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## Articles

# Peahens prefer peacocks displaying more eyespots, but rarely

Roslyn Dakin\*, Robert Montgomerie

Department of Biology, Queen's University, Kingston

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Recent studies have reported conflicting evidence for the influence of train-feather eyespots on the mating success of peacocks, *Pavo cristatus*. In this study we address this controversy, using observation and experiment to evaluate the effect of train morphology and the number of eyespots displayed during courtship on female choice. We show first that the maximum number of eyespots in the train is consistent among adult peacocks in feral populations at about 165–170 eyespots, and that most of the observed variation in eyespot number appears to be due to feather breakage or loss. Although we confirm a previous report that removing a large number ( $\geq 20$ ) of the outermost eyespots from a male's train decreases his mating success compared to unmanipulated males, this experimental modification produces an ornament that is outside the range of eyespot number typically displayed during courtship. Thus, the considerable variation in the mating success of feral peacocks cannot be explained by natural variation in the number of eyespots visible in the train. Peafowl mate choice is clearly more complex than previously thought: females may reject a few males with substantially reduced eyespot number, while using some other cue to choose among males with typical trains.

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The iridescent train of the lek-breeding peacock is an obvious visual display, long thought to be the result of sexual selection for increased ornament size and complexity (Darwin 1871). Studies of feral peafowl populations in the United Kingdom and France provide evidence that females prefer to mate with males that display a greater number of eyespots in their trains during courtship (Petrie et al. 1991; Petrie & Halliday 1994; Loyau et al. 2005a), lending support to Darwin's (1871) idea that elaboration of the train is the result of selection mediated by female mate preferences.

Manning (1989) was the first to use the number of eyespots displayed during courtship as a measure of ornamentation in peacocks. Based on a positive relation between male age and the number of eyespots visible in the train, he suggested that the number of displayed eyespots might honestly advertise male age. However, two subsequent studies found that the number of eyespots in the train does not reliably increase with male age (Petrie 1993; Takahashi et al. 2008), and that it often decreases (Petrie 1993).

Nevertheless, several lines of observational and experimental evidence indicate that eyespot number is an important cue for mate choice by peahens: (1) the number of eyespots visible in the train is correlated with the number of copulations a male achieves during

a breeding season (Petrie et al. 1991; Loyau et al. 2005a); (2) male copulation success declined precipitously when 20 of the outermost eyespots were removed experimentally (Petrie & Halliday 1994); (3) peahens biased the sex ratio of their offspring towards females when they were mated, experimentally, with males from which 20 eyespots were removed (Pike & Petrie 2005); and (4) female investment of resources into eggs increased with the number of eyespots visible on the train of her experimentally chosen mate (Loyau et al. 2007a). In addition, the rate of recovery from an immune challenge is correlated with eyespot number (Loyau et al. 2005b), suggesting that more ornamented males have better immune system genes, thus providing a potential adaptive explanation for female choice based on eyespot number.

Despite this evidence for female choice based on male eyespot number, a recent 7-year study of feral peafowl in Japan (Takahashi et al. 2008) failed to find a relation between mating success and the number of eyespots visible in the train, suggesting that peahens may not use eyespot number to assess mate quality, and calling into question Darwin's (1871) original theory about train elaboration in this species. The authors of the Japanese study suggested that 'the peacock's train is an obsolete signal for which female preference has already been lost or weakened' (Takahashi et al. 2008).

In the present study, we address these apparently conflicting results. We began by studying the geometric arrangement of train feathers and natural variation in the number of eyespots displayed during courtship in three feral peafowl populations in North America. We then evaluated the relation between train

\* Correspondence: R. Dakin, Department of Biology, Queen's University, Kingston, ON K7L 3N6, Canada.  
 E-mail address: [2rd@queensu.ca](mailto:2rd@queensu.ca) (R. Dakin).

morphology and peacock mating success by (1) repeating the *Petrie & Halliday (1994)* experiment, removing a large number of eyespots from the trains of some males and observing their subsequent mating success compared to control males, (2) examining the relations between measures of mating success and both the number of eyespots displayed and train length in our study populations, and (3) re-examining the general relation between the number of eyespots visible in the peacock's train and male mating success in all studies to date.

The full train of the adult peacock is a very complex ornament, comprising upper-tail coverts that have been modified into four specialized feather types (*Fig. 1*; *Sharma 1974*; *Manning 1989*): (1) the longest 'fish-tail' feathers delimit the upper edge of the raised train (*Manning 1989*); (2) the large 'major eyespot' feathers are distributed regularly throughout the central part of the erect train and form the majority of its feathers; and the lower edges of the erect train are delimited by (3) curved asymmetrical 'sword' feathers and (4) asymmetrical 'minor eyespot' feathers (*Sharma 1974*). Only feather types (3) and (4) have eyespots near their distal end. All four feather types are shed annually over an 8-week period from late August to early October, following the breeding season, and are regrown over the subsequent 6–8 months or more (*Sharma 1974*; R. Dakin, personal observations). Adult peacocks that moult in captivity have, at most, about 169 eyespot (major and minor) feathers (*Sharma 1974*). Males do not grow their full train until they are at least 3 years old (*Kannan & James 1998*); some subadult males grow a stunted and asymmetrical train with 5–40 eyespot feathers (R. Dakin, personal observations).

