (paired t-tests: wing-shaking, $t=0.91$, $p=0.38$; train-rattling, $t=0.48$, $p=0.64$, $n=11$). Finally, the relation between bout length and the vector length for the mean male bearing was not significant ($r=0.17$, $p=0.62$, $n=11$).

Female position during displays

When males performed the wing-shaking display, females were generally standing behind them in sectors 4–6 (Fig. 4a; mean=83% of point samples per male, range=53–100%, $n=11$ males). This mean percentage is significantly greater than 50% (one sample t-test, $t=8.8$, $p<0.0001$, $n=11$ males). In fact, females were most often in sectors 4 and 6 and rarely in sector 5 when they were standing behind the male as he performed this wing-shaking display. In contrast, males performed the train-rattling display almost exclusively when females were standing directly in front (mean=98.6% of point samples per male, range=90–100%). Males often moved or turned during the wing-shaking display when females were present (mean=37% of point samples per male, range=0–86%), but they generally did not move during the train-rattling display (moving in mean=6% of point samples per male, range=0–30%). On average, males were significantly more likely to move or turn during wing-shaking compared to train-rattling, pooling across bouts for each male (Fig. 4b; paired t-test, $t=3.9$, $p=0.004$, $n=10$ males).

Male orientation during displays

Although male displays were observed only on sunny days, many of the male display courts were in full shade during our observation periods. Despite this, there were no significant differences between sun and shade in sun–male angles (angle B in Fig. 3b) for either the wing-shaking (two-sample Hotelling test, $F=1.63$, $p=0.24$, $n=7$ males in sun, 8 males in shade) or train-rattling displays ($F=0.76$, $p=0.50$, $n=4$, 7) nor for sun–female angles (angle C in Fig. 3b) in sun or shade for either the wing-shaking ($F=1.54$, $p=0.25$, $n=7$, 8) or train-rattling displays ($F=0.62$,
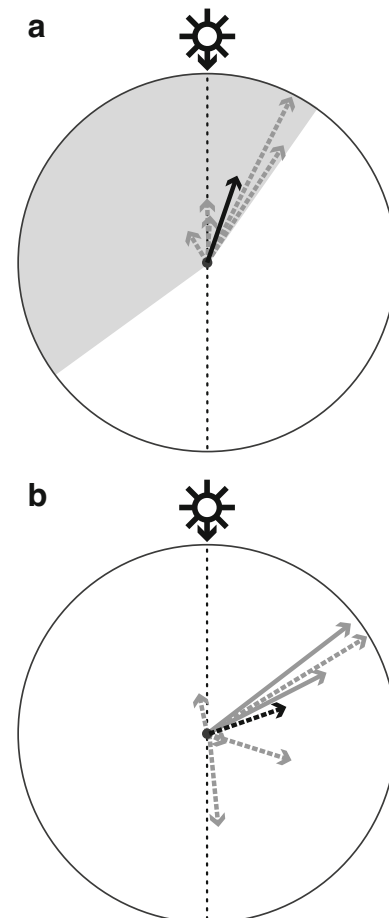
absence of females, the direction that males with their trains erect faced on shaded courts was not significantly directional (Fig. 5b; $\bar{a}=70.8°$, VL=0.41, $p=0.08$, $n=7$). Nonetheless, the difference between mean sun–male angles in sun and shade was significant ($F=8.19$, $p=0.01$, $n=5$, 7), with males facing more directly towards the sun when they displayed on sunlit courts.

When males had their trains erect and performed the wing-shaking display while females were present, the grand mean sun–male angle was not significantly directional (Fig. 6a; VL=0.18, $p=0.21$, $n=11$ males), though the mean sun–male angle (B) was fairly consistent for each male (mean male VL=0.35±0.17 SD, 95% CI=0.24–0.47, $n=11$), and seven of 11 males were significantly directional (Fig. 6a). The grand mean sun–female angle (C) was also not significantly directional during the wing-shaking display (Fig. 6c; VL=0.15, $p=0.40$, $n=11$), but mean sun–female angles were significantly directional for six of

Fig. 4 Tukey *box plots* showing **a** the proportion of point samples where target females were positioned in each of the 60° sectors around the male (see Fig. 3a) during wing-shaking displays and **b** the proportion of point samples where males moved or turned during the wing-shaking and train-rattling displays. Data were pooled over all display bouts for each of 11 males, taking a mean for each male, so that each box plot shows the distribution of the 11 male mean proportions

$p=0.56$, $n=4$, 7). Thus, for these display situations, we pooled data from displays in both sun and shade for subsequent analyses.

