



## ARTICLES

# Peahens do not prefer peacocks with more elaborate trains

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The elaborate train of male Indian peafowl, *Pavo cristatus*, is thought to have evolved in response to female mate choice and may be an indicator of good genes. The aim of this study was to investigate the role of the male train in mate choice using male- and female-centred observations in a feral population of Indian peafowl in Japan over 7 years. We found no evidence that peahens expressed any preference for peacocks with more elaborate trains (i.e. trains having more ocelli, a more symmetrical arrangement or a greater length), similar to other studies of galliforms showing that females disregard male plumage. Combined with previous results, our findings indicate that the peacock's train (1) is not the universal target of female choice, (2) shows small variance among males across populations and (3) based on current physiological knowledge, does not appear to reliably reflect the male condition. We also found that some behavioural characteristics of peacocks during displays were largely affected by female behaviours and were spuriously correlated with male mating success. Although the male train and its direct display towards females seem necessary for successful reproduction, we conclude that peahens in this population are likely to exercise active choice based on cues other than the peacock's train.

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The striking contrast of showy male and sober female birds in nature is sometimes rather puzzling. Darwin (1871) proposed the idea of sexual selection through female mate choice to explain why such patterns of sex differences in appearance have evolved in animals, and many behavioural ecologists have applied his idea to explain conspicuous, extravagant plumage ornaments in male birds (e.g. Andersson 1994). Sexual selection is generally expected to be strong in species with highly skewed mating success among males, such as lek-breeding birds. In these species, the tight coevolution of female mate preferences and male sexual displays seems particularly

plausible because this relationship explains both why only males of the species have ornaments and why only few males achieve matings with females. However, reviews have revealed that male plumage ornaments in general are not always accompanied by strong sexual selection (e.g. Gontard-Danek & Møller 1999) and that the trend is similar for lekking birds, despite their large potential for sexual selection (Fiske et al. 1998; Rintamäki et al. 2001). Perhaps counterintuitively, numerous studies have experienced difficulties in identifying the cues that cause variation in mating among males on leks (Sæther et al. 2005), whereas few studies have found male plumage ornaments to be the primary cues used by females in mate choice on leks (Andersson 1989; Petrie et al. 1991; Stein & Uy 2006).

Researchers have achieved exceptional success in explaining male plumage ornaments in Indian peafowl, *Pavo cristatus*, as the direct target of female choice. To date, the peacock's train has been proposed not only as a target of current female choice (e.g. Petrie et al. 1991), but also as

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an indicator of good genes (Petrie 1994). However, there may be at least four problems with these hypotheses.

First, male train morphology seems not to be the universal cue of choice because there is evidence both for and against the effect of male train morphology on male mating success. Successful peacocks are individuals either with (Yasmin & Yahya 1996) or without (Rands et al. 1984; Loyau et al. 2005a) longer trains and with (Petrie et al. 1991; Loyau et al. 2005a) or without (Hasegawa 1995) a greater number of eyespots (see Appendix in Gontard-Danek & Møller 1999 for effect sizes). The trait itself does not seem to be the single cue for choice; several peafowl researchers have pointed out the functional importance of behavioural cues (Rands et al. 1984; Yasmin & Yahya 1996; Loyau et al. 2005a). Second, the ways in which females assess male trains (unless females have the ability to count eyespots per se) have been questioned repeatedly (e.g. Manning 1989; Petrie et al. 1991; Gadagkar 2003; Loyau et al. 2005a) but have not been fully investigated. Third, there is no consensus on which traits characterize males with the most elaborate trains (Gadagkar 2003). Petrie and colleagues have reported relationships between (1) the number of eyespots and male mating success (Petrie et al. 1991; Petrie & Halliday 1994), (2) the train length and male survival (Petrie 1992), (3) the train mass and number of eggs produced per male (Petrie & Williams 1993), (4) the area of eyespots and growth rate and survival of offspring (Petrie 1994), (5) the proportion of feathers with eyespots in the train and male body condition (Petrie et al. 1996) and (6) the diameter of eyespots and male immunocompetence (Møller & Petrie 2002). However, they found no consistent relationships among the above descriptors of train elaborateness (Petrie & Williams 1993; Petrie et al. 1996). Moreover, a group of French researchers found that peacocks that successfully mated with females were those with more eyespots and shorter trains (Loyau et al. 2005a). Fourth, to our knowledge, mate choice based on a male plumage ornament that is under oestrogen control is very rare. In galliform birds, male-like (often showy) plumage, including the peacock's train, develops in the absence of oestrogen (e.g. Owens & Short 1995), and conspecific females generally disregard these traits in mate choice (Davison 1981; Gibson et al. 1991; Beani & Dessì-Fulgheri 1995; Buchholz 1995; Hannon & Eason 1995; Ligon & Zwartjes 1995; Leonard & Zanette 1998; Hagelin & Ligon 2001). The assumption that higher levels of male hormones may contribute to more elaborate trains (Petrie et al. 1996) is now known to be endocrinologically incorrect (e.g. Owens & Short 1995).