**METHODS**

*Field Methods*

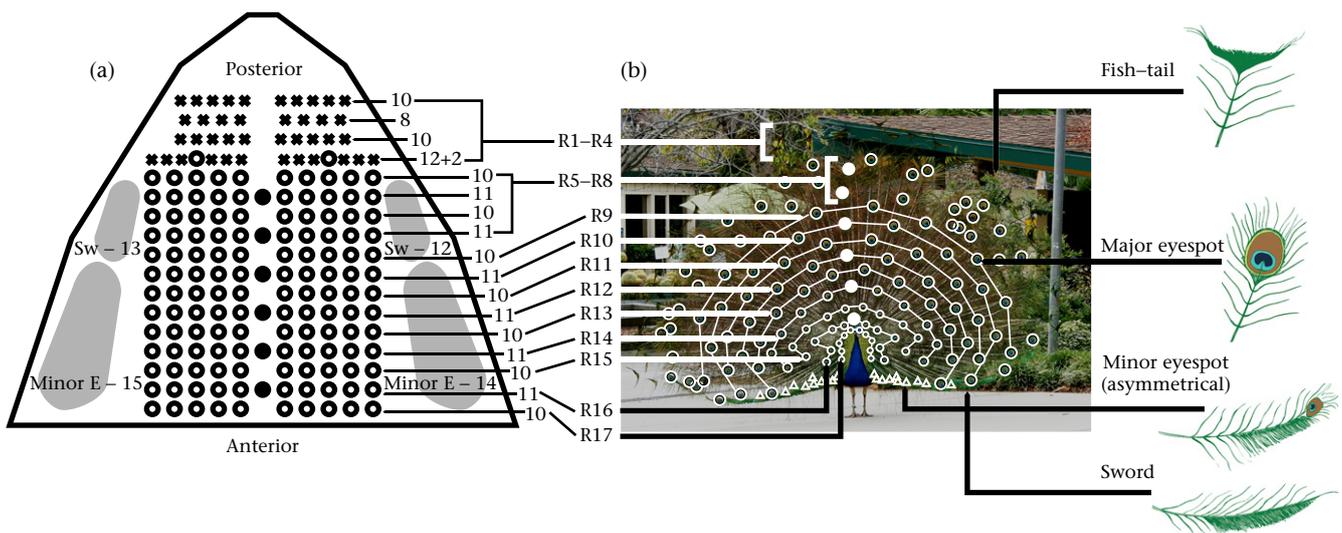
We studied the feral populations of peafowl at (1) Assiniboine Park Zoo (APZ) in Winnipeg, MB, Canada (April–May 2007), where about 60 peafowl range freely over 50 ha of pens and woodland, (2) Toronto Zoo (TZ) in Toronto, ON, Canada (April–June 2007), where about 30 peafowl are free-ranging over 250 ha of pens and

woodland, and (3) Los Angeles Arboretum (LAA) in Arcadia, CA, U.S.A. (February–April, 2008–2010), where more than 100 peafowl live in 50 ha of urban parklands and residential areas. The APZ and TZ populations are housed in large indoor pens during the coldest winter months (December–March), whereas the LAA birds are feral year-round. Peafowl in all three populations are wild-type, lek-breeding birds, and thus are expected to be similar to this species in the wild (*Hillgarth 1984*; *Harikrishnan et al. 2010*).

*Measurement of Train Morphology*

Males were caught prior to the start of the breeding season (April at APZ and TZ; January–March at LAA) and marked for individual identification with a numbered leg band. All males were caught by hand, either inside their winter enclosures at APZ and TZ, or when displaying on leks or visiting baited enclosures at LAA. At the time of this capture, we measured body mass ( $\pm 0.01$  kg), the lengths of the left and right tarsi ( $\pm 1$  mm) as a measure of body size, and the longest 'fish-tail' feather in the train ( $\pm 0.5$  cm) as a measure of train length (*Petrie et al. 1991*; *Loyau et al. 2005a*; see *Fig. 1* for feather terminology). To use residual mass as an index of body condition, we included both body mass and average tarsus length in general linear models. For a separate study of plumage colours, we initially removed five eyespots from each male captured before the breeding season at all of our study sites, by cutting the rachis immediately below the eyespot on the longest five major eyespot feathers on all males (*Fig. 1*). In addition, we also removed one of the shortest major eyespot feathers from each male captured in 2010 at LAA.

