Intra- and Intersexual Selection for Multiple Traits in the Peacock (*Pavo cristatus*)

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Abstract

Animal communication involves a multitude of signals ranging from morphological to behavioural traits. In spite of the diversity of traits used in animal signalling, most studies of sexual selection have focused on single male traits. Moreover, the two forces of sexual selection (male–male competition and female preference) may target different traits and favour the diversification of male signalling. Still, little is known on the combined effects of intra- and intersexual selection on the evolution of multiple signals. The peacock is often cited as one of the best examples of the strength of sexual selection in producing exaggerated traits. Here, we investigated traits under intra- and intersexual selection in a population of free-ranging common peafowl. Peacocks with longer trains and tarsi were more likely to establish a display territory in a central position within the lek and had a higher number of intrusions and agonistic interactions. These traits appeared therefore to be under intrasexual selection. Female selection was assessed as the number of copulations. Mating success was positively correlated with behavioural traits (display activity) and with train ornamentation (number and density of ocelli) suggesting that females use multiple cues during mate selection. Therefore, intra- and intersexual selection seem to operate on different sets of traits. Overall, our results stress the role of multiple receivers on the evolution of multiple signals.

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Introduction

In many species males exhibit complex courtship displays, using multiple sexual characters such as ornamentation coupled with vigorous display. Never-

theless, the evolution of the multicomponent nature involved in most sexual displays remains poorly understood because the majority of studies on sexual selection have focused on single traits involved in male–male competition or in female mate choice.

Empirical and theoretical studies have only recently begun to examine how both processes of sexual selection (male–male competition and female choice) may interact to promote the evolution of multiple signals (see Arnold & Wade 1984a,b and references therein). Several studies on the ring-necked pheasant, *Phasianus colchicus*, tried to identify male traits used in male–male competition or for attracting females but failed in establishing a clear distinction between them as the same traits (including spur and tail length, wattle display duration) seem to be used both in intra- and intersexual selection (reviewed by Mateos 1998). However, in the yellow-browed leaf warbler, *Phylloscopus inornatus*, it has been shown that females use more than one character to choose their mates, and these traits differ from those used during male contests (Marchetti 1998). Female scarlet-tufted malachite sunbirds, *Nectarinia johnstoni*, and female red-collared widowbirds, *Euplectes ardens*, show a strong preference for one signal (tail elongation), whereas another trait (pectoral feather tufts or the red collar respectively) is used during male agonistic interactions (Evans & Hatchwell 1992a,b; Pryke et al. 2001).

To date, several hypotheses have been proposed to explain the evolution and maintenance of male multiple traits. According to the multiple message hypothesis, different signals might convey information on different properties of male quality (Møller & Pomiankowski 1993; Johnstone 1995). The redundant signal hypothesis states that although each signal reflects the same information about male quality, the addition of several signals enhances the precision and the reliability of mate choice (Zuk et al. 1992; Møller & Pomiankowski 1993). Finally, the unreliable signal hypothesis postulates that signals do not reflect current male quality and have evolved as a consequence of a pre-existing female sensory bias unrelated to mate choice (Ryan 1990; Møller & Pomiankowski 1993; Rowe 1999). Holland & Rice (1998) put forward another hypothesis for the evolution of multiple signals based on the antagonistic coevolution between the sexes or, in the case of lekking species on male–male signal-receiver antagonistic coevolution. More recently, Pryke et al. (2001) developed the idea that multiple signalling can be stable not because of multiple messages but because of multiple receivers, in this case males and females.

Although the peacock (*Pavo cristatus*) train is the classical example of an extravagant trait evolved under the action of sexual selection, few studies have addressed the issue of multiple signalling in this species (Rands et al. 1984; Petrie et al. 1991; Yasmin & Yahya 1996). Peahen mate choice has been shown to be based on both morphological and behavioural traits (number of eyespot in the peacock's train: Petrie et al. 1991; Petrie & Halliday 1994; train length: Yasmin & Yahya 1996; call length: Yasmin & Yahya 1996).

In lekking species, such as the peafowl (Rands et al. 1984), males congregate on a communal display area during the breeding season. They first compete with

other males to establish a breeding territory that contains no resources. They then defend it from intruders. Intrasexual agonistic behaviour is frequent among males who jockey for a status or a position that conveys maximal attractiveness to females (Bradbury 1981). Central positions are often occupied by older, more dominant, males that achieve a disproportionate share of female copulations (Bradbury & Gibson 1983). Therefore male–male competition can indirectly affect mating success. Females visit the lek when sexually receptive and 'sample' numerous males before selecting a mate. The distribution of mating is highly skewed among males who provide nothing to their offspring but genes (Davies 1978; Payne 1984). Despite territory is obviously a valuable resource for a male as it is a prerequisite for attracting a female, the role of male–male competition has not previously been investigated.