Sæther et al. (2000) pointed out that gathering evidence from a wide range of populations, a long span of observation and from the perspective of both sexes will aid in testing the universality and persistence of female preference for a certain male trait and thus in reconciling differences among previous results. Here, we present data from a feral population of Indian peafowl observed over 7 years using both male- and female-centred monitoring for further investigation of the role of the male train in mate choice. Our objectives were to determine (1) whether peahens prefer peacocks with longer trains or more ocelli on their trains in this population, (2) whether the symmetry of the ocellar

arrangement affects male mating success as expected (but untested) from earlier studies of other populations (e.g. Petrie et al. 1991), and (3) which features of the male shivering display using the train affect male mating success.

## METHODS

### General Observations

A free-ranging population was observed at Izu Cactus Park (34°35'N, 139°05'E; ca. 15 ha), Shizuoka, Japan since 1994. We identified individuals in a total population of 75–104 birds. We used coloured leg rings for 90.7% of males and 61.5% of females. To identify the remaining birds, we used differences in unchanging physical characteristics such as the colours of wing, shoulder or throat feathers (Somes & Burger 1991, 1993) and the shape of the fleshy white skin on the face. Observers compared individuals to photographs of these characteristics whenever necessary. The ratio of adult males (older than 3 years) to adult females (older than 1 year) ranged 0.92–1.69, indicating that the population was generally male biased. Territorial males defending their own territories for display accounted for 72.9–84.1% of adult males. Most males annually formed a lek with males located at distances of 7–10 m from each other, which is intermediate between classical (e.g. Petrie et al. 1991) and exploded (e.g. Galusha & Redd 1992) leks. Data were collected mainly from early April to mid-June in 1995–2001 for a total of 307 days. One to five observers and three video cameras (for male birds only) monitored birds from 0500 to 0900 hours and from 1530 to 1730 hours, the time when females visited males. We related the train morphology of adult territorial males to individual mating success for a total of 200 male-years (52 individuals). In addition, we monitored adult females for 45 female-years (25 individuals) on at least 7 days and averaged 18.0 h of observation in 1998–2001. Behaviours of focal individuals were recorded at 1-min intervals in all cases.

### Male Mating Success

We used two measures of male mating success for two types of analysis as follows. First, for male-centred population-level analyses, the total number of copulations gained by a male in a specific year was defined as a measure of male mating success. Neither forced copulations nor successful mating attempts by nonterritorial males were observed. Second, for individual female choice analyses, we estimated male mating status using female courtship behaviours. This was done to decrease the likelihood of excluding possible mates from the analyses because of limited observations. Female attitudes in a male territory could be divided into three categories: passing by the male, passively receiving his display or actively soliciting his display using repetitive 'run-round' behaviours (the typical courtship sequence of this species has been well described by Ridley et al. 1984 and Petrie et al. 1992). We observed that females repetitively engaged specific male(s) in courtship interactions and copulated with these males

later (see also Petrie et al. 1992). Accordingly, we recorded all run-rounds by a focal female in a male territory and treated any visit accompanied by more than two successive female run-rounds as 'a preferred visit' (i.e. we excluded visits with less than three run-rounds). Each male visited by a focal female was scored as 'chosen' or 'rejected', where males that received at least one preferred visit were considered 'chosen' and others were 'rejected'. The number of preferred visits received by a male (range 0–41) was strongly related to the number of copulations achieved by the male (range 0–12) in all 4 years ( $r = 0.87–0.98$ ,  $N = 34–38$ , all  $P < 0.001$ ). Moreover, copulations were always preceded by preferred visit(s) by the female; this guaranteed that the occurrence of a female preferred visit was a valid estimate of male mating status.

### Measures of Male Morphology

We photographed the train of each male in each season on several days when the trains were fully displayed. More than one observer separately evaluated the number of eyespots and calculated a fluctuating asymmetry (FA) index for each male using the same sets of photographs. Single values for individual males were then determined by agreement. We defined the FA index as a percentage of the number of eyespot pairs having lost one of the pair from a symmetrical linear position divided by the total number of eyespot pairs on the train; therefore, a smaller FA value indicates a more symmetrical arrangement of eyespots on the train (a value of 0 indicates complete symmetry). We used this novel index because the index used previously in other peafowl studies to determine the FA (a simple difference in the numbers of eyespots in the right and left sides of the train; cf. Manning & Hartley 1991; Hasegawa 1995) does not always reflect the actual symmetry of the arrangement. For other morphological traits, we performed measurements at the end of the breeding season before the moult. Sixteen (1997), 10 (1999) and eight (2000) males were captured in enclosures or directly baited with food, as the staff of the park usually did. We generally followed the methods of Petrie et al. (1991) to measure the body weight and lengths of the spurs, bill, wings, tail and train, although we added crest length (from base to tip of the longest crest feather) and excluded the length of the metatarsus from that of the tarsus. For bilateral traits, the size of the trait was defined as the mean of the left and the right trait values. We were able to relate male train length to male mating success in 33 male-years (24 individuals).