When males had their train erect and females were not present, males performed the wing-shaking display on average 34% (range 0–100%) of the time, pooling across bouts for each male ($n=10$ males; one male was never observed without a female present). When they were not performing this display, they simply stood or walked about. For males with their trains erect on sunlit courts when females were absent, the grand mean sun–male angle (angle B) was significantly directional when males had their trains erect (Fig. 5a; second-order Hotelling procedure, VL=0.46, $p=0.02$, $n=5$) and the grand mean angle ($\bar{a}=19.3°$, 95% CI=234–35°) was not significantly different from 0° (i.e. males were facing generally towards the sun). In the

Fig. 5 Sun–male angles when females were absent ($n=10$ males), for displays on: **a** sunlit courts and **b** shaded courts. *Grey vectors* are the means for each male, and the *black vector* is the grand mean across all males. Mean vectors are drawn as *solid lines* when samples are significantly non-random. The 95% confidence interval (*shaded*) is shown for the grand mean. The outer circle has a radius of VL=1

Fig. 6 Sun–male (**a**, **b**) and sun–female (**c**, **d**) angles during **a**, **c** wing-shaking (*n*=11) and **b**, **d** train-rattling (*n*=10) displays. See Fig. 5 for description of vectors
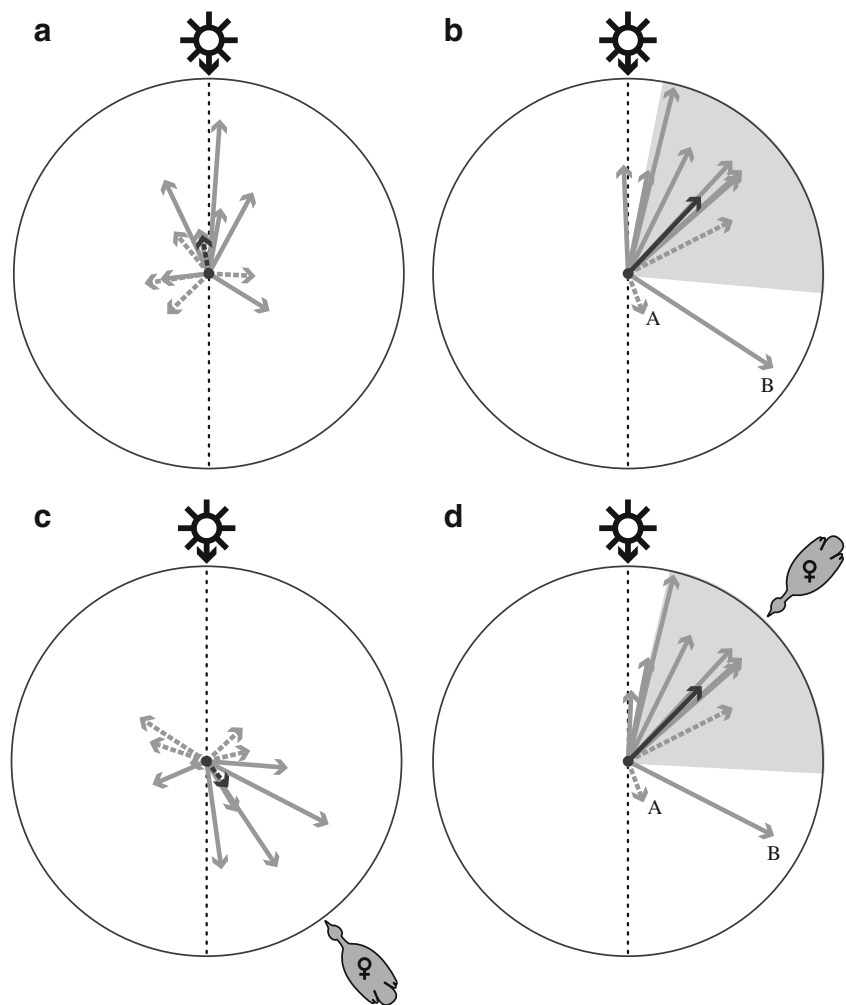
the 11 males. It is noteworthy that females were on average located on the shaded side of the male (i.e. away from the sun) for all of these significant means (Fig. 6c).

