Behav Ecol Sociobiol (1994) 35:213–217

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Experimental and natural changes in the peacock's (*Pavo cristatus*) train can affect mating success

Received: 18 December 1993 / Accepted after revision: 2 July 1994

Abstract Petrie et al. (1991) demonstrated a correlation between the degree of elaboration of peacocks' trains and their mating success, and also showed that this correlation occurred because females preferred to mate with the male that had the most elaborate train of those sampled on the lek. Although these data suggest that female choice is responsible for non-random mating in this species, they do not conclusively show that train morphology is the cue that females respond to, because they do not rule out the possible influence of another unidentified variable which is correlated with train elaboration. This paper presents an experimental test of the importance of the peacock's train in determining male mating success. If the number or arrangement of eye-spots in the peacock's train influences mating success, then changing the number of eye-spots should change mating success. This prediction was tested in an experiment where the trains of male peafowl (*Pavo cristatus*) were manipulated by removing a number of eye-spots between mating seasons. Peacocks with eye-spots removed showed a significant decline in mating success between seasons compared with a control group. This result, together with the observational data, supports the hypothesis that the peacock's train has evolved, at least in part, as a result of female choice.

Key words *Pavo cristatus* · Female choice
Male morphology · Experimental manipulation
Mating success

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Introduction

The evolution of elaborate male ornaments, of which the peacock's train provides the classic example, presents some severe theoretical and empirical problems (see Harvey and Bradbury 1991). While such characters are generally assumed to have evolved through the action of female choice, they are also subject to other selection pressures. For example, they may play a role in competition among males, as 'badges' of status (Halliday 1990). Many studies have demonstrated that some form of sexual selection is involved in the evolution of epigamic characters. The commonest approach is to show a positive correlation between the development of a male character and mating success. An increasing number of studies have taken the necessary next step, eliminating the possibility that such a correlation merely reflects the influence of some unidentified third factor, by experimentally manipulating the male character and showing a predicted increase or decrease in male mating success (e.g. Andersson 1982; Møller 1988; Höglund et al. 1990; Barnard 1990; Andersson 1992). Not all of these studies have conclusively shown that this change in mating success occurs solely through the action of female choice for male morphology. The study of Andersson (1982) does not rule out an effect of the experimental treatment on competition between males and the manipulation of Barnard (1990) also resulted in a change in male display behaviour.

Petrie et al. (1991) demonstrated a correlation between the degree of elaboration of peacocks' trains and their mating success and also showed that this correlation occurred because females preferred to mate with the male that had the most elaborate train of those sampled on the lek. Although the data on female sampling behaviour suggest that female choice is responsible for non-random mating in this species, they do not conclusively show that train morphology is the cue that females respond to. This paper presents an experimental test of the importance of the peacock's train in determining male mating success.