To quantify the number of eyespots actually visible in each male's train ornament when it was erect during the train display, we digitally photographed displaying males during the breeding season, 1–4 weeks after we had captured them and removed five to six eyespots for colour analysis. We call this 'displayed eyespot number' to distinguish it from the number of eyespots the male had before we removed any ('counted eyespot number' = displayed eyespot number + number of eyespots removed + number of eyespots shed during handling). Note that this 'counted eyespot



**Figure 1.** The peacock's train is composed of four specialized types of upper-tail coverts, shown to the right. (a) Diagram of feather insertion in the caudal feather tract of male PC72. The fish-tail and major eyespot feathers were arranged in a regular pattern of rows (R1–R17). Fish-tail feathers are marked with an 'x' and major eyespots with an 'o' (filled for feathers on the midline of the uropygium). Numbers on this diagram give the total number of feathers in each row. The sword ('Sw') and minor eyespot ('Minor E') feathers were grouped to the left and right sides of the rows of major eyespots, and are also labelled with the number of feathers removed. (b) Photograph of male PC72 with his train erect, with major eyespots marked with white circles corresponding to the size of each eyespot. Major eyespots in rows R9–R17 are joined together with white lines. For the remaining rows, major eyespots visible in the photograph are circled but could not be identified to row. Minor eyespots visible in the photograph are marked with white triangles.

number' is almost certainly slightly less than the total number of eyespot feathers grown by each male, as several eyespots are likely to be hidden on the photographs of displaying males (Fig. 1).

#### Natural Train Morphology and the Arrangement of Eyespots

To examine the structure of the peacock's train, we recaptured one male (PC72) at the end of the breeding season at LAA in 2010 and systematically removed all of his train feathers by cutting them close to the base of the rachis. We recorded where each feather was inserted in the caudal feather tract on top of the uropygium. This also allowed us to compare his 'counted eyespot number' with the total number of eyespot feathers in the train at the end of the breeding season.

#### Eyespot Removal Experiment

Following Petrie & Halliday (1994), we experimentally tested the effect of removing a large number of eyespots from the trains of males at APZ and TZ. On treatment males, we cut the rachis immediately below the eyespot on 20 of the longest major eyespot feathers on seven adult males (1 at TZ, 6 at APZ, including one male for which only 15 eyespots were removed, in error), in addition to the five eyespots removed from each of those males for colour analysis. We chose males for this treatment haphazardly, using the first males captured in their winter holding quarters during the annual inspection at each site. Control males (8 at APZ, 4 at TZ) were handled the same way, except that we removed only the five eyespot feathers for colour analysis. The seven treatment males had, on average, 22 fewer eyespots (mean  $\pm$  SE =  $127 \pm 2.5$ ) than the 12 control males ( $149 \pm 1.6$ ) when we photographed them during the breeding season.

To measure mating success, we observed male leks during the morning (0700–1200 hours local times) and early evening (1600–1800 hours) periods of lekking activity (Petrie et al. 1991; R. Dakin, personal observations). We watched one to four males at a time for 0.5–2.5 h per observation period, resulting in 195 h of lek observation (80 h at APZ, 115 h at TZ). We recorded the duration of each male's attendance at his display court, the duration of his train displays (i.e. train erect) and the number of his 'train-rattling' bouts (Dakin & Montgomerie 2009), copulation attempts ('hoot-dashes'; Petrie et al. 1991) and successful copulations (cloacal contact). We observed 238 copulation attempts, 40 of which resulted in successful copulations (34 at APZ, 6 at TZ).

During focal watches, we counted the number of females present at each lek at 5 min intervals and estimated the distance ( $\pm 1$  m) between each female and the closest male. We defined a female as a visitor when she was less than 5 m from a male with an erect train and not closer to any other adult male. We defined female visit rate as the number of 5 min intervals where a male had at least one female visitor present, divided by the number of 5 min intervals that the male was on the lek during our observation periods.

We attempted to distribute our focal male watches equally among the different lek sites within each population. Each focal male was observed on the lek for  $8.6 \pm 1.4$  h at APZ (range 1.0–16.2,  $N = 14$  males) and  $14.5 \pm 2.3$  h at TZ (range 9.3–22.3,  $N = 5$  males); variation within populations was due to differences in male attendance rather than a biased distribution of observation periods at leks. As a measure of male display rate, we divided the total time that a male spent with his train erect by the total time that he was observed on the lek. Not surprisingly, male display rate was highly correlated with female visit rate (Pearson correlation:  $r_{17} = 0.87$ ,  $P < 0.0001$ ), since the mere presence of females usually causes males to raise their trains (Takahashi et al. 2008; R. Dakin, personal

observations). To compare eyespot removal and control males, we calculated rates of train-rattling bouts, female visits, copulation attempts and successful copulations as measures of mating success for each male. Copulations occurred only after the train-rattling display, and males performed this display only when female visitors were close by, typically less than 3 m away (Dakin & Montgomerie 2009). Thus, the rate of train-rattling bouts should be correlated with female preference (Takahashi et al. 2008). Similarly, the rate of copulation attempts should be correlated with female preference because these generally occur after a female has been viewing a male at close range for an extended period (R. Dakin, personal observations).

Neither the morphology nor the behaviour of peacocks differed significantly between these two populations (Table 1, see Appendix Table A1 for descriptive statistics), so we pooled data from the two sites for analyses of the eyespot removal experiment. There were also no differences between the treatment and control males with respect to either train morphology prior to eyespot removal, or measures of body size and condition (Table 1, see Appendix Table A1 for descriptive statistics).

