



Do peahens not prefer peacocks with more elaborate trains?

ADELINE LOYAU*, MARION PETRIE†, MICHEL SAINT JALME‡ & GABRIELE SORCI§

*Station d'Ecologie Expérimentale du CNRS à Moulis, CNRS UMR 2936

†Evolutionary Biology Group, Newcastle University

‡Muséum National d'Histoire Naturelle (MNHN), UMR 5173

§Biogéosciences, CNRS UMR 5561, Université de Bourgogne

(Received 17 June 2008; initial acceptance 9 July 2008;
final acceptance 23 July 2008; published online 7 September 2008; MS. number: D-08-00401)

Keywords: female mate choice; interpopulation variability; ornament; *Pavo cristatus*; peafowl

Ever since Darwin (1871), the peacock's train has been cited as the icon of an extravagant conspicuous secondary sexual trait that has evolved through female mate choice. However, Takahashi et al. (2008) recently challenged this idea. They monitored female mate choice during 7 years in a feral peafowl, *Pavo cristatus*, population in Japan and found no correlation between male mating success and three morphological train traits. They concluded that 'combined with previous results, our findings indicate that the peacock's train is not currently the universal target of female choice' and proposed 'that the peacock's train is an obsolete signal for which female preference has already been lost or weakened' (Takahashi et al. 2008, page 1216). We feel that their conclusions are far too strong, particularly since three independent studies have found a relationship between train features and mating success (Petrie et al. 1991; Petrie & Halliday 1994; Yasmin & Yahya 1996; Loyau et al. 2005a). The purpose of this article is therefore to draw attention to alternative explanations and conclusions that are essential for the understanding of the complexity of mate choice. We first suggest some possible nonadaptive and adaptive explanations for the reported differences in female preferences in the peafowl. We then show that plasticity in mate choice is a widespread phenomenon across a large spectrum of species. Therefore, we suggest that findings based on a single

population can be misleading if generalized to the whole species.

The peacock's train is a complex structure that cannot be summarized with only three morphological traits (number of eyespots, train symmetry and train length). Two previous studies showed that the density and the coloration and iridescence of eyespots in the train have the potential to be involved in mate choice (Loyau et al. 2005a, 2007a). Consequently, Takahashi et al. (2008) cannot discard the possibility that they did not measure elements of the signal most relevant for female mate choice. Their main concern was the absence of correlations between the number of eyespots and mating success, consistent over the 7 years of their study. One explanation for this absence of correlation could be that, in the Japanese population, the train contains a trait preferred by the females that is not always positively correlated with the number of eyespots. Hence, it would not be possible to detect whether the train contains a signal under sexual selection. On the basis of their results, Takahashi et al. (2008) also concluded that train symmetry and train length were not components of the signal received by the females. However, does that mean that no signal exists? More recently, a correlational study suggested that females may use eyespot density in the train (Loyau et al. 2005a) rather than the number of eyespots, perhaps because this feature is more quickly assessed. This finding is not inconsistent with the fact that experimentally reducing the number of eyespots in the train decreased mating success (Petrie & Halliday 1994) since, by removing eyespots, Petrie & Halliday (1994) also reduced the eyespot density. Petrie et al. (1991) found positive correlations between eyespot number, train length and mating success, although the relationship between eyespot number and train length was negative in a sample of culled birds from one lek, all shot on the same day

Correspondence: A. Loyau, Station d'Ecologie Expérimentale du CNRS à Moulis, CNRS UMR 2936, 09200 Saint Girons, France (email: al@adeline-loyau.net). M. Petrie is at the School of Clinical Medical Sciences, William Leech Building, Newcastle University, Newcastle-upon-Tyne NE1 4HH, U.K. M. Saint Jalme is at the Muséum National d'Histoire Naturelle (MNHN), UMR 5173, MNHN-CNRS-Paris 6, France. G. Sorci is at Biogéosciences, CNRS UMR 5561, Université de Bourgogne, Dijon, France.

because of a change of paddock (Petrie et al. 1996). Takahashi and colleagues may be able to test for an effect of eyespot density, since they measured the number of eyespots and the train length of 24 peacocks for 3 years. This would be a valuable addition to our understanding of how the various components of the signal in the male's train affect female mate choice.