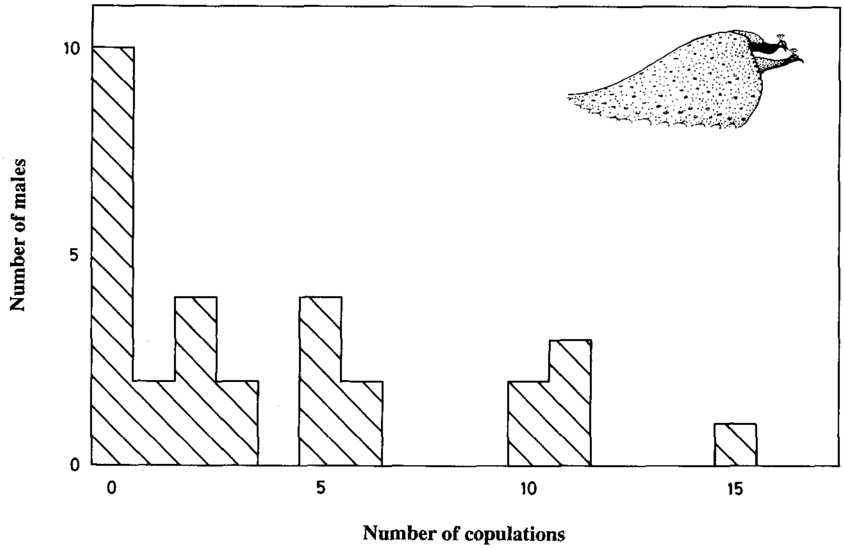

Fig. 1 Frequency distribution showing the number of copulations a male gains

Methods

A free ranging, feral population of blue peafowl has been observed at Whipsnade Park, Bedfordshire, U.K., since October 1987. For a description of basic research methods see Petrie et al. (1991). The main data presented here were collected during the 1989 and 1990 mating seasons when four leks were observed every day from the time birds started to display in the morning until they stopped around midday (c. 0800–1300 hours). Additional data on mating success were obtained in 1988 when one lek was observed in the same manner. Observations were made from either canvas hides or vehicles positioned in order to maximise the number of males in view. The total number and identity of all marked birds present at or near the lek sites was recorded. If a female approached a male, and he displayed and shivered his train to her, their identities and any subsequent mating behaviour were recorded.

During the mating season displaying males were photographed and the number of feathers ending in eye-spots (ocelli) was later counted from enlarged transparencies. Each male was photographed several times and the maximum count was used. Care was taken to photograph the entire train and where an object obscured part of the train the number of eye-spots obscured was estimated by comparison with other photographs of the same male or very occasionally with the other non-obscured side of the train.

During the winter of 1989–1990 we caught 22 full-trained males, removed eye-spots from 11 and then released them. We removed 20 eye-spots from each of the experimental males, cutting the eye spot from the end of the feather shaft with a pair of scissors. Each time we cut a feather we chose the longest shaft and therefore removed the 20 outermost eye-spots. This manipulation did not affect the overall length of the train which is determined by feathers which end in a "V" rather than an eye-spot. Not all of the males captured and released established display sites where they could be observed. We therefore had fewer experimental birds than originally planned. We decided to look at the effect of the experimental manipulation on the *change* in mating success of marked birds between successive years (1989 and 1990), in comparison to a control group whose mating success was also measured in 2 successive years. Control birds were captured and handled in the same way; the 20 outermost eye-spots were singled out but not removed from their trains. Mating success was highly skewed and not normally distributed, so non-parametric tests were generally used for analyses involving this variable. However, change in mating success was normally distributed and therefore parametric tests were used in analyses involving this variable.

Results

Variation in mating success within a season

Figure 1 shows the frequency distribution of mating success across the four leks observed in 1989. As in other lekking species, there are a relatively few successful males and most males gain zero or only a few matings. Petrie et al. (1991) identified variation in the male's train as an important factor contributing to this variance in mating success. However, that analysis only considered variation at one lek site and it is important to establish whether variation in train morphology significantly accounts for variation in mating success when males at several lek sites are considered together. Figure 2 shows that there is a significant positive correlation between mating success, measured as the total number of copulations that a male achieves, and the total number of eye-spots in his train ($n = 27$, $r_s = 0.475$, $P < 0.015$). This analysis is valid so long as mating success is independent of which particular lek a male belongs to. A multiple regression with mating success (log-transformed) as the dependent variable and eye-spot number and lek site as independent variables revealed that lek site was not a significant correlate of mating success after controlling for the other variable (overall regression $F_{2,26} = 4.404$, $P = 0.0176$; total number of eye spots, coefficient $= 0.48$, $t = 2.77$, $P = 0.035$, lek site, coefficient $= -0.22$, $t = -1.29$, $P = 0.21$).

Effect of changes in train morphology on mating success

If the number or arrangement of eye-spots in a male's train influences his mating success, then reducing the number of eye-spots should reduce mating success. We tested this prediction by comparing the change in the number of copulations between years of the experimen-