In contrast, during the train-rattling display, the grand mean sun–male angle (B) was highly directional (Fig. 6b, VL=0.52, *p*=0.001, *n*=10 as one male was not observed train-rattling). In this context, males faced generally towards the sun, though the grand mean sun–male angle ($\bar{a}$=43°) was significantly different from 0° (95% CI=11–95°). The mean sun–male angle (B) during the train-rattling display was also consistent within males (mean male VL= 0.67, 95% CI=0.51–0.83, *n*=10), with eight of ten individual mean sun–male angles significant (Fig. 6b). Results are nearly identical for the grand mean sun–female angle (C) in this context (Fig. 6d; VL=0.52, *p*=0.002, *n*= 10 males), with a grand mean angle of 44° (95% CI=13– 93°), because females were almost always in sector 2 during this display. Thus, during the train-rattling display, males were on average facing towards the sun at about 45° to the right of the sun azimuth, and the female was almost always standing directly in front of the male.

The two individuals who deviated most from this pattern during train-rattling displays had the largest sun–male angles ($\bar{a}$=123° and 159°, VL=0.87 and 0.20, males A and B, respectively, in Fig. 6b). Both of these individuals maintained display courts that were completely shaded during our observations. Removing these two individuals does not change the results for sun–male angle (VL=0.66, *p*=0.0001, *n*=8); the grand mean sun–male angle (B) without these two males shifts to 32°, but it is still significantly different from 0° (95% CI=6–186°). Similarly, the grand mean sun–female angle (C) does not change substantially when excluding these two males (VL=0.64, *p*= 0.0005, *n*=8, mean=33°, 95% CI=8–58°). Like the other eight males, these two oriented their displays with the sun on their left and the female directly in front.

Model presentation experiment

The type of display initially performed by a male after he was presented with the female model (Table 1) did not significantly depend upon either the time of day (AM vs.

Table 1 Initial display responses of males to a model female presented in different experimental contexts: morning or afternoon and on the east or west side of the male. For AM-EAST and PM-WEST trials, the model was on the sunlit side of the male's erect train; for AM-WEST and PM-EAST trials, she was on the shaded side

Experimental context (n)	Male display	
	Wing-shaking	Train-rattling
Time of day		
AM (10)	6	4
PM (7)	6	1
Model location (compass)		
EAST (10)	6	4
WEST (7)	6	1
Model location (sun)		
Sunlit side (9)	4	5
Shaded side (8)	8	0

PM; Fisher exact test, $p=0.34$) or the location of the model (EAST vs. WEST; $p=0.34$). Instead, the type of display performed depended upon the position of the model relative to the sun. Males were initially more likely to perform the train-rattling display when the model was presented on the sunny side of their erect trains (i.e. EAST in the AM and WEST in the PM trials) and were significantly more likely to perform the wing-shaking display when the model was presented on their shaded side (Fisher exact test, $p=0.03$). As when courting live females, males usually (10/12 trials) positioned themselves with the model female behind their erect train when they performed the wing-shaking display and with the female directly in front for the train-rattling display (all five trials where they performed this display).

The grand mean male compass bearing (angle A in Fig. 3b) was not significantly directional when pooling EAST and WEST trials but was significantly directional (or nearly so) when pooling trials by time of day (Table 2). The grand mean

sun–male angle (B) tended to be significantly directional regardless of the trial context and did not differ significantly from 0° (i.e. facing directly towards the sun; Table 2).