### Measures of Male Shivering Displays

Shivering is a display in which a peacock shows and shakes his train directly towards a visiting female at close range, producing a rustling noise (e.g. Ridley et al. 1984). During a female visit, males sometimes performed more than 20 shivering bouts. Each bout lasted 1 to >400 s and consisted of quick changes in the intensity of the noise produced; these changes were termed 'shivers' and were generated approximately twice per second. We

recorded 2039 shivering bouts performed by focal males in 2 years (1997 and 1998) that were used for population-level analyses and 5209 shivering bouts received by focal females in 4 years (1998–2001) that were used for individual female choice analyses. In the latter cases in which females were monitored, we also recorded whether a focal female performed a run-round whenever the male territory owner commenced a new shivering bout. We then calculated four behavioural variables for each male for each season: (1) the number of shivering bouts (bouts/min), (2) the time spent shivering (s/min), (3) the mean length of a single shivering bout (s) and (4) the mean shiver rate (shivers/s; excluding bouts lasting <5 s). For individual female choice analyses, we calculated bouts/visit for (1) and s/visit for (2) instead because we were unable to distribute equal observation times for each male given the nature of the female-centred investigation.

### Analyses

Several separate analyses were performed on male-centred population-level data. First, we constructed a generalized linear mixed model (GLMM) using all observations across years to test the overall effect of the male measure on the number of copulations among males using R 2.5.1 (R Development Core Team 2007), with a Poisson distribution of errors, male identity and year incorporated as random effects to avoid pseudoreplication of the same individuals. For analyses using GLMM, each male trait was included as a fixed effect in individual analyses of male mating success. Second, we performed two types of multiple regression analyses using male mating success as the dependent variable in each year. One included eyespot number and the FA index as independent variables, whereas the other included these two train measures and two behavioural variables as independent variables. Train length was excluded from the multiple regression analyses because of the small sample size; moreover, train length showed no correlation with the other two train measures (see Results), and no significant statistics were obtained when we added train length as an independent variable.

Two additional analyses were performed for train measures. One was to determine whether changes in two train measures (number of eyespots and rank of the FA index) covaried with changes in mating success among males: we compared train measures between occasions when the same male was successful (i.e. obtained at least one copulation) and occasions when he was unsuccessful (i.e. obtained no copulations) for 24 males whose mating status changed during the study. In the other analysis, we compared train measures of surviving males to those of males that were predated during the breeding season by dogs, *Canis lupus familiaris*, or red foxes, *Vulpes vulpes*.

For individual female choice analyses, we compared train morphology and shivering variables in chosen and rejected males in 45 cases of female mate sampling. We tested the overall effect of the male measure on the male mating status using GLMM, using all data of males

sampled by focal females, with a binomial error distribution and female identity and year incorporated as random effects to control female choosing.

Variables that departed significantly from a normal distribution or those with small sample sizes were analysed using nonparametric statistics; all others were analysed using parametric statistics. Values presented in the Results are mean  $\pm$  SD, and all probability values are two tailed.

## RESULTS

All 268 observed matings involved territorial males. The most successful male achieved 14.9–31.4% of all copulations per year; thus, mating success was nonrandomly distributed among territorial males (Kolmogorov–Smirnov test:  $D = 0.49$ – $0.76$ ,  $N = 20$ – $37$ , all  $P < 0.01$ ). Males who obtained more copulations in 1 year tended to obtain more in the next year (six pairs of two consecutive years:  $r_s = 0.51$ – $0.87$ ,  $N = 18$ – $34$ , all  $P < 0.03$ ). Based on our records of 45 mate-sampling cases, per 10 h, females on average met 11.2 territorial males 30.0 times (including 5.9 preferred visits), received 78.7 shivering bouts and accepted 0.9 copulations in response to 5.4 male-initiated copulatory attempts. The proportion of chosen male(s) to the total number of males sampled by a focal female was  $23.8 \pm 10.2\%$ . Roughly half of the females (40.9–56.5% of individuals) mated multiple times. All monitored females returned to previous male(s) for copulation or courtship, indicating that they probably use best-of- $N$  tactics for mate choice (see also Petrie et al. 1991, 1992).

### Male Morphology and Mating Success

#### Male train morphology

Males tended to have a similar number of eyespots on their trains compared to that in the previous year (six pairs of two consecutive years:  $r = 0.53$ – $0.88$ ,  $N = 20$ – $31$ , all  $P < 0.05$ ), but this was not the case for the FA index ( $r_s = -0.20$ – $0.38$ ,  $N = 20$ – $31$ , all  $P > 0.08$ ). The relationships among the three train measures were as follows: the number of eyespots showed a negative relation (or trend) with the FA index in 4 of 7 years, but not in the other 3 years ( $r_s = -0.46$  to  $-0.04$ ,  $N = 24$ – $37$ ,  $P = 0.01$ – $0.83$ ) and the train length had no relation with the number of eyespots ( $r_s = -0.13$ – $0.43$ ,  $N = 8$ – $14$ , all  $P > 0.26$ ) or with the FA index ( $r_s = -0.10$ – $0.37$ ,  $N = 8$ – $14$ , all  $P > 0.27$ ) in all 7 years.