The aims of the present study were to: (1) investigate which character(s) may be under intrasexual selection in peacocks, (2) elucidate peahens mating preferences, (3) investigate whether these two processes of sexual selection target one or multiple traits; and (4) discuss possible mechanisms for the origin and maintenance of complex ornamental and behavioural displays.

Methods

The study was carried out at the Parc zoologique de Clères, National Museum of Natural History, France, on a population of free-ranging common peafowl. The age of the population (peafowl were already present in the Park 30 yr ago when the National Museum of Natural History acquired it) as well as the number of founders are unknown. Peafowl were not used to be caught or manipulated but were acclimated to humans visiting the zoo. All individuals used in the study were 3-yr-old or older. Males and females were caught in early spring 2001 and marked with numbered and coloured metallic rings. Tarsus, spur and train length (from the base of the tail to the tip of the longest feather) were measured. Number of eyespots in the train was recorded from digital photographs (AGFA E Photo 1280) of males facing the camera with all the eyespots fully displayed. We successfully photographed 28 males.

Peafowl were observed between 29 May and 5 July 2001. In total 120 h of focal observation sequences were performed between 09:00 and 17:00 h with a mean duration of about 3 h per sequence. During observations, displaying positions and agonistic interactions were mapped in order to identify males defending a display site. Males clustered territories at two areas separated by at least 200 m, we therefore assumed they were forming two leks and focused on the largest one (34 territorial males). Territory size was not constant within the lek. Territories were smaller at the centre of the lek, as it is usually observed (Höglund & Alatalo 1995). Accordingly we used the number of neighbours as an index of central position within the lek rather than measuring the distance between sites.

Because of time constraints, we focused our observations on 34 territorial males (out of a total population of 61 males). For these 34 males, we recorded the following behaviours: (1) number and duration of displays; (2) number of calls,

and for each call the number of notes (e.g. we considered one call and three notes when a male called 'kian kian kian') (see Yasmin & Yahya 1996); (3) number of female visits; (4) number of copulations accepted by a female; (5) number of male intrasexual interactions (i.e. a male giving up his place to an approaching male, a territorial male threatening or chasing a floater male). Aggression between two neighbouring territorial males involved walking parallel to one another along the boundary between their territories with their train down, or physical contact with the males jumping up and striking at each other with their spurs (Petrie et al. 1991).

Statistical Analyses

We used generalized linear models (proc GENMOD; SAS Institute, Cary, NC, USA, 1999) to explore correlates of territory establishment and mating success. The distribution of error terms was binomial, normal, or Poisson, depending on the dependent variable analysed (with the corresponding link function: logit, identity and log). We started with the saturated model and we subsequently dropped step by step all non-significant terms. Differences in sample sizes indicate missing values (e.g. not all territorial males were photographed and therefore number of eyespots was unavailable).

Variables describing displays (number and duration of displays, song rate, number of notes) were highly correlated (all $r > 0.5$). We therefore ran a principal component analysis (PCA) with all behavioural variables. The first axis explained 55% of the total variance and loaded positively on all the variables entered in the PCA. The second axis explained 22% of variance (cumulative variance explained 77%) and loaded positively on the variables describing display frequency and duration and negatively on variables describing song characteristics. Both axes were used in the statistical analyses but axis 2 was never retained in the final model.

Results

Intrasexual Selection for Territory Establishment

We identified three types of males. Seventy-four per cent (45/61) exhibited 'territorial' behaviours. For example, they defended display territories and displayed to and mated with females on these territories. Twenty-three per cent (14/61) did not show any site attachment. These floating males displayed their train to females on different non-defended places, or they displayed on the territories of territorial males that rapidly chased them. Finally, two of 61 males (3%) were never seen displaying.