Comparisons of grand mean angles between different trial types also indicate that the position of the sun, rather than the model female, determined male display orientation. Using data only from the first trial performed with each individual (to avoid pseudoreplication), the grand mean male compass bearing (A) was significantly different between AM and PM trials (parametric two-sample second-order test, $F=11.9$, $p=0.0009$, $n=10$, 7 males) but not between EAST and WEST trials ($F=0.5$, $p=0.64$, $n=10$, 7). There was no significant difference between grand mean sun–male angles (A) when comparing either AM and PM ($F=0.5$, $p=0.61$, $n=10$, 7) or EAST and WEST trials ($F=0.4$, $p=0.66$, $n=10$, 7).

Discussion

Our observational and experimental results demonstrate that the direction that peacocks face during their pre-copulatory courtship display is influenced by the position of the sun. The train-rattling display was significantly directional, with males oriented at about 45° to the right of the sun azimuth, on average, and with the target female almost always positioned directly in front of the male's erect train (Fig. 6b, d). Moreover, these angles were the same whether or not the male displayed in sun or shade. This finding is remarkable for three reasons. First, it strongly suggests that the males' iridescent plumage colours are an important component of courtship signalling and female choice (see also Loyau et al. 2007a). Thus, although the number of eyespots on the male's train may not influence female choice in some populations (Dakin and Montgomerie unpublished data; Takahashi et al. 2008), the colour of those eyespots or other male colours appear to be important

Table 2 Directionality of male display responses to a model female by experimental context. For male bearing, 0° refers to true north; whereas for sun–male angle (B in Fig. 3b), 0° refers to the sun azimuth. (Statistics are for parametric second-order tests of directionality for circular data; samples that are significantly directional are in italics)

Experimental context (n)	Mean angle				
	VL	F	p	$\bar{a}$	95% CI
Male bearing					
AM (12)	0.33	3.0	0.10	99.7°	
PM (9)	*0.61*	*26.8*	*0.0005*	*277.2°*	*236–321°*
EAST (14)	0.19	0.9	0.44		
WEST (13)	0.08	0.1	0.91		
Sun–male angle					
AM (12)	0.34	3.1	0.09	357.4°	
PM (9)	*0.59*	*20.7*	*0.001*	*5.8°*	*321–54°*
EAST (14)	*0.36*	*4.4*	*0.04*	*16.1°*	*318–101°*
WEST (13)	*0.53*	*12.6*	*0.001*	*358.6°*	*324–42°*

sexual signals. Second, our results suggest that males either use the plane of polarization or their previous experience to locate the position of the sun as it changes through the day. There is some evidence that birds can detect the e-vector of polarized light (Able 1982), and this would be visible as long as the birds could see open sky. Males clearly knew where the sun was, and they attempted either to move themselves or to manipulate the target females (live and experimental) so that the target female was on the sunny side of their erect train, whether or not they displayed in the full sun. Finally, we found that the males consistently oriented their erect trains in such a way that the sun was always on the male's left side. The reasons for the consistency of this sun–male angle are unknown and will require further study, but the lateralization of courtship behaviour may also be important in maximizing signal efficacy.

Males usually performed the wing-shaking display while facing away from females (Fig. 4a) and, as a result, their conspicuously moving, orange-coloured wings could serve to attract female attention. Males may use the wing-shaking display to corral target females into a position on the sunny side of their erect train for subsequent train-rattling displays. This hypothesis is strongly supported by our model presentation trials—by controlling female movement, this experiment demonstrates that males will generally perform the wing-shaking display when the female is positioned on the shaded side of their erect train, versus always train-rattling when the female is positioned on the sunny side (Table 1). Thus, the directionality of the train-rattling display that we observed under natural conditions is clearly due to male behaviour and not simply to peahens attempting to view the males' trains from the sunny side, although it is possible that females also prefer to do this.