Population-level analyses using all observations across years in GLMMs revealed no significant effects of the three train measures on male mating success (Table 1). Other population-level analyses for train measures produced similar results. First, the between-year changes in male train morphology did not result in corresponding changes in male mating success: 24 males that changed their mating status between years did not tend to be successful when they had trains with more eyespots (successful years:  $149.9 \pm 5.8$ ; unsuccessful years:  $150.4 \pm 5.3$ ; paired  $t$  test:  $t_{23} = 0.67$ ,  $P = 0.42$ ) or a smaller FA index (successful years:  $2.75 \pm 1.93$ ; unsuccessful years:  $2.98 \pm 2.57$ ;

Wilcoxon signed-ranks test:  $z_{23} = -0.43$ ,  $P = 0.67$ ). Second, we observed no combined effect of train measures on the variance of mating success among males for all 7 years ( $R^2 = 0.01$ – $0.08$ ,  $N = 20$ – $37$ ,  $F = 0.13$ – $0.92$ , all  $P > 0.41$ ).

Similarly, in our analyses of individual female choice, GLMMs revealed no effects of these two measures of the male train on choice by focal females (number of eyespots:  $z = 0.92$ ,  $P = 0.36$ ; FA index:  $z = -0.07$ ,  $P = 0.95$ ; both  $N$  of observations = 577).

#### Other male morphological traits

We observed sexual dimorphism in adult birds (larger size of males during the breeding season) in all other measured morphological traits except crest length (M. Takahashi & H. Arita, unpublished data). However, positive correlations of trait values with mating success were rarely observed (one case was for wing length in 1997 and the other case was for body weight in 1999), and no measure consistently showed a specific relation with mating success in more than 1 year (data not shown). GLMM analyses using all observations across 3 years produced similar results (Table 1).

#### Predation

Comparing the trains of males that survived to those that were predated, we obtained the following results: (1) no difference in the number of eyespots (surviving:  $149.4 \pm 4.9$ ,  $N = 44$ ; predated:  $149.0 \pm 14.0$ ,  $N = 7$ ; Mann–Whitney  $U$  test:  $U = 101.5$ ,  $P = 0.15$ ), (2) slightly greater FA index in predated individuals (surviving:  $2.98 \pm 1.74$ ,  $N = 44$ ; predated:  $8.95 \pm 9.96$ ,  $N = 7$ ;  $U$  test:  $U = 91.5$ ,  $P = 0.08$ ) and (3) significantly greater length in predated individuals (surviving:  $153.5 \pm 6.9$ ,  $N = 20$ ; predated:  $161.4 \pm 1.46$ ,  $N = 3$ ;  $U$  test:  $U = 7.0$ ,  $P = 0.04$ ; although the sample size of predated individuals was very small). There was no significant difference in the proportion of predated males that had mated (4/7) and the proportion of surviving males that had mated (21/44; chi-square test:  $\chi^2_1 = 0.21$ ,  $P = 0.64$ ), indicating that unmated males did not suffer disproportionate predation (cf. Petrie 1992).

### Male Shivering Displays and Mating Success

#### Behavioural differences between males

Male-centred population-level analyses using all observations across years revealed that more successful males performed more shivering bouts and spent longer times shivering; in contrast, on average, more successful males did not perform longer single shivering bouts and did not show intensive shiver rates (Table 1). The results were similar in individual female choice analyses. Significant differences were observed in chosen and rejected males in the number of shivering bouts (GLMM:  $N$  of observations = 566,  $z = 8.32$ ,  $P < 0.001$ ) and the time spent shivering ( $N$  of observations = 529,  $z = 7.22$ ,  $P < 0.001$ ), whereas no differences were found in the mean length of individual shivering bouts ( $N$  of observations = 450,  $z = 0.95$ ,  $P = 0.34$ ) or the mean shiver rate ( $N$  of observations = 440,  $z = 1.11$ ,  $P = 0.27$ ). To appropriately

**Table 1.** Relationships between male morphological and behavioural measures and mating success (number of copulations) in peacocks

Male measures	N			<i>b</i> ±SE	<i>z</i>	<i>P</i>
	Obs	Male	Year			
<b>Train morphology</b>						
Number of eyespots*	200	52	7	0.03±0.02	1.35	0.18
FA index†	200	52	7	0.01±0.02	0.33	0.74
Train length‡	33	24	3	0.02±0.06	0.35	0.72
<b>Other morphology</b>						
Body weight§	29	22	3	-1.75±2.48	-0.70	0.48
Tarsus length**††	33	24	3	0.01±0.03	0.43	0.67
Spur length††	33	24	3	-0.05±0.09	-0.52	0.60
Bill length††	27	22	3	0.04±0.12	0.32	0.75
Wing length‡	33	24	3	-0.04±0.32	-0.11	0.91
Tail length‡	34	25	3	-0.07±0.12	-0.58	0.56
Crest length††	29	21	3	0.02±0.06	0.27	0.79
<b>Shivering display</b>						
Number of shivering bouts (bouts/min)	45	27	2	20.36±5.83	3.49	<0.001
Time spent shivering (s/min)	45	25	2	0.49±0.16	3.00	<0.01
Mean length of a single shivering bout (s)	41	24	2	0.01±0.02	0.53	0.59
Mean shiver rate (shiver/s)‡‡	39	24	2	0.29±1.12	0.26	0.80

Statistical values (*z*, *P*) are based on GLMM using all observations across study years (1995–2001) to test the effect of the male measure on the number of copulations among males, with a Poisson distribution of errors, male identity and year incorporated as random effects to avoid pseudoreplication of the same individuals. CVs of the train measures refer to the coefficients of variation in Table 2. See text for general methods of focal observations and measurements of males.

