J. evol. Biol. 2: 379–384 (1989)

1010–061X/89/05379–06 $ 1.50 + 0.20/0

Age-advertisement and the evolution of the peacock's train

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Key words: Age-advertisement; evolution; peacock's train.

Introduction

The males of many polygynous species of bird have bright plumage, elaborate crests, pectoral bibs or elongated tail feathers. Outstanding among these species is the blue peacock (*Pavo cristatus*) with its long covert feathers, most of which end in vividly coloured ocelli. Such structures are probably costly, so how did they evolve? There are four possible answers which invoke female preference for male ornaments. Firstly, if there are some choosy females in the population then the sons of a choosy female will possess the preferred ornament and themselves be preferred by the daughters of other choosy females (Fisher, 1930; O'Donald, 1980). Secondly, if the ornament is a handicap then discriminating females should mate with males who have demonstrated their fitness by surviving to breed (Zahavi, 1975). Thirdly, the condition of ornaments may be dependent on parasite load. Females may choose "bright" males which will have a low parasite load and therefore advantageous genes for parasite resistance (Hamilton and Zuk, 1982). Finally, the development of male ornaments may indicate male age (Halliday, 1983; Manning, 1985). Choosy females should prefer old males who have demonstrated their genetic quality by surviving an array of selective pressures.

It is difficult to make testable predictions for the first two models. The bright bird theory predicts that highly coloured males should be best developed in species which have high parasite loads and also that females should prefer unparasitised males. While the former appears to be true (Read, 1987; Ward, 1988), two tests of the latter prediction have produced negative results (Borgia, 1986; Zuk, 1987).

The age-advertisement model predicts that male ornaments should contain age-dependent information and that females should on average prefer old males. There is some evidence for the latter prediction from field crickets (Zuk, 1987) and argus pheasants (Davison, 1981). The blue peafowl is an appropriate species to investigate the former question. It is intensely sexually dimorphic and almost invariably referred to in discussions on female choice and the evolution of sexual dimorphism. However, little is known of its biology. Attention is of course focussed on the male's train which originates from the back of the peacock and consists of three types of covert feather. The longest end in a fish-tail like structure, the striking ocellus-bearing feathers vary considerably in their length and finally there are curved feathers which form the edge of the train when erected (Fig. 1).

Most recent workers seem to feel that the train reaches its maximum development in the fourth year (Sharma, 1974) or at the very most the fifth or sixth year (Delacour, 1951). The older literature however contains hints that the train's development is more closely related to age. Jerdon (1864) states, "The train of course increases in length for many years at each successive moult." In the same vein Darwin (1871) suggested that the train increases in "beauty" for many years after maturity. More recently Manning (1987) has shown that train length, colour intensity of the ocelli, and ocellus size are significantly correlated with age up to 12 years. The ocelli of the train are the most striking feature of the peacock's display and the sheer number of these structures may be an age indication to the peahen. Manning (1987) found a weak association between the total number of train feathers and the age of males ($r = 0.33$, not significant at the 5 % level). It was suggested that this was worth investigating further as these feather collections, made in 1986, were to assess such features as feather length and colour and many of the smaller feathers were probably missed. In addition only two of the males were in aviaries which had fine wire mesh so that many of the smaller feathers would be blown away. Therefore reliable feather counts from 1986 data were only available for two birds. This paper reports results of (a) feather collections made in 1987 and

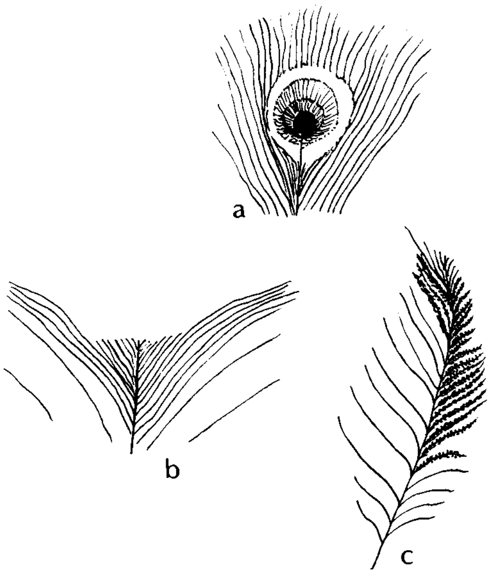

Fig. 1. The three kinds of feather in the train of the peacock (a) the ocellus-bearing feather, (b) the longest type which ends in a fish-tail structure, (c) the curved feather found at the edge of the train.

1988 together with (b) photographs of displaying males. Both methods reveal a strong correlation between male age and the number of feathers in the train and in particular the number of ocellus feathers.