#### Train Morphology and Mating Success

To examine the effect of train morphology on mating success across the normal range of variation for feral peacocks, we analysed a larger data set that included observations from the LAA population over 3 years of study (2008–2010). To avoid including the same male sampled at LAA in different years, we first included in our data set all 11 males from 2010 when we made the most extensive focal male observations, followed by males studied in 2009 ( $N = 5$ ) and 2008 ( $N = 5$ ) respectively, that were not already in our sample.

As a measure of relative male mating success that could be compared across populations and previous studies (Petrie et al. 1991; Petrie & Halliday 1994; Loyau et al. 2005a), we standardized the number of copulations each male achieved within each population-year sample. Note that this is not a copulation rate, but because these birds are highly visible and the distribution of observations tends to be uniform across males in a given study population, this variable is highly correlated with copulation rate (e.g. this study, repeated measures ANOVA:  $b = 3.55$ ,  $F_{1,27.83} = 38.4$ ,  $N = 30$  measurements of 25 males,  $P < 0.0001$ ). Since copulation number is the usual measure in previous studies of this species, it is

**Table 1**

Comparisons of morphological and behavioural traits of male peacocks between populations (APZ:  $N = 14$ , TZ:  $N = 5$ ) used for the eyespot removal experiment, and between treatment ( $N = 7$ ) and control ( $N = 12$ ) males

	APZ vs TZ		Treatment vs control	
	Test statistic	<i>P</i>	Test statistic	<i>P</i>
<b>Morphology</b>				
Train length	1.17	0.26	1.02	0.32
Mean tarsus length	1.18	0.25	0.49	0.63
Body mass	1.15	0.26	0.95	0.35
Body condition (residual body mass)	0.52	0.61	1.15	0.27
<b>Behaviour</b>				
Display rate	0.18	0.86	2.01	0.06
Female visit rate	0.25	0.80	1.08	0.30
Rate of train-rattling bouts	0.35	0.73	<b>2.24</b>	<b>0.04</b>
Rate of copulation attempts	0.60*	0.55	<b>66*</b>	<b>0.047</b>
Copulation rate	0.67*	0.50	64.5*	0.053

All analyses are *t* tests, unless otherwise noted; significant differences are highlighted in bold. See Appendix for descriptive statistics.

\* Nonparametric Wilcoxon tests (*W*).

the only measure available for comparing males within and among populations.

*Statistical Analysis*

For general linear models we included male identity as a random effect (repeated measures ANOVA) and report the partial regression coefficient (*b*) for the effect of interest. All means are presented ± SE; for repeated measures we report least squares means (LSM), but we show the range from the raw data. We used JMP 8.0.2 or R 2.12.0 (R Development Core Team 2010) for all analyses.

*Ethical Note*

The methods used in this study were approved by the Queen's University Animal Care Committee (Animal Utilization Protocols Montgomerie-2005-044-Or and Montgomerie-2009-006-Or), as well as by the animal care and research committees of the Assiniboine Park Zoo, Toronto Zoo and Los Angeles Arboretum. We attempted to minimize handling time for all captured birds. All procedures and manipulations used herein resulted in no injury to the animals and have been performed with this species in previous studies.

**RESULTS**

*Train Length*

The train lengths of males measured in our study populations ranged from 104 to 153 cm (LSM 132 ± 2.1 cm, *N* = 54 measurements, 38 males), similar to the range reported in other studies (means 116–157 cm; Table 2). Train length is often measured

before the breeding season, during the period when feathers are still growing, so this accounts for some of the observed variation both within and between populations. LAA males, for example, were captured for train measurements in February before train plumage growth was complete, and thus had significantly shorter trains (LSM 121 ± 1.6 cm, *N* = 19 males) than those at APZ and TZ (144 ± 2.3, *N* = 14 and 140 ± 3.8 cm, *N* = 5, respectively; repeated measures ANOVA:  $F_{2,46.6} = 39.9, P < 0.001$ ; Tukey–Kramer HSD:  $P < 0.05$ ), which we measured in April. As a result, our pooled data across all three populations showed a significant positive relation between train length and measurement date (repeated measures ANOVA:  $b = 0.44, F_{1,42.8} = 83.2, N = 38$  males,  $P < 0.0001$ ), so we controlled for measurement date in subsequent analyses that included train length.

*Eyespot Number*

To calculate the total number of eyespots on the train of each male in our study populations at the start of the breeding season (counted eyespot number), we added the number of feathers we removed when we first captured the male to the number of eyespots on the erect train (displayed eyespot number) on our photographs of males taken up to 49 days later (24.7 ± 1.5, *N* = 54 measurements of 38 males). The counted number of eyespots of males in our study populations ranged from 139 to 167 (LSM 155 ± 0.9, *N* = 54 counts of 38 males), similar to the total number of eyespots reported for other feral populations (mean of means = 149 for 16 feral populations, range 144–160; Table 2).