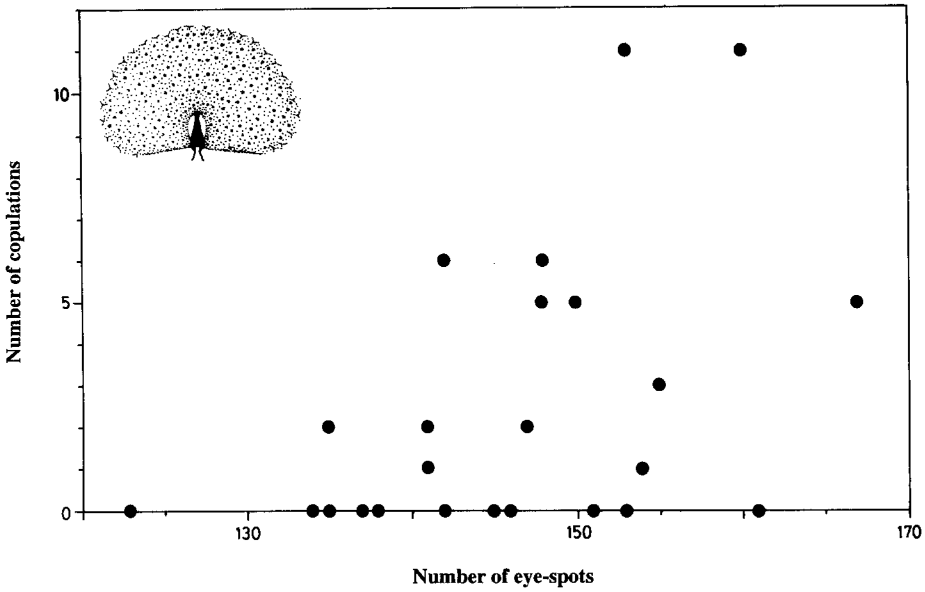

Fig. 2 The relationship between the number of copulations a male obtains and the number of eye-spots he has in his train, as counted from enlarged photographs

tal group of males with that of the control group (see above). The experimental males were marked individuals for whom 20 eye-spots have been removed when caught in the winter ($n = 6$) and the control group were marked males who were caught in the winter but whose trains were left intact ($n = 3$) in addition to marked males who were not caught between years ($n = 12$). There were only three males in the control group for whom we had collected data on mating success in both years, which had been caught in the winter and had received virtually identical treatment to the experimental group. There was no significant difference between the change in mating success of this group ($n = 3$) and the experimental group (one male in this control group also showed a marked decline in mating success). It could be argued that this control group is too small to allow for a meaningful direct comparison with the experimental group, and since the change in mating success of these three males did not differ from that shown by 12 males who were not caught in the winter but for whom we had mating success data ($n_1 = 3$, mean change $= -2$ SE $= 1.5$, $n_2 = 12$, mean change $= 1$, SE $= 0.718$, $t = 1.8$, n.s.) we combined these groups to provide a large enough sample of males to compare with the experimental group.

Both groups include males who failed to gain any matings at all in the first year of observation, 2 out of 6 in the experimental group and 4 out of 15 in the control group. Although these males cannot achieve fewer than zero matings, there is the possibility that their mating success can increase between years (as well as stay the same) and, since the proportion of these males does not differ substantially between the groups, we decided to include these males in the analyses that follow. There was also no difference in the absolute mating success of the two groups in 1989 ($n_1 = 6$, mean number of copulations 3.833 (range 0–11) $n_2 = 15$, mean $= 3.619$ (range 0–11).

We found that there was a significant decline in mating success between seasons in the experimental group in comparison to the combined control group (see Fig. 3) ($n_1 = 6$, $n_2 = 15$, $t = 1.923$, $P = 0.0347$, one-tailed), and we could therefore reject our null hypothesis that a reduction in the number of eye-spots in the train does not result in a decline in mating success. Since the control group mainly consists of males that were not caught (12 out of 15) it is possible that the difference in the change in mating success between the experimental and combined control groups is a result of capture