Methods

It proved impossible to find a flock of peafowl of known ages. Aviculturists were therefore located who had males of known age. The housing of these birds varied (i. e. in aviaries, gardens or farms), as did their diets. However, any variation this introduced into feather number would tend to obscure rather than enhance an age/feather number correlation. The sample consisted of 28 males, ranging in age from 3 years (when the first ocellus feathers appear) to 14 years. Potential longevity i. e. "the maximum life span of an individual of a species under optimal conditions" (Lindstedt and Calder, 1976) seems to be about 20 years. Potential natural longevity in the field is not known. Two methods of obtaining feather counts were used. (a) Shed train feathers were collected and classified as fish-tail, ocellus or curved feathers. There were difficulties with this method. Firstly, it was impossible to be sure that all feathers had been found. This was particularly so for the very small ocellus feathers near to the neck of the male which tended to blow away. Secondly, a proportion of feathers were broken and difficult to assign to one of the three classes. (b) For free-range birds and others when more than one male was enclosed the displaying males were photographed – the difficulties here were of the male's head obscuring some feathers and the impossibility of counting the curved feathers. However this method works well for estimating the number of ocelli and is less stressful for the bird than catching it and counting feather number. It was decided to include only those ocelli which could be seen in the photographs and not to infer their presence behind, say the head of a male.

Results

Data obtained from feather collections are presented in Fig. 2. Feathers were obtained from twelve males. Collections made in 1986 and discussed in Manning (1986) were considered unreliable for total feather number except in the case of two males enclosed in aviaries. All other feather collections were made in 1987 and 1988. This meant that counts were available over 3 years for two males while other counts were for two or one year. Correlations of feather number with age were calculated for a sample size of 12. That is, when two or three years counts were available for a bird only the first was used to calculate the correlation coefficient. Values of r were as follows: number of ocellus feathers 0.76, $p < 0.01$; number of fish-tail feathers 0.62, $p < 0.05$; number of curved feathers 0.47, $p < 0.05$; all train feathers 0.81, $p < 0.001$. The inclusion of second and third year feather counts tended to increase values of r. For example the count for all train feathers increased in subsequent

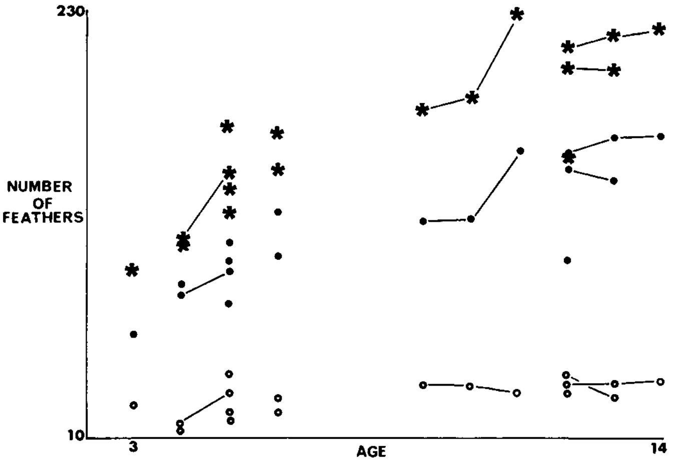

Fig. 2. Data from feather collections from twelve peacocks. Stars indicate counts of all feathers, closed circles are numbers of ocellus feathers and open circles are numbers of fish-tail feathers.

years for both birds for which three years counts were available and for one bird in which two years counts were available.

Data obtained from photographs of 16 displaying males are shown in Fig. 3. The correlation between number of ocellus feathers and age is $r = 0.67$, $n = 16$, $p < 0.01$. In general it seems that the number of ocelli was greater for the phogographed birds than for their conspecifics of the same age from which feathers were collected. This is probably accounted for by broken feathers and perhaps more importantly by the

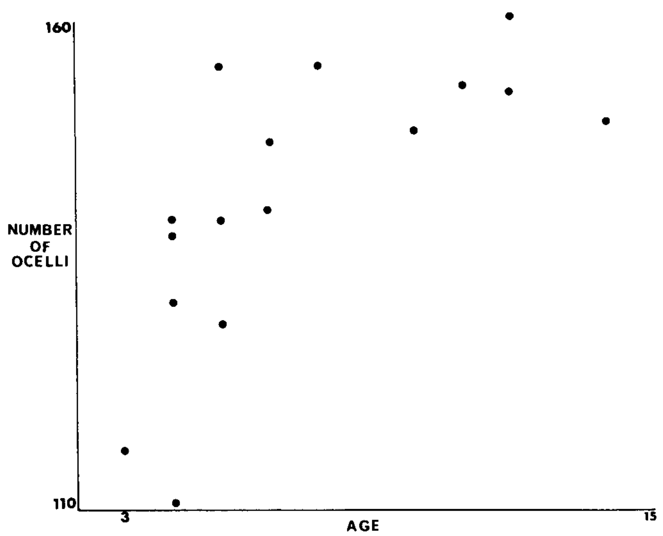

Fig. 3. Counts of ocellus – number from photographs of 16 displaying blue peacocks.

very short ocellus feathers being lost as birds tend to trample them into the soil or they are blown away. Photographing a displaying male is therefore the best way of measuring the number of ocelli he possesses.