The likelihood to establish and defend a display territory was positively and significantly correlated with tarsus length and more strongly with train length (stepwise multiple logistic regression with binomial error: tarsus length, $\chi^2_1 = 3.844$, $p = 0.0499$; train length, $\chi^2_1 = 8.163$, $p = 0.0043$; $n = 61$; Fig. 1a,b). Spur length was not significantly correlated with territory establishment ($p > 0.2$) and was not retained in the final model. Adding number of ocelli to the stepwise model
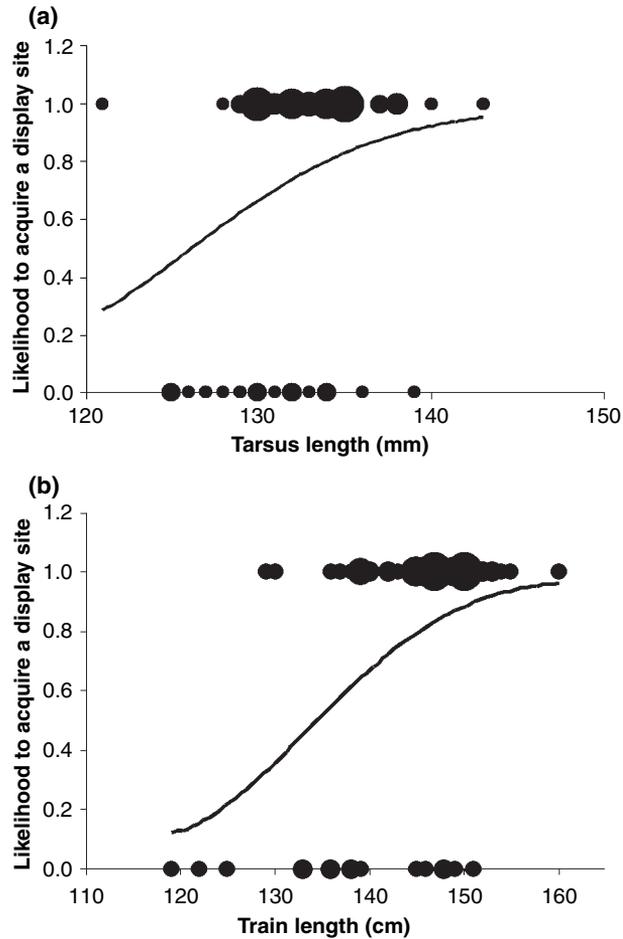
Fig. 1: Effect of tarsus (a) and train length (b) of peacocks on the probability to acquire a display site. Dots of different size indicate overlapping values (from 1 to 8)

did not change the results as train and tarsus length were again the only significant predictors of territory establishment (stepwise multiple logistic regression with binomial error: train length, $\chi_1^2 = 4.578$, p = 0.0324; tarsus length, $\chi_1^2 = 4.437$, p = 0.0352, n = 41).

There was intense competition for a display site as witnessed by the number of male–male agonistic interactions and intrusions. Tarsus length explained a significant proportion of the variation in the number of neighbours within the lek with males with longer tarsi having more neighbours (generalized linear model with Poisson distribution of errors: $\chi_1^2 = 4.77$, p = 0.029, n = 34). Moreover, the variation in number of agonistic interactions was explained by both train length and display activity (PCA 1) (generalized linear model with Poisson distribution

of errors: $\chi^2_1 = 10.63$, p $= 0.0011$ and $\chi^2_1 = 22.17$, p $<$ 0.0001, n $= 34$, respectively), whereas the number of intrusions was positively correlated only with train length (generalized linear model with Poisson distribution of errors: $\chi^2_1 = 6.85$, p $= 0.0088$, n $= 34$).

Intersexual Selection

We defined mating success as the total number of copulations accepted by females for a given male. The distribution of copulations was highly skewed towards a few males. We observed a total of 24 copulations performed by 12 different males among 34 observed birds. The preferred male gained nine matings (37.5%) and mated with five different females, one mated three times (with three different females), two twice (with two different females) and eight once. Among non-territorial birds, only one secured a single copulation. Five of 17 mated females copulated more than once and three did it with two different males. Unfortunately these numbers were relatively small to draw any conclusion.

We also assessed female preference by scoring the number of female visits experienced by a given male. This variable was positively correlated with number of copulations ($r_s = 0.421$, p $= 0.0032$, n $= 34$). The only significant predictor of number of female visits was the number of ocelli (generalized linear model with Poisson distribution of errors: $\chi^2_1 = 8.11$, p $= 0.0044$, n $= 28$), so the most ornamented males were the most visited by females.