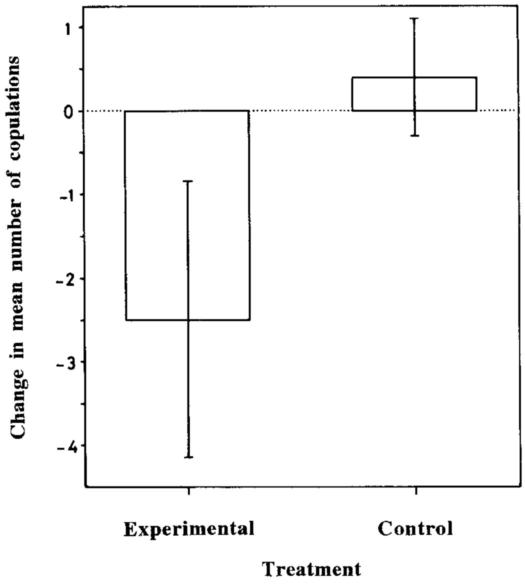

Fig. 3 Change in number of copulations between seasons for those males who had 20 eye-spots removed ($n = 6$, mean $= -2.5$, SE $= 1.6$) in comparison with those males whose trains were not manipulated ($n = 15$, mean $= 0.4$, SE $= 0.7$), $t = 1.923$, $P = 0.035$, one-tailed test. The control group includes 3 males who were caught overwinter but whose trains were not manipulated

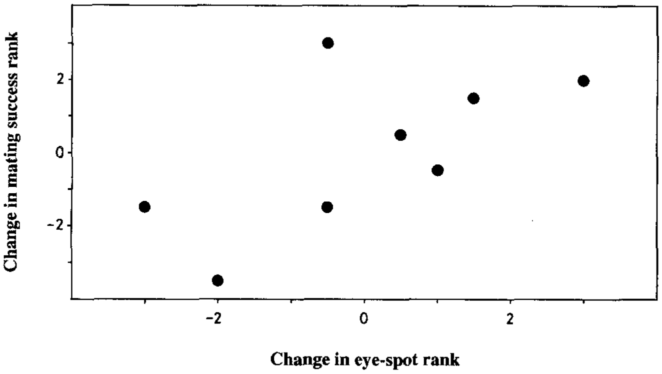

Fig. 4 The relationship between the change in the rank position of a male on a lek between years in terms of his mating success and the between year change in the rank position of that individual in terms of the number of eye-spots in his train ($n = 8$, $r_s = 0.637$, $P = 0.054$)

rather than the manipulation of the trains. Although we cannot completely rule out this possibility we feel that it is unlikely, because the following analysis provides no evidence that winter capture by itself reduces mating success. Of the 12 control birds who were not caught in the winter 1989/1990, 4 were caught in the winter 1988/1989 and 8 were caught in winter 1987/1988. If capture reduces mating success, the four birds caught in winter 1988/1989 would have a relatively low success in 1989 and a increased mating success in 1990 in comparison to the eight males which were not caught prior to either the 1989 or 1990 breeding seasons. However, we did not find any difference between the change in mating success between these groups ($n_1 = 4$, mean change = 1.5, SE = 0.86, $n_2 = 8$, mean change = 0.375, SE = 1.224, $t = 0.603$, n.s.), although it should be pointed out that small sample sizes mean the power of this test is quite low (0.3) and therefore the probabilty of making a type II error is quite high (0.7).

It could also be predicted that an increase in the number of eye-spots in a male's train would result in an increase in mating success. However, it proved impossible to effectively increase the number of eye-spots in the train for two reasons. First, we found it difficult to catch a sufficient number of displaying males and, second, the number of feathers in the train (approx. 230) and their complex arrangement precluded crude manipulation. There are however naturally occuring changes between years, both in train morphology and in mating success, and these include increases in train elaboration as well as decreases. To see whether these natural changes in train morphology correlate with changes in mating success we looked at the change in rank of birds with respect to these two factors at one lek site where the largest number of males had been measured in 2 successive years and where there were no captures and experimental manipulations. Ranked data were used in this analysis because, unless a change in eye-spot number resulted in an individual having more or less eye-spots than other displaying males, these changes were unlikely to result in a change in mating success. Figure 4 shows that there is a non-significant positive relationship between the change in mating success and the change in eye-spot number. If the relative number of eye-spots alters, with respect to the number of eye-spots in the trains of other males at a lek site, then the relative number of copulations that male achieves tends to change in the same direction ($n = 8$, $r_s = 0.637$, $P = 0.054$).