\*Counted using several photographs of fully opened trains for each male.

†Evaluated as a percentage in which the number of eyespot pairs having lost one of the pair from a symmetrical linear position is divided by the total number of eyespot pairs on the train.

‡Measured to the nearest 1 mm using a metal tape measure.

§Measured to the nearest 100 g using a spring balance.

\*\*Excluding the length of the metatarsus (cf. Petrie et al. 1992).

††Measured to the nearest 0.01 mm using digital Vernier callipers.

‡‡Excluding bouts lasting <5 s.

interpret the result in which males that performed more or longer displays were more successful, we then explored differences in shivering measures of the same individual males in relation to female soliciting behaviour.

#### Behavioural differences within males

Female sampling activity varied from day to day (see also Petrie et al. 1992). Females visited the preferred male(s) repeatedly but did not always perform run-rounds. We therefore compared shivering displays on the occasions in which the same male received repetitive female run-rounds during the display and the occasions in which he did not. In total, 38 males chosen by at least one focal female in 1998–2001 were used in these comparisons. We found that some features of male displays changed between occasions, whereas other features did not. For example, in 1998, we found significant differences between two occasions in the number of shivering bouts (preferred occasions:  $9.28 \pm 6.17$ ; other occasions:  $2.04 \pm 0.62$ ; paired *t* test:  $t_{10} = 4.11$ ,  $P = 0.002$ ) and the time spent shivering (preferred:  $307.13 \pm 157.89$ ; others:  $78.34 \pm 34.60$ ; paired *t* test:  $t_{10} = 5.26$ ,  $P < 0.001$ ), whereas no differences were found in the mean length of individual shivering bouts (preferred:  $41.83 \pm 18.49$ ; others:  $37.48 \pm 16.74$ ; paired *t* test:  $t_{10} = 1.07$ ,  $P = 0.31$ ) and the mean shiver rate (preferred:  $0.40 \pm 0.08$ ; others:  $0.40 \pm 0.05$ ; paired *t* test:  $t_{10} = -0.12$ ,  $P = 0.91$ ). The same results were obtained for three other years. Between-male and within-male

differences in shivering behaviour showed the same patterns when we partitioned samples based on the presence or absence of female preference, suggesting that certain measures of male shivering displays (i.e. the number of shivering bouts and the time spent shivering) change on occasion, with or without female motivation.

Accordingly, we included only two behavioural measures (mean length of a single shivering bout and mean shiver rate) in addition to two train measures (number of eyespots and FA index) as the independent variables in our second multiple regression analysis. The combination of these four variables explained little variance in male mating success in both 1997 and 1998 ( $R^2 = 0.14$  and  $0.20$ ,  $F = 0.51$  and  $0.79$ , both  $N = 18$ , both  $P > 0.55$ ), and none showed a significant partial correlation with male mating success in either year (data not shown).

## DISCUSSION

### Effects of Male Morphology on Mating Success

Peafowl researchers have almost reached a consensus indicating few effects of male morphological traits other than the train on mating success (Petrie et al. 1991; this study). However, evidence is contradictory for the effects of the number of eyespots and train length (see Table 2). According to our data, the FA of the ocellar arrangement

**Table 2.** Effect of two measures of train morphology on mating success in peacocks with the CVs of the traits from studies of five different feral populations

Train measures	UK (Oxford)	UK (Whipsnade)	India	France	Japan
Number of eyespots (CVs)	—	Positive† (4.3–8.5%)	—	Positive**, No††	No (3.2–5.9%)
Train length (CVs)	No* (4.5%)	(4.7, 6.8%)‡	Positive§ (4.6%)	Negative**	No (3.8–6.9%)

The specific relation (positive, negative or no relation) between male train measures and the mating success of a given male in a specific population is shown with CVs of the traits in parentheses. When the CVs were not provided in the original papers, we computed the values from tables or figures if they contained the necessary information. The CVs of the traits are consistently small across populations, despite discordant relationships between the trait values and male mating success.

\*Rands et al. (1984); CV was computed from Table 1.

†Petrie et al. (1991); CVs were computed from Figure 3 of Petrie et al. (1991) and refer to Table 1 of Petrie & Williams (1993); Table 1 of Petrie et al. (1996).

‡Table 1 of Petrie & Williams (1993); Table 1 of Petrie et al. (1996).

§Yasmin & Yahya (1996); CV was computed from Table 1.

\*\*Loyau et al. (2005a).

††Loyau et al. (2007).

showed no consistent relationship with the size of the trait or male mating success, suggesting that this trait is not under directional selection. Females did not choose males with a combination of more and symmetrically positioned ocelli on the train. In addition, population-level analyses in each year indicated that none of the male train measures was a consistent cue of female choice (see Appendix).