We used a multiple generalized linear model with a Poisson distribution to assess factors affecting mating success (i.e. number of copulations). Display behaviours were not correlated with any of the ornamental traits (all p $>$ 0.15). Male copulation success was explained by display activity (generalized linear model with Poisson distribution of errors: PCA 1, $\chi^2_1 = 5.13$, p $= 0.0235$, n $= 28$), number of ocelli ($\chi^2_1 = 6.80$, p $= 0.0091$, n $= 28$, Fig. 2), and train length ($\chi^2_1 = 3.88$, p $= 0.0490$, n $= 28$). Surprisingly, males with shorter trains were more successful than peacocks with longer trains. As number of ocelli and train length were positively correlated (r $= 0.324$, p $= 0.0386$, n $= 41$), it might be difficult to explain female preference for short-tailed males. One possible explanation could be that females actually use a visual cue to assess number of ocelli based on the density of eyespots. To investigate this hypothesis we computed the density of ocelli as the number of eyespots divided by the surface of the train (we assumed that the train has a semicircle shape with a radius equal to train length). Density of ocelli was negatively correlated with train length (r $= -0.672$, p $<$ 0.0001, n $= 41$) and, as expected, was a good predictor of male mating success (generalized linear model with Poisson distribution of errors: $\chi^2_1 = 6.05$, p $= 0.0139$, n $= 28$).

Discussion

We found that several morphological and behavioural traits determine the outcome of intra- and intersexual selection in peafowl. Tarsus and train length are
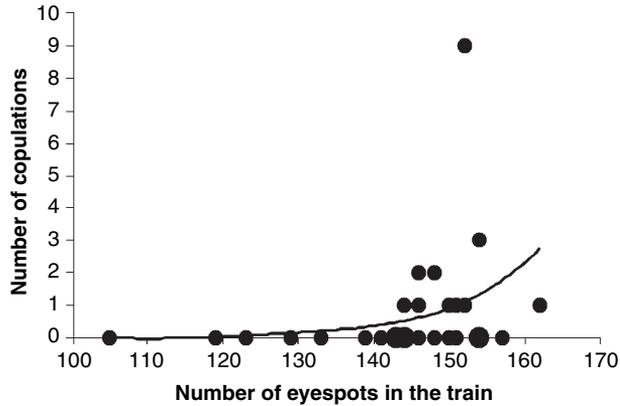
Fig. 2: Positive correlation between number of copulations and number of eyespots in the train in peacocks

involved in territory acquisition within the lek, whereas train ornamentation (number and density of eyespots), and visual and vocal displays are used by females during mate choice.

Intrasexual Selection for Territory Establishment

Establishing and defending a territory is a major determinant of mating success as all but one of the males who succeeded to attract a mate, also successfully acquired and defended a display site within the lek. The probability of acquiring and defending a territory was related to morphological features including train and tarsus length that may reflect male competitive ability. Although spurs are usually involved in agonistic behaviours (pers. obs.), we did not find any evidence suggesting that spur length might affect the likelihood to acquire and defend a display site. Our result supports previous findings indicating that territorial peacocks are heavier and have longer train than floating males (Petrie et al. 1991) suggesting that more vigorous males are more dominant. Moreover, the peacock's train may by itself play a role in agonistic behaviours. Indeed an intruder spreading its train encourages an attack from the resident male, and territorial males usually use their train as a threat in aggressive interactions to chase floating males without physical contact (Petrie et al. 1991). It is well documented that an elongated tail may be a handicap to the bearer because it is costly to produce and maintain (Møller 1989; Evans & Thomas 1992; Balmford et al. 1993; Savalli 1994; Møller & Petrie 2002). Hence in the peacock, only high quality males may be able to bear a long train, and train length may act as an honest badge of status during male contest. Territorial birds might benefit from displaying their status if this prevents escalation and the related costs (energy expenditure and injury risk) (Rohwer 1982).

Empirical studies on spatial and territorial features of male lekking species state that males often compete for central positions (reviewed by Höglund & Alatalo 1995). It seems to be the same in the peafowl as males with longer tarsus length acquired a display site in a more central position within the lek. Furthermore, males with the longest trains and the highest display activity showed the highest number of agonistic interactions and intrusions. Hence, tarsus length may be involved in territory establishment and position into the lek, whereas train length may play a role on territory maintenance. Finally, higher quality males with longer tarsus and longer trains might be more dominant males that have preferential access to high quality display sites.

Intersexual Selection

We showed that peahens use multiple signals to choose their mates. Both morphological (train ornaments) and behavioural (visual and vocal displays) male attributes were used by peahens during mate choice.