Discussion

The experimental result supports our observational evidence and suggests that the quality of the male's train could be an important determinant of mating success. As we considered the change in mating success of individuals as a result of a reduction in the number of eye spots between seasons, there is no possibility that chance differences between the experimental and control groups as a result of sampling error could have contributed to the result. However, there is a possibility that capture *per se* may have contributed to the decline in mating success.

When we removed the eye-spots we only "nipped" out the eye at the end of the feather. The overall length of the train is determined by those feathers that end in a "V" and not an eye-spot, so we were not altering the overall length of the train by this manipulation. However, it is possible that we altered other aspects of the train by our manipulation, such as its overall symmetry and consequently its aesthetic appearance to peahens. A recent theory suggests that females are attracted not merely by the degree of development of a male character, but also by its symmetry. There are theoretical grounds for predicting that less-fit males will have less symmetrical epigamic characters (Møller 1990). There is some direct evidence that females do prefer males with symmetrical characters; female swallows (*Hirundo rustica*) appear to pay direct attention to the level of fluctuating asymmetry in the tails of their mates (Møller 1992, 1993). Symmetry may well be important in the peacock; Manning and Hartley (1991) have shown that the symmetry of a male's train increases as the number of eye-spots increases. Although we manipulated the number of eye-spots, it is also unsafe to assume that peahens count eye-spots when choosing a mate; they could be responding to the overall amount of colour in the train which is affected by the number of eye-spots but could also be affected by eye-spot size.

Manning (1987, 1989) found a relationship among known-age peacocks between age and degree of train development and suggested that the benefit that females derive from preferring males with elaborate trains is that their young are sired by older males that have demonstrated their ability to survive. However, results from Whipsnade suggest that the degree of train development is not necessarily age related and females do not always show a preference for older males (Petrie 1993).

The evidence presented here supports the idea that variation in male morphology affects mating success. We have shown previously that female choice is the most likely mechanism leading to variation in male mating success (Petrie et al. 1991) and we next need to consider why females have developed a preference for males with elaborate trains. Peacocks form leks and do not contribute to the care of the offspring, so females do not gain material benefits when choosing to mate with particular males. The classical view of a lekking species is that females must be gaining genetic benefits for their offspring when choosing particular males and that their preference has evolved through indirect selection. Either females gain genes which increase the chances that their offspring survive to maturity, or females gain for their sons those genes which have made their fathers attractive. This view has recently been challenged (Kirkpatrick and Ryan 1991; Reynolds and Gross 1990). These authors stress that, even though males do not contribute parental care in a lekking species, there may still be direct selection for female preferences. Females, by choosing particular lek males, may reduce the chance of predation on themselves by mating at a particularly safe site, or they may mate with a more fertile male, or they may gain a disease-free copulation, and it may not be necessary to invoke indirect selection for the evolution of female preferences.

Recent research at Whipsnade has shown that females will remate if they do not at first gain access to the more successful males (Petrie et al. 1992). This suggests that females are not merely interested in obtaining a "safe" copulation or a disease-free copulation, but are more interested in obtaining the sperm of particular individuals. Moreover, if females were gaining good viability genes for their offspring, it would be expected that attractive males would also have higher viability, and this is what has been found; males of low mating success were more likely to suffer predation (Petrie 1992). A similar result has also been found in lekking black grouse (*Tetrao tetrix*) where successful males are more than twice as likely to survive than unsuccessful lek males (Alatalo et al. 1991). These lines of evidence, although pointing towards the idea that females gain genetic benefits for their offspring through mate choice, do not provide a conclusive test of this hypothesis. What is urgently needed is a field study which relates paternity to offspring survival and subsequent mating success.

Acknowledgements We are grateful to Richard Kock and Peter Olney for their support and permission to work at Whipsnade Park, to Louise Barker, Ruth Cooper, Jonathan Cooper, Jonathan Daisley, Nigella Hillgarth, Emma Jerman, Chris Pierpoint, Carolyn Sanders and Frances Scott for their excellent assistance in the field and to the Research Committeee of the Open University and the Natural Environment Research Council for financial support.

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Communicated by M.A. Elgar