What is surprising is that two suites of field studies have reached opposite conclusions: (1) monitoring from the perspective of both sexes has detected a positive effect of male train morphology on mating success in Britain (Petrie et al. 1991) but not in Japan (this study), (2) increases and decreases in the number of eyespots appeared to result in corresponding changes in mating success in Britain (Petrie & Halliday 1994: experimental) but not in Japan (this study: observational) and (3) males with longer trains showed better survival (in winter) in Britain (Petrie 1992) but not in the breeding season in Japan (this study). It is unclear why some researchers have detected both correlation and causality between male train elaboration and female preference, whereas others have failed to detect either. First, our results did not change when we used the total number of females that copulated with a male as a measure of male mating success (M. Takahashi, unpublished data); thus the currency of male success was not the cause of these differences (cf. Petrie et al. 1991). Second, individual female choice analyses performed by Petrie et al. (1991) and those described here allowed us to avoid some confounding factors that might arise among different populations (e.g. physical or genetic environments, degree of male clustering or mating skew). Third, we recognized no definitive differences among studies in the variation in the traits in question; train morphology showed relatively low variance among males across populations (maximum CV 8.5%; Table 2). Although it is generally assumed that females may use traits with high variance as mate choice cues (e.g. Jennions & Petrie 1997), the variance in the length of the ornamental train is almost the same as that of nonornamental tails in males (3.8–6.9% for the train versus 4.0–6.6% for the tail in our population: M. Takahashi, unpublished data; see also Appendix in Cuervo & Møller 2001).

One potential factor generating the discordant outcomes among studies may be the differences in observation times. Some previous observations (Petrie et al. 1991; Petrie & Halliday 1994) missed the evening mating period, during which we recorded 21.1% of all copulations. In a previous study (Petrie et al. 1991), peahens that often mated with multiple males on different days (Petrie et al. 1991, 1992) were monitored only for a single mating each. On the other hand, we avoided the problem of small effect size due to a small number of observations (Møller & Jennions 2001; Jennions & Møller 2003) by conducting a 7-year survey; we then obtained the 'least' effect size from the longest observation with the largest sample size among peafowl studies. Another potential factor may be the age effect. Previous analyses have frequently included measures of trains taken from 2- or 3-year-old males with regard to male mating success and territory acquisition (Petrie et al. 1991; Loyau et al. 2005a), condition dependency (Petrie et al. 1996; Møller & Petrie 2002), or immunocompetence (Møller & Petrie 2002). However, at these ages, the train measures may not be fully expressed (Sharma 1974; Hillgarth 1984; Manning 1987, 1989; Petrie 1993; Møller & Petrie 2002). Although male age per se is not likely to be the target of choice (Rands et al. 1984; Petrie et al. 1991; Petrie 1993; cf. Hillgarth 1984), it appears more appropriate to conduct such analyses while making a distinction between 4-year-old and younger males because males younger than 4 years are normally unsuccessful in the feral condition (M. Takahashi, unpublished data). In fact, the second- or third-best males with respect to the number of eyespots achieved no matings in most populations (Petrie et al. 1991; Petrie & Halliday 1994; Loyau et al. 2005a; this study). In a British population, more than 80% of focal females missed the chance to access the best male before mating on 10-male leks (see Appendix in Petrie et al. 1991). Could these observations require an explanation other than unanimous, prudent female choice based on male train morphology?

Positive results are likely to be published and distributed in the research field of sexual selection (Alatalo et al. 1997; Gontard-Danek & Møller 1999; Simmons et al. 1999). However, it is equally important to publish negative results (e.g. Sæther et al. 2000; Møller & Jennions 2001).

and present a variety of results to ensure proper interpretation. Future research should first gather data extensively to re-evaluate the universality of female preference for males with more elaborate trains. This needs to be done because researchers working on specific populations may consecutively observe the same relationship (positive, negative or none) between train elaboration and male success regardless of female preference because of high between-year constancy in both train elaboration (probably due to genetic background (M. Petrie, unpublished data cited in Pike & Petrie 2005)) and male success (probably due to female fidelity to previous mates (M. Takahashi, unpublished data)). It is then necessary to elucidate which criteria are used by peahens to assess peacock's trains other than FA (e.g. volume of shivering noise (Manning 1989), total area (Petrie 1994), overall amount of colour (Petrie & Halliday 1994) or the density of eyespots (Loyau et al. 2005a)). Studies of peafowl vision will be helpful (Harper 2006), although the visual systems are essentially identical among galliform birds (including the absence of UV-sensitive visual pigments (Hart 2002)), despite considerable interspecific variation in plumage coloration (Hart 2001).