To assess potential sources of variation in total eyespot number, we examined the effects of photograph date, male body condition and the length of the train. Petrie et al. (1996) suggested that body condition might be an important factor influencing eyespot number. If a male's eyespot number is also influenced by the degree

**Table 2**  
Studies quantifying the number of eyespot feathers in trains of adult peacocks

Source	Details*	Number of eyespots			Main findings	Mean±SE train length (cm) (range)
		<i>N</i>	Mean±SE (range)	% Sample <144†		
Sharma 1974	T, O, C	NA	169	–	Description of train feather moult	
Manning 1989	T/D, O, C	16	142±3.7 (110–161)	50	Eyespot no. increases with age	
Manning & Hartley 1991	D, O, F	17	146±3.4 (117–167)	35	Symmetry of train increases with eyespot no.	
Petrie et al. 1991	D, O, F	10	151±2.1 (141–161)	20	Number of copulations obtained increases with eyespot no.	116.0±3.6
Petrie 1992	D, O, F	17	153	NA	Probability of predation negatively related to eyespot no.	
Petrie & Williams 1993	T, E, F	8	144±4.3	NA	Female egg production not related to eyespot no.	134.7±3.2
Petrie & Halliday 1994	D, E, F	24‡	146±2.0 (123–167)	42	Removal of 20 eyespots decreases number of copulations obtained relative to previous year	
Petrie et al. 1996	T, O, F	17	160±2.3 (143–177)	6	Eyespot no. is not related to body mass or muscle size	139.0±1.6 (125–149)
Loyau et al. 2005a	D, O, F	28	144±2.3 (105–162)	32	Number copulations obtained increases with eyespot no.	
Loyau et al. 2005b	D, O, F	24	152±1.4 (137–162)	13	Immunological recovery faster with greater eyespot no.	
Pike & Petrie 2005	T, E, C	21	158±2.4	NA	Offspring sex ratio biased towards females when hens are mated to peacocks with 20 eyespots removed	
Loyau et al. 2007a	D, E, F	24	154±1.0 (146–163)	0	Female egg investment increases with mate's eyespot no.	
Petrie et al. 2009	D, O, C	6	139±3.2	NA	Eyespot no. not significantly heritable	
Takahashi et al. 2008	D, O, F 1995	20	150±1.9 (127–164)	NA	Number copulations obtained not related to eyespot no.	
	D, O, F 1996	20	146±2.1 (118–159)	NA		
	D, O, F 1997	20	150±1.2 (139–158)	NA		156.9±1.5 (149.2–170.0)
	D, O, F 1998	30	147±1.1 (127–157)	NA		
	D, O, F 1999	36	148±0.9 (139–158)	NA		152.0±2.5 (138.5–163.0)
	D, O, F 2000	37	149±1.3 (125–159)	NA		154.8±3.8 (137.4–168.5)
	D, O, F 2001	37	151±0.8 (140–160)	NA		
This study	T/D, O/E, F	42	155±0.9 (139–167)	5	Mating success not related to displayed eyespot no. Removal of 20 eyespots decreases mating success	

For each study, we summarize the main statistically significant findings relevant to variation in eyespot number.

\* D: displayed eyespot number; T: total eyespot number removed and/or shed; O: observational; E: experimental; C: captive or farm-bred birds, F: free-ranging feral populations.

† Percentage of the sample that had fewer than 144 eyespots in the train. NA indicates that the relevant data were not available and could not be extracted from a figure.

‡ Data extracted from their Figure 2.

to which his train feathers have grown in, one might predict a positive relation between train length and eyespot number, so we examined this factor as well.

There was a significant negative relation between counted eyespot number and the date the males were photographed (repeated measures ANOVA, controlling for population and the interaction between date and population:  $b = -0.97$ ,  $F_{1,38,2} = 5.46$ ,  $P = 0.025$ ; Fig. 2). This pattern shows that eyespots are lost slowly but progressively through the breeding season. There was no relation between male body condition and the total number of eyespots (counted eyespot number) on a male's train in our study populations (repeated measures ANOVA, controlling for average tarsus length, eyespot count date and population:  $b = -1.36$ ,  $F_{1,41,0} = 0.33$ ,  $P = 0.57$ ). Nor was there a relation between counted eyespot number and train length (repeated measures ANOVA, controlling for the dates of both train measurement and eyespot count as well as population:  $b = 0.01$ ,  $F_{1,38,8} = 0.011$ ,  $P = 0.92$ ). Thus, variation in total eyespot number was not due to variation in body condition or the extent of train growth among the males in our populations.

#### Natural Train Morphology and the Arrangement of Eyespots

Train feathers on male PC72 were inserted in a regular pattern of rows on the uropygium (Fig. 1a) with only fish-tail feathers making up the posterior three rows, followed by a row of both fish-tail and major eyespot feathers. The remaining anterior 13 rows comprised only major eyespot feathers in an alternating pattern of 10 or 11 feathers (Fig. 1a). The length of the feathers and the size of the eyespots generally decreased towards the anterior. The pattern of eyespots in the erect train was bilaterally symmetrical (Fig. 1a, b). The shapes of the major eyespots themselves became increasingly asymmetrical in a regular fashion towards the left and right sides of the train, such that the central dark blue lobes of the eyespot pattern were larger on the left side for feathers on the left side of the train (and vice versa).