The number and the density of eyespots were the only morphological traits that predicted female visits and mate choice. Contrary to previous results reported by Petrie et al. (1991) and Yasmin & Yahya (1996), train length was not positively correlated to mating success in this peafowl population. Actually, our results suggest that females might prefer short tailed peacocks. This result might appear difficult to explain, especially because number of eyespots and train length were positively correlated. However, we suggest that the negative correlation between train length and mating success could be a by-product of female preference for higher eyespot density. Theory on animal communication tells us that a signal sent by a signaller has to be received and perceived by the receiver to be functional (see Swaddle 1999 for a discussion of perception thresholds in asymmetric traits). A key question concerning the role played by eyespots on female preference is how can peahens assess the number of eyespots. It is possible that the visual perception of a dense cluster of ocelli is more informative than a diluted number of eyespots over a large surface. By assessing eyespot density, females might therefore favour males with larger number of ocelli for a given unit of surface. Interestingly, given that train length is under positive intrasexual and negative intersexual selection, there is scope for conflicting forces operating on the same trait. Andersson et al. (2002) found the same pattern of conflictual selection in the red-collared widowbird with male competition selecting for redder collar and shorter tail, while females prefer males with longer tails. Given the small sample size and the correlation nature of the present study, this hypothesis of antagonistic selection on tail length definitely deserves more data and an experimental approach to be tested.

Surprisingly, behavioural components of the peacock's display (i.e. vocal and visual displays) have received little attention. Our results suggest that behavioural cues affect the outcome of female choice in addition to, and independently of, male ornaments. Although this is the first study, to our knowledge, to report peahen preference for display activity, females of other lekking species are known

to assess male quality using behavioural cues (e.g. Höglund & Lundberg 1987; Andersson 1989).

In lekking species, males do not contribute to offspring care and females are often believed to obtain nothing but indirect benefits through gametes (Höglund & Alatalo 1995). The good genes theory of sexual selection postulates that female preference for males with particular phenotypes is driven by the benefits of transmitting viability and/or pathogen resistance genes to the progeny (Hamilton & Zuk 1982). Phenotypic cues used by females therefore have to be reliable signal of male 'genetic quality'. Costly traits are the most likely candidates as honest indicators of male quality. Both train ornaments and visual and vocal displays of peacocks are likely to be energetically costly to produce and maintain (Møller & Petrie 2002). Although no study has measured the energetic costs of display in peacocks, the strut display of another lekking species, the sage grouse, *Centrocercus urophasianus*, induces substantial energetic demands and only males with the highest display rate and therefore the highest energy expenditure successfully mate (Vehrencamp et al. 1989). In agreement with the view that females use male phenotypic characteristics to gather indirect benefits, peahens mated with more ornamented males produce offspring with higher growth rate and survival prospects compared to females mated to less ornamented males (Petrie 1994). Recent studies have however also stressed the role of differential maternal investment as a determinant of offspring phenotype and life-history traits (see Sheldon 2000 for a review). Definitely more work is needed to disentangle the effect of paternal genes from maternal effects.

Evolution of Multiple Traits

Our results show that, in the peafowl, the two forces of sexual selection (male–male competition and female preference) may target different traits and favour the diversification of male signalling. Separate agonistic and epigamic signals can coexist because they are selected by different receivers, in this case males and females (Pryke et al. 2001). For a given male, one trait can reflect the ability to fight and could be involved in the outcome of contests between males, whereas another trait can reflect the ability to raise offspring, or a low parasite load, and therefore be used by females. The multiple receiver hypothesis, however, does not exclude that each display might signal a single property of the overall quality of an individual. Experimental manipulation of traits thought to be involved either in male/male competition or female choice might elucidate the role of such forces on the evolution of multiple signalling.

It is not obvious why peahens use multiple traits to choose a mate. Rowe (1999) reviewed studies that support the idea that two components enhance message transfer and therefore are better received than one trait alone. Multiple signals might increase the probability of detection, lower the intensity at which detection occurs, and reduce the reaction time, through the exploitation of female pre-existing sensory bias (Rowe 1999). During the peacock display, movement and calling could increase the detectability of visual traits such as the number or

the density of eyespots. It may also be easier for receivers to distinguish between signallers on the basis of differences in two or three signal components rather than a single one (Rowe 1999).

According to the multiple message hypothesis, different signals might convey information on different properties of male quality (Møller & Pomiankowski 1993; Johnstone 1995). This might be particularly true for plumage ornaments and behavioural displays for several reasons. Plumage ornaments are static traits produced during the annual moult that might indicate male quality during moult but not necessarily reflect male quality when mate choice occurs. Conversely, behavioural displays are flexible traits that might reflect current health status or general phenotypic condition of males. Costs of production and maintenance are also likely to differ between feather ornaments, and visual and vocal displays, reinforcing the idea that they convey different types of information to prospective mates.

Acknowledgements

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