We may have failed to detect mate choice based on the male train that actually occurred in our population for unknown reasons. If we did, then the male train does not necessarily indicate male quality because equivocal evidence describes the costs or condition dependency of its expression. For direct costs, predated males had shorter (Petrie 1992) or longer (this study) trains than survivors, whereas measures of the train were (Petrie et al. 1996) or were not (N. Hillgarth, M. Petrie & T. R. Halliday, unpublished data cited in Petrie et al. 1991; H. Arita, unpublished data) related to male ectoparasite loads; for indirect costs, train length was (Møller & Petrie 2002) or was not (Petrie et al. 1996) related to male residual weight (i.e. condition index), whereas the number of eyespots was (Loyau et al. 2005b) or was not (Møller & Petrie 2002) related to male immunocompetence. These results do not suggest that the male train is more likely a good-genes trait rather than a runaway trait, although one train measure (the area of eyespots) has suggested the greatest good-genes effect (Petrie 1994) among species studied in the past century (Møller & Alatalo 1999). Moreover, the expression of male plumage ornaments that are under the control of oestrogen, such as the peacock's train, are typically poor indicators of the phenotypic and genotypic condition of males (e.g. Owens & Short 1995; Ligon et al. 1998; Mateos 1998; Kimball & Ligon 1999). Perhaps, therefore, female galliforms generally pay attention to testosterone-dependent traits rather than to male plumage ornaments (Brodsky 1988; Moss et al. 1988; Beani & Dessi-Fulgheri 1995; Buchholz 1995; Hannon & Eason 1995; Fusani et al. 1997; Mateos 1998; Hagelin & Ligon 2001; Parker & Ligon 2003). Therefore, peahens appear to be quite exceptional if they indeed select mates based on the male train.

### Effects of Male Shivering Display on Mating Success

We observed that occasions with or without female courtship could cause differential continuation of displays

by the same male, such that female repetitive run-rounds directly provoked increased shivering bouts and increased time spent displaying. Thus, the measures of display continuation (how long or how many males displayed) appear almost entirely dependent on female, rather than male, motivation. Researchers of lekking birds have stressed the difficulty in differentiating causes and effects: do males display actively because they are successful or are they successful because they display actively (Gibson & Bradbury 1985; McDonald 1989; Höglund et al. 1997; Shorey 2002)? All measures of shivering previously investigated (Rands et al. 1984; Petrie & Williams 1993; Loyau et al. 2005a,b) are problematic in this respect, whereas other measures that we investigated (how intensely males displayed once a female was in their territories) showed neither this sort of problem nor a correlation with male success. Even if a high level of performance in shivering somehow provides females with information on male quality (e.g. health status (Loyau et al. 2005b)), it does not act as a cue in mate choice by itself because a female should initially solicit a given male to display based on other cues.

### What Factors Affect Male Mating Success?

Rands et al. (1984) proposed four factors that potentially affect the mating success of peacocks: (1) attraction of females to their display sites (e.g. by calling), (2) stimulating displays, (3) male appearance and (4) site position. As described above, observations from five separate populations do not provide unequivocal support for factors (2) and (3), although the auditory component of shivering was an unmeasured variable. For factor (4), peahens seem to pay little attention to territory size (Rands et al. 1984) or the position of males (Petrie et al. 1991; M. Takahashi, unpublished data; cf. Hillgarth 1984; Rands et al. 1984; Loyau et al. 2007). The fact that Indian peafowl has the smallest spurs among extant and fossil *Pavo* species (Louchart 2003) suggests the decreased importance of male physical conflicts and related traits in this species. Therefore, Rands's first factor, especially male acoustic signalling, is now worth considering (see Yasmin & Yahya 1996; Loyau et al. 2005a; Takahashi & Hasegawa, in press) for at least three reasons: a prominent sex difference in vocalizations (e.g. Takahashi & Hasegawa, in press), a correlation between the number of male multinote calls and the mating success (Yasmin & Yahya 1996) and the general implication that acoustic displays improve male mating opportunities in galliforms (Davison 1983; Gibson & Bradbury 1985; Gratson 1993; Beani & Dessi-Fulgheri 1995; Guyomarc'h et al. 1998; Rintamäki et al. 2001) and nongalliform lekking birds (McDonald 1989; Pruett-Jones & Pruett-Jones 1990; Westcott & Smith 1997). Peacock researchers will need to become more multimodal, as pointed out by Maynard Smith (Harper 2006), in reference to the current findings of universality, advantage, or functions of multimodal signals in mate choice (reviewed in Candolin 2003). Different studies are prone to different conclusions if females of the species use a combination of cues in their mate selection sequences (Fiske et al. 1994; Mateos 1998) or if between-female and/or within-female variations in preferences occur (Jennions & Petrie 1997; Widemo & Sæther 1999; Badyaev & Qvanström 2002).

## Phylogenetic Inferences for Evolution of Sex Differences in Indian Peafowl

The CVs of peacock trains and nonornamental tail feathers did not differ in our population, suggesting that train length is not currently under directional selection. The symmetrically arranged ocelli on the feathers and the male display thereof are universal features among the pavonine clade, although there is no evidence of mate choice using male ocellar arrangement among other pavonines (Davison 1981, 1983). Interestingly, a recent molecular phylogeny of peacock-pheasants (Kimball et al. 2001) revealed the ocelli to be primitive in this sister taxon of peafowls, and losses of ocelli and male frontal displays were observed in the most derived species.