The asymmetrical minor eyespot and sword feathers along the lower edges of the left and right sides of the erect train (Fig. 1b) were curved and arranged with their concave edges downwards, such that a dense fringe of green barbs bordered the bottom edge of the erect train. On the uropygium, these feathers were inserted outside the rows of major eyespot feathers, with sword feathers posterior to the minor eyespot feathers (Fig. 1a). Asymmetrical

minor eyespot and sword feathers decreased in length as well as in the size of the minor eyespots themselves towards the anterior.

Male PC72 had 161 eyespot feathers (major and minor) when we captured him at the end of breeding season, and thus 167 at the start of the breeding season since we removed six when we first captured him. This total is remarkably close to the maximum of 169 eyespots collected from males moulting in captivity (Sharma 1974). Note that we counted only 154 eyespots on his photograph (Fig. 1b) taken during the breeding season, indicating that not all of the 161 eyespots were visible in the erect train. Although Petrie et al. (1996) reported removing 171–177 eyespots from three males in a feral population, we can find no other evidence that peacocks can grow this many eyespot feathers.

We conclude from this analysis that adult peacocks grow about 169 eyespot feathers (139 major, 30 minor), and we propose that this number may be anatomically determined and relatively invariant among males. Further anatomical work will be needed to test for variation in the number and arrangement of eyespot feathers among males both within and between populations, but our working hypothesis, which is consistent with all of the data currently available, is that adult peacocks typically grow 169 eyespot feathers in their train.

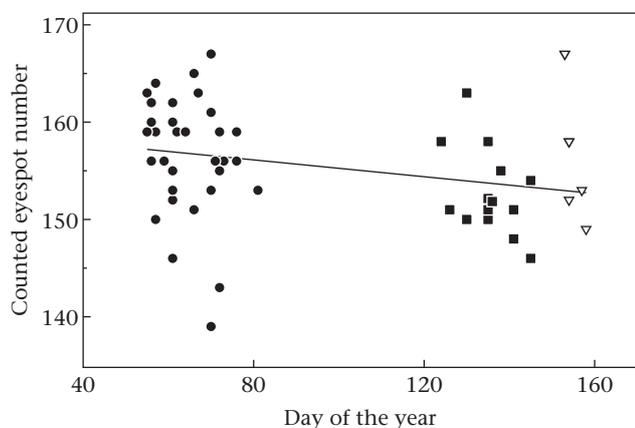
#### Eyespot Removal Experiment

Experimental removal of a large number of eyespots had no significant effect on the rate of female visits to a male (Table 1). It did, however, influence male mating success, significantly reducing the rates of train-rattling bouts, copulation attempts and successful copulations (Fig. 3, Table 1). Males with a large number of eyespots removed also had lower train display rates. Although this difference was not statistically significant (Table 1), we cannot rule out the possibility that eyespot removal affected male mating success via this or some other change in male behaviour that we did not detect. Nevertheless, our results confirm the effect of eyespot removal on male mating success. Descriptive statistics for morphological and behavioural traits of peacocks in the two feral populations (APZ and TZ) that were used in the eyespot removal experiment are given in the Appendix.

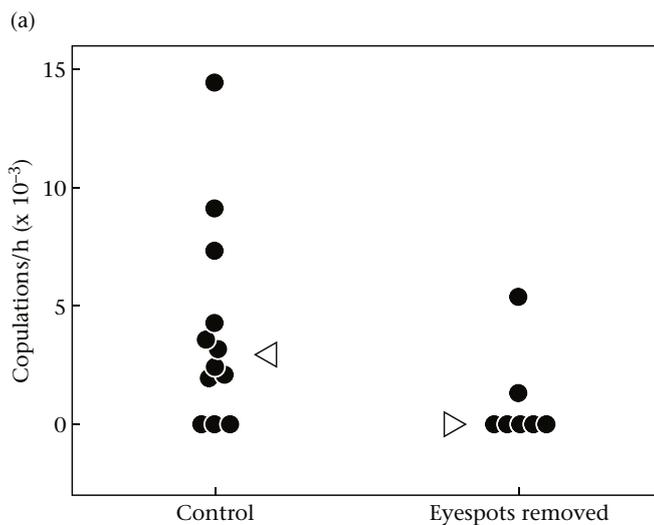
#### Mating Success

Among males that did not have the number of eyespots experimentally reduced, there was no evidence for an overall relation between the number of copulations a male obtained (standardized for population–year) and his train length (repeated measures ANOVA controlling for train measurement date:  $b = 0.02$ ,  $F_{1,39,4}$ ,  $P = 0.32$ ). Nor was there any relation between the number of copulations obtained (standardized) and the number of eyespots displayed by these males (repeated measures ANOVA:  $b = -0.02$ ,  $F_{1,42,9}$ ,  $P = 0.46$ ).

Our analysis of data pooled from all previous studies of feral peafowl populations showed a significant overall relation between a peacock's mating success (number of copulations standardized by population–year sample) and the number of eyespots displayed on his train ( $r = 0.28$ ,  $N = 102$ ,  $P = 0.004$ ; Fig. 4). However, there was no relation between the numbers of copulations and eyespots among males with at least 144 eyespots displayed (Pearson correlation:  $r_{68} = 0.08$ ,  $P = 0.52$ ; Fig. 4), the 25th percentile of total eyespot count of males in these populations ( $N = 102$ , Table 2). Nor was there a significant correlation for males with fewer than 144 eyespots displayed in their train ( $r_{30} = -0.001$ ,  $P = 0.99$ ; Fig. 4). Thus, variation in eyespots is not a good predictor of mating success for most males in feral populations.