While there was no overall consistency across males in the orientation of their wing-shaking displays, the majority of individual males did show significant directionality during this display (Fig. 6a). Male display courts varied in the size and location of sheltering features and in their location relative to preferred female foraging and resting sites and thus high female traffic (unpublished data). As a consequence, the most common direction of approach for females, and thus the direction males faced when attempting to attract new visitors, varied among males.

While we have focused this study on the analysis of peacock displays on sunny days, peacocks will certainly display on overcast days (unpublished data). Hamilton (1965) reported that, on cloudy days, the directionality normally seen in Anna's hummingbird dives was no longer apparent, and this might be expected in peacocks. It would be an interesting natural experiment to compare the patterns of male display behaviour and directionality on clear days with those of overcast days when light is diffuse. It would

also be interesting to compare male display behaviour in different peafowl populations worldwide, since birds in North American populations experience different light environments and lek in different habitats than those in India and Southeast Asia. Nonetheless, our comparison of sunlit and shaded courts suggests that males know the position of the sun at different times of day and orient their displays accordingly, and they should be able to do this anywhere in the world.

If orientation towards the sun is important for male signal efficacy, why do some peacocks choose shaded display courts? Display court selection most likely involves a number of factors, including proximity to food sources where females congregate (Loyau et al. 2007b), proximity to closely related males (Petrie et al. 1999), distance from agonistic males and predators, and shelter from the wind. For example, one male in this study maintained a display court directly to the west of a tall building and thus his court was completely shaded throughout the morning. Nevertheless, he received a high rate of female visitation apparently because his territory was adjacent to a popular dust-bathing site that attracted many females, consistent with the hot-spot theory of lek formation (Bradbury and Gibson 1983). Display court selection is no doubt complex, and presumably it would not be advantageous for males to choose a well-lit territory in an area that would receive no visitors or for males to forego display during periods of shade or cloud.

Of the train-rattling display, Darwin (1871) said that "peacocks and birds of paradise rattle their quills together, and the vibratory movement apparently serves merely to make a noise, for it can hardly add to the beauty of their plumage". However, we believe these rapid feather movements might help to display the feathers' iridescence. Preliminary evidence suggests that the iridescent eyespot coloration of the peacock's train is important for mate choice (Loyau et al. 2007a; Dakin and Montgomerie, unpublished data) and may be an honest signal of male quality.

The benefit to males of orienting at such a consistent angle relative to the sun is not yet clear. One possibility is that it improves the efficacy of the colour signal from their train, allowing females to discriminate more easily among individual males and to more accurately assess male quality. Perhaps a 45° sun–male angle minimizes specular reflectance from the eyespots or produces a particular iridescent effect or hue that females prefer. None of these explanations, however, help us to understand why males were usually oriented to the right of the sun during train-rattling displays (Fig. 6b). Laterality in courtship displays (Snow 1961; Workman and Andrew 1986) and copulation behaviour (Ventolini et al. 2005) has been documented in several other bird species, and in bird song is thought to be

due to the laterality of avian brain function (Nottebohm 1971). Interestingly, all of the phylogenetically closest relatives of peafowl (genus *Polyplectron* and the argus pheasants *Argusianus argus* and *Rheinartia ocellata*) display their fan-like ornamental tail plumage in a lateral posture, where males present only one side of their body to visiting females (Kimball et al. 2001). Although peafowl do not use this side-on posture, there may be strong lateralization for courtship function throughout the clade.

While there is still much to be learned about the complex displays and ornaments of peacocks, our study strongly, albeit circumstantially, argues against the notion that the male train is not an important signal to females, as Takahashi et al. (2008) contend. It seems to us unlikely that the complex male displays that we describe here would be maintained with such precision if they did not influence female choice. That the males appear to be orienting their trains to influence the efficacy of their colour signals further reinforces the evidence that the train ornament and the iridescent colours of the eyespots (e.g., Loyau et al. 2007a) are products of sexual selection that females attend to when choosing a mate.