Discussion

An interpretation of these results using the age-advertisement theory would be that peahens may choose the oldest available male if they prefer the male with the largest number of ocelli. Such a choosy female would therefore mate with a peacock who has demonstrated his genetic quality by avoiding death by predation, disease and evironmental extremes. Whether peahens can and do assess numbers of ocelli remains to be demonstrated. However the strong correlation between number of feathers in the train and age may explain a puzzling aspect of peacock display. When the train is erect the peacock often rattles the feathers together to produce a curious rustling noise. The volume of this noise may well be related to the number of feathers in the train and therefore the female may be using this noise as an age cue.

Data from the feather collections indicate that total number of feathers per train is more strongly correlated with age than any one feather type. This suggests that a mutation which increases say the number of ocellus feathers will do so at the expense of one or both of the other types of feather. Similarly Manning (1987) has shown that a combined ranking of ocellus colour intensity, mean size of ocelli and maximum length of fish-tail and ocellus feathers per train is more strongly related to age than any one of these variables by itself. This interdependence of age-related variables may provide a check against cheating mutations if females are assessing a range of male characters. For example a mutation which increases the length of fish-tail feathers but which reduces the development of other characters of the train would not enhance male reproductive success. The peacock's train as a whole seems therefore to be an honest advertisement of his age.

Acknowledgements

This work would not have been possible without the help of many aviculturists. My grateful thanks go to G. H. Ball, L. Bennett, T. Bona, P. Cookson, J. Crewdson, Ms L. Farrington, H. Hunter, P. King, D. Marrable, B. Melling, F. Mosford, T. Moss, E. Newhouse, P. J. S. Olney, D. Petrie, W. Prescott, F. Sheratt, G. Sowerby, Mr & Mrs Van Suchtelen, D. Wallis. I am also grateful to Professor A. J. Cain who read and commented on an earlier version of the manuscript. Financial support was provided by the World Pheasant Association and collected feathers are deposited with the Department of Vertebrate Zoology, Liverpool Museum.

References

Borgia, G. 1986. Satin bower bird parasites: a test of the bright male hypothesis. Beh. Ecol. Sociobiol. 19: 355–358.

Darwin, C. 1871. The Descent of Man and Selection in Relation to Sex. John Murray, London, UK.

Davison, G. W. H. 1981. Sexual selection and the mating system of *Argusianus argus* (Aves: Phasianidae). Biol. J. Linn. Soc. 15: 91–104.

Delacour, J. 1951. The Pheasants of the World. Country Life, London, UK.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford, UK.

Halliday, T. R. 1983. The study of mate choice, pp 1–32. *In* P. Bateson (ed), Mate Choice. Cambridge Univ. Press, Cambridge, UK.

Hamilton, W. D., and M. Zuk. 1982. Heritable and true fitness and bright birds: a role for parasites? Science 218: 384–387.

Jerdon, T. C. 1864. Birds of India, vol. 3. G. Wyman, Calcutta, India.

Lindstedt, S. L., and W. A. Calder. 1976. Body size and longevity in birds. Condor. 78: 91–94.

Manning, J. T. 1985. Choosy females and correlates of male age. J. theor. Biol. 116: 349–354.

Manning, J. T. 1987. The peacock's train and the age-dependency model of female choice. J. World Pheasant Ass. 12: 44–56.

O'Donald, P. 1980. Genetic models of sexual selection. Cambridge University Press, Cambridge, UK.

Read, A. F. 1987. Comparative evidence supports the Hamilton and Zuk hypothesis on parasites and sexual selection. Nature 328: 68–70.

Sharma, I. K. 1974. Ecological studies of the plumes of the peacock (*Pavo cristatus*). Condor. 76: 344–346.

Ward, P. I. 1988. Sexual dichromatism and parasitism in British and Irish freshwater fish. Anim. Behav. 36: 1210–1215.

Zahavi, A. 1975. Mate selection: a selection for a handicap. J. theor. Biol. 53: 205–214.

Zuk, M. 1987. Variability in attractiveness of male field crickets (Orthoptera: Gryllidae) to females. Anim. Behav. 35: 1240–1248.

Received 3 Oct. 1988;
accepted 21 Feb. 1989.
Corresponding Editor: P. Schmid-Hempel