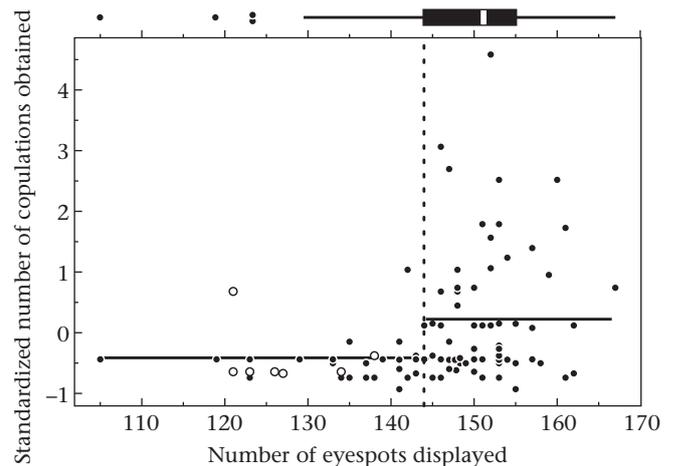


**Figure 2.** Relation between the counted eyespot number and the date that eyespots were counted on photographs. Graph shows 54 eyespot counts from 38 adult male peacocks, with 10 males counted in two or three different years. Regression line is plotted on the raw data to illustrate the trend; see text for analysis. ●: LAA; ■: APZ; ▽: TZ.



**Figure 3.** Results of eyespot removal experiment showing (a) the effect of removing 20–25 eyespots on the mating success (copulations/h) of seven peacocks compared to 12 control males that had only five eyespots removed, and photographs of (b) control and (c) removal treatment males. In (a), all data are shown, with medians indicated by open triangles; in (b) and (c), each eyespot is marked with a white dot on the photograph.

Following Takahashi et al. (2008), we also checked whether natural year-to-year changes in displayed eyespot number influenced a given male's copulation success between years at LAA. For the 11 males that we observed in two different years at LAA, there was no relation between the changes in the number of eyespots displayed and the standardized number of copulations ( $r_9 = -0.17$ ,  $P = 0.62$ ).



**Figure 4.** Relation between the number of copulations obtained (standardized by population–year) and the number of eyespots displayed on a peacock's train ( $N = 102$ ). Data are from four studies (Petrie et al. 1991; Petrie & Halliday 1994; Loyau et al. 2005a; this study). The seven open circles are from the removal experiment in this study. Vertical dotted line is at the 25th percentile of displayed eyespot number shown in the main graph; horizontal solid lines are mean values for trains below and above that 25th percentile. Tukey box plot above graph shows the distribution of total number of eyespots displayed per train.

## DISCUSSION

Our findings with respect to peacock mating success and eyespot number are consistent with all previous studies. Like Takahashi et al. (2008), we found no effect of natural variation in train morphology, including displayed eyespot number and train length, on male mating success. We also confirmed the experimental result of Petrie & Halliday (1994) that removing a large number of eyespots reduces male mating success.

Loyau et al. (2008) outlined a number of possible reasons for the apparent contradiction between previous studies (e.g. Takahashi et al. 2008; Loyau et al. 2005a). Our results provide a simpler explanation: the eyespot removal treatment (Petrie & Halliday 1994; this study) changes the appearance of male trains substantially when compared with normal males. All treatment males in our study displayed fewer than 138 eyespots, approximately the 10th percentile of displayed eyespot number in our study populations, and a relatively rare number of eyespots displayed by males in other populations studied to date (Fig. 4, Table 2). Because this experimental treatment removed only the outermost eyespots in the erect train, female choice might also have been influenced by its potential effects on apparent train size, the density of eyespots in the train, or bilateral asymmetry in the distribution of eyespots.

In our study, two of the seven males in the removal treatment copulated successfully, with one male obtaining five copulations and ranking fourth in copulation success overall (including control males) in this experiment (Fig. 3). This male was apparently preferred, despite having only 121 eyespots. In all feral populations studied so far, females have tended to avoid mating with males with fewer than 144 eyespots in their trains, and yet none of the variation in reproductive success among males with at least 144 eyespots displayed, or indeed with fewer than 144 eyespots displayed, can be explained by variation in the number of eyespots shown to females (Fig. 4; this study; Loyau et al. 2007b; Takahashi et al. 2008). These two results indicate that female mating preferences in feral peafowl populations are not solely based on eyespot number, and that they are often based on some other cue.