References

Able KP (1982) Skylight polarization patterns at dusk influence migratory orientation in birds. Nature 299:550–551

Anonymous (2008) Peahens do not prefer peacocks with the best tails. New Scientist 197:16

Bradbury JW, Gibson RM (1983) Leks and mate choice. In: Bateson P (ed) Mate choice. Cambridge University Press, Cambridge, UK, pp 109–133

Darwin C (1871) The descent of man, and selection in relation to sex, 1st edn. John Murray, London, UK

Endler JA, Théry M (1996) Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. American Naturalist 148:421–452

Gronbeck C (2005) SunAngle. http://susdesign.com/sunangle/. Accessed May 2008

Hamilton WJ (1965) Sun-oriented display of the Anna's hummingbird. Wilson Bulletin 77:38–44

Heindl M, Winkler H (2003) Vertical lek placement of forest-dwelling manakin species (Aves, Pipridae) is associated with vertical gradients of ambient light. Biological Journal of the Linnean Society 80:647–658

Henwood K, Fabrick A (1979) A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. American Naturalist 114:260–274

Hillgarth N (1984) Social organization of wild peafowl in India. Journal of the World Pheasant Association 9:47–56

Kannan R, James DA (1998) Common peafowl (*Pavo cristatus*). The Birds of North America Online. http://bna.birds.cornell.edu/bna/species/377. Accessed October 2008

Kimball RT, Braun EL, Ligon JD, Lucchini V, Randi E (2001) A molecular phylogeny of the peacock-pheasants (Galliformes: *Polyplectron* spp.) indicates loss and reduction of ornamental traits and display behaviours. Biological Journal of the Linnaean Society 73:187–198

Loyau A, Gomez D, Moureau B, Théry M, Hart NS, Saint Jalme M, Bennett ATD, Sorci G (2007a) Iridescent structurally based coloration of eyespots correlates with mating success in the peacock. Behavioral Ecology 18:1123–1131

Loyau A, Saint Jalme M, Sorci G (2007b) Non-defendable resources affect peafowl lek organization: a male removal experiment. Behavioral Processes 74:64–70

Loyau A, Saint Jalme M, Sorci G (2005) Intra- and intersexual selection for multiple traits in the peacock (*Pavo cristatus*). Ethology 111:810–820

Morell V (2008) Peacock feathers: that's so last year. ScienceNOW Daily News. http://sciencenow.sciencemag.org/cgi/content/full/2008/331/2. Accessed March 2008

National Geophysical Data Center (2008) Estimated value of magnetic declination. http://www.ngdc.noaa.gov/geomagmodels/struts/declZipE. Accessed June 2008

Nottebohm F (1971) Neural lateralization of vocal control in a passerine bird: I. Song. Journal of Experimental Zoology 177:229–262

Petrie M, Hall M, Halliday T, Budgey H, 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? Behavioral Ecology and Sociobiology 31:1–10

Petrie M, Halliday T (1994) Experimental and natural changes in the peacock's (*Pavo cristatus*) train can affect mating success. Behavioral Ecology and Sociobiology 35:213–217

Petrie M, Halliday T, Sanders C (1991) Peahens prefer peacocks with elaborate trains. Animal Behaviour 41:323–331

Petrie M, Krupa A, Burke T (1999) Peacocks lek with relatives even in the absence of social and environmental cues. Nature 401:155–157

Snow BK (1961) Notes on the behavior of three Cotingidae. Auk 78:150–161

Takahashi M, Arita H, Hiraiwa-Hasegawa M, Hasegawa T (2008) Peahens do not prefer peacocks with more elaborate trains. Animal Behaviour 75:1209–1219

Ventolini N, Ferrero EA, Sponza S, Chiesa AD, Zucca P, Vallortigara G (2005) Laterality in the wild: preferential hemifield use during predatory and sexual behaviour in the black-winged stilt. Animal Behaviour 69:1077–1084

Walther BA (2003) Do peacocks devote maintenance time to their ornamental plumage? Time budgets of male blue peafowl *Pavo cristatus*. Lundiana 4:149–154

Workman L, Andrew RJ (1986) Asymmetries of eye use in birds. Animal Behaviour 34:1582–1584

Yasmin S, Yahya HSA (1996) Correlates of mating success in Indian peafowl. Auk 113:490–492

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, Upper Saddle River, NJ