In addition, peacock-like plumage is inhibited by a high level of female hormones, suggesting that there has been selection on females for dull-coloured plumage, as would be expected in ground-nesting species with little or no male parental care where females suffer high predation risk during incubation (Wallace 1889; Andersson 1994; Götmark et al. 1997). Peahens were actually twice as vulnerable as males in our population (24 female versus 11 male adult birds were predated during our study, even though the sex ratio of the population was generally male biased; H. Arita & M. Takahashi, unpublished data). Phylogenetic studies have suggested that oestrogen-dependent plumage dichromatism such as that in Indian peafowl was preceded by bright monochromatism in both sexes, followed by natural selection for duller coloration in females (Kimball & Ligon 1999; Badyaev & Hill 2003), whereas selection on male bright plumage may not be as strong (Møller & Pomiankowski 1993; Bleiweiss 1997; Kimball & Ligon 1999). This scenario appears to some extent to be in contrast with the conventional explanation of sexual selection in which current plumage sex differences are predominantly the result of selection for greater ornamentation in males, rather than selection for lesser ornamentation in females.

## CONCLUSION

Combined with previous results, our findings indicate that the peacock's train (1) is not currently the universal target of female choice, (2) shows small variance among males across populations, (3) does not appear to reliably reflect male condition and (4) is perhaps ancestral and static rather than recently derived. Nevertheless, this trait is thought to have evolved and to function for almost exclusively epigamic purposes (Ridley et al. 1984; Petrie et al. 1991; cf. Loyau et al. 2005a) and is thought to be a necessary condition for successful reproduction. Combining these considerations, we propose that the peacock's train is an obsolete signal for which female preference has already been lost or weakened, but which has none the less been maintained up to the present because it is required as a threshold cue to achieve stimulatory levels in females before mating (Holland & Rice 1998) and/or it is maintained as an unreliable cue (Møller & Pomiankowski 1993). Peahens probably use the male train in their mate choice sequences, but we should not

necessarily assume that the male trait is a costly and/or informative cue (use of uninformative cues can be beneficial for females, e.g. through facilitation of mate detection; Candolin 2003). For birds in which male-like plumage develops in the absence of oestrogen, it is typical for existing male ornaments to be unreliable Fisher traits (Johnsen & Zuk 1996; Omland 1996) or traits that do not attract females (see Introduction). On the other hand, females could shift their attention from obsolete signals to more informative signals (e.g. Møller & Pomiankowski 1993; Holland & Rice 1998; Wiens 2001), as we observed peahens exercising active best-of-*N* choice, presumably on some trait other than the male's train.

Researchers of sexual selection have focused their interests largely on the question of why but not how only males have elaborate trains in this species. The endocrinological basis and phylogenetic inferences for the peacock's train coincidentally caution against the conventional attitude of unidirectional presumption that greater plumage ornamentation in males is always the most recently derived condition (see Kimball & Ligon 1999; Kimball et al. 2001; Wiens 2001; Badyaev & Hill 2003). 'The sight of the peacock's tail makes me sick': although we have come far in some ways since Darwin's writing (Hiraiwa-Hasegawa 2000), it is too early to regard his question as settled until the whole evolutionary track of diversification in peacocks' displays has been revealed by integrated perspectives of physiology, phylogeny and field ecology.

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## Appendix

Ranges and means and SDs of three measures of train morphology in peacocks and relationships between the measures and the mating success (number of copulations) in different years

Train measures	Year	Range	$\bar{X} \pm \text{SD}$	N	r	P
Number of eyespots	1995	127–164	150.3±8.4	20	0.10	0.68
	1996	118–159	146.4±9.5	20	0.13	0.60
	1997	139–158	149.6±5.4	20	0.26	0.28
	1998	127–157	146.8±5.9	30	0.21	0.26
	1999	139–158	147.9±5.3	36	0.08*	0.62
	2000	125–159	148.7±7.6	37	0.10	0.56
	2001	140–160	151.2±4.9	37	0.18*	0.29
FA index	1995	0.0–22.1	3.49±4.91	20	–0.27	0.39
	1996	0.0–28.8	6.29±7.39	20	–0.27	0.26
	1997	0.0–6.8	2.67±2.10	20	–0.09	0.70
	1998	0.0–37.3	4.65±6.89	30	–0.23	0.23
	1999	0.0–30.1	3.03±3.38	36	0.02*	0.90
	2000	0.0–20.9	3.41±4.64	37	–0.22	0.19
	2001	0.0–12.3	3.25±2.30	37	–0.04*	0.81

(continued)

Train measures	Year	Range	$\bar{X} \pm SD$	<i>N</i>	<i>r</i>	<i>P</i>
Train length (cm)	1997	149.2–170.0	156.88±5.89	15	−0.17*	0.53
	1999	138.5–163.0	151.99±8.01	10	0.30*	0.38
	2000	137.4–168.5	154.79±10.62	8	−0.24*	0.53

Statistical values (*r*, *P*) refer to correlations between the male train measures and the number of copulations among males. Asterisks (\*) indicate that the value is  $r_s$  (instead of  $r$ ) based on Spearman rank correlation tests for variables that were not normally distributed or that had small sample sizes. More successful males did not have more eyespots on their trains or longer trains, nor did they exhibit smaller indices of fluctuating asymmetry (FA; i.e. a more symmetrical ocellar arrangement). See text for general methods of observation and measurements of males.