Our detailed examination of the arrangement of train feathers on one male and the consistent maximum number of eyespots

found on males in all populations (Table 2) suggests to us that all adult males grow more or less the same number of eyespot feathers. Thus, males appear to grow 165–170 eyespot feathers during the autumn moult, some of which are later lost by breakage or by being pulled out (e.g. by a predator). The regular arrangement of train feathers that we observed on the uropygium of one adult male suggests a constant number and arrangement of follicles in the caudal tract that produce the specialized feathers in the train. As with the development of the wing primaries or the rectrices, the maximum number of dermal papillae that will eventually produce eyespot feathers may be genetically determined in all males (Lillie 1942). Among the feral populations studied to date, there appears to be little (if any) variation in the total number of eyespot feathers grown by adult males. It is possible that adult males in wild Indian populations show more variation, either due to genetic variation or because train growth rates are more variable in the wild, causing differences in the degree to which the shortest eyespot feathers have developed and are thus visible during the breeding season (e.g. Sharma 1974). So far, there have been no studies on eyespot number in wild populations, and the sole study looking at correlates of mating success in wild peacocks did not count eyespot number (Yasmin & Yahya 1996).

In the feral populations we studied, the loss of individual feathers appears to be the primary source of variation in eyespot number among males. First, we showed that displayed eyespot number decreased with time. Second, eyespot number does not appear to be related to the extent that feathers have grown in or developed in our feral populations; despite substantial variation in train length, there was no relation between the number of eyespot feathers counted and train length. The breakage and loss of individual eyespot feathers is not unusual; during the breeding season, males were often observed with broken eyespot feathers that had not yet fallen out (R. Dakin, personal observations).

If feather loss is the main source of variation in displayed eyespot number in feral males, the reported positive correlation between the number of eyespots and the symmetry of eyespot number on left and right sides of the train (Manning & Hartley 1991) is inevitable, and thus unlikely to be adaptive (contra Manning & Hartley 1991). Haphazard feather loss would necessarily cause both the number of eyespots and the mean bilateral symmetry of eyespot numbers to decrease. Similarly, Petrie et al. (2009) may have failed to find significant heritability in the number of eyespots displayed in the train if there is no genetic variation in the number of eyespot feathers grown, and variation in eyespot number is instead influenced mainly by environmental factors. It is also possible that males with fewer eyespots took longer to recover from an immune challenge (Loyau et al. 2005b) because they had experienced greater levels of physical stress associated with the loss of eyespot feathers.

### Conclusion

The weight of evidence from studies of feral peafowl populations now suggests that mate choice in this species is more complex than previously thought: females may mate less often with males missing a large number of eyespots, while choosing among the remaining males based on other aspects of their plumage and behaviour. Perhaps females benefit by avoiding mating with males that have experienced extreme feather loss through predation or physical stress. They may also perceive that males missing the outer rows of eyespots are subadult individuals. Displayed eyespot number may be a cue that is only rarely used in mate choice in feral populations such as the ones studied here and in Takahashi et al. (2008), because individuals missing a large portion of the train are relatively rare in these populations.

However, display and observation of the train appear to be critical components of courtship (Dakin & Montgomerie 2009), so it seems likely that other characteristics of the train's colours and patterns are critical for mate choice in this poster boy for sexual selection (Loyau et al. 2007b; R. Dakin & R. Montgomerie, unpublished data).

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## APPENDIX

**Table A1**Morphological and behavioural traits of peacocks in the eyespot removal experiment conducted in the APZ and TZ populations, with mean  $\pm$  95% CI

	Population		Experiment	
	APZ	TZ	Control	Treatment
	N=14	N=5	N=7	N=12
<b>Morphology</b>				
Train length (cm)	144.0 $\pm$ 4.0	140.1 $\pm$ 5.2	144.1 $\pm$ 4.1	141.0 $\pm$ 5.7
Mean tarsus length (cm)	15.0 $\pm$ 0.2	15.2 $\pm$ 0.5	15.0 $\pm$ 0.3	15.1 $\pm$ 0.3
Body mass (kg)	4.70 $\pm$ 0.21	4.91 $\pm$ 0.31	4.81 $\pm$ 0.17	4.65 $\pm$ 0.43
Body condition (residual body mass)	-0.12 $\pm$ 0.23	-0.02 $\pm$ 0.36	-0.02 $\pm$ 0.19	-0.22 $\pm$ 0.43
<b>Behaviour</b>				
Display rate (proportion)	0.23 $\pm$ 0.08	0.24 $\pm$ 0.05	0.27 $\pm$ 0.07	0.16 $\pm$ 0.13
Female visit rate (proportion)	0.15 $\pm$ 0.07	0.13 $\pm$ 0.05	0.16 $\pm$ 0.07	0.11 $\pm$ 0.09
Train-rattling bouts/h	4.75 $\pm$ 2.46	4.05 $\pm$ 2.01	<b>5.88<math>\pm</math>2.47</b>	<b>2.31<math>\pm</math>1.89</b>
Copulation attempts/h	1.18 $\pm$ 0.54	0.75 $\pm$ 0.53	<b>1.40<math>\pm</math>0.53</b>	<b>0.49<math>\pm</math>0.48</b>
Copulations/h	0.20 $\pm$ 0.15	0.09 $\pm$ 0.16	<b>0.24<math>\pm</math>0.16</b>	<b>0.06<math>\pm</math>0.11</b>

Significant differences are highlighted in bold.