Takahashi et al. (2008) discussed the discordance between studies and suggested that missed observations of mating and small sample sizes of previous studies may play a part, claiming that their study had 'the longest observation with the largest sample size among peafowl studies' (Takahashi et al. 2008, page 1214). We agree that the number of copulations observed is critical to a meaningful analysis of variance in mating success. However, Takahashi et al. (2008) saw only 268 copulations in 7 years, which amounts to ca. 38 copulations per annum from 20 to 37 territorial males observed in any 1 year. In contrast, Petrie & Halliday (1994) saw 116 copulations in 1 year (1989) from observations of 30 territorial males (almost three times as many). We suspect the difference in the number of copulations observed may be caused by a difference in population size and in particular the number of reproductively active hens observed. The Japanese study reported a total population of 75–104 birds, which Takahashi et al. (2008) stated is male biased, whereas the Whipsnade population was estimated at 179 birds. Unfortunately, watching the same small population for a number of years does not overcome the problem of error associated with small sample size, as the dependent variable is the number of copulations per male per annum; the possibility therefore remains that there may be insufficient observations of copulations to detect an effect in the Japanese study.

There are other possible explanations for the discordance between studies, including uncontrolled variation as a result of small methodological differences. For example, train length was measured 'in early spring' in France (Loyau et al. 2005a), 'during the peak mating period' at Whipsnade (Petrie et al. 1991) and from the beginning to the peak of the mating season in Japan. This could confound the relationship, as there is marked variation in the timing of the start and length of time over which feathers drop. The number of feathers lost by the end of the season could relate to performance during the mating season, if expenditure on reproductive effort or mating success leads to an earlier or compressed train feather drop.

Takahashi et al. (2008) found an unusually low skew in male mating success. The most successful male obtained only 14.9–31.4% of copulations per year whereas in earlier studies these values were consistently higher (36.4% in Petrie et al. 1991; 32.3% in Yasmin & Yahya 1996; 37.5% in Loyau et al. 2005a). In the population studied by Takahashi et al. there appeared to be a low consensus among females about whom to mate with, an unusual finding in a lekking species. Could that be a result of low variation in train morphology which does not allow peahens to distinguish between the different potential mates? In the French population, we found that eyespot

density was the trait with the highest coefficient of variation (10.3%) while the coefficient of variation of the eyespot number was only 3.05% (Loyau et al. 2007b). It is unfortunate that Takahashi et al. did not provide the pattern of variation of the eyespot density in their population. Low variation in train morphology could arise if genetic variability is low. Consideration of variation is relevant because, apart from Yasmin & Yahya (1996), all the studies of peahen mate choice were carried out in an unnatural environment. Apart from the obvious problem that feral populations of peafowl do not undergo the same selection pressures as wild populations, these populations were established outside the original distribution range of the species several centuries ago, usually using a small number of individuals which could have created a strong genetic bottleneck. Isolated small populations are expected to have reduced genetic variability because of a combination of founder effects, inbreeding and genetic drift (Jaenike 1973). There are a number of instances where the conspicuous coloration of mainland birds has been lost on small island populations and genetic drift is often cited as a cause (Wiens 2001 and references therein). Another possibility is that, in some captive populations, not all founders have come from the same place in the native range of the species, resulting in a higher genetic diversity. Therefore, isolation combined with relaxed or modified selection pressures and/or mixed origins of founders could explain why Takahashi et al. found different results to those of previous researchers.

Reasons for the discrepancy between Takahashi et al.'s results and previous studies may not only reflect differences in methodology. There are several other explanations for what might be called plastic female choice. Indeed, divergence in behaviour among populations of a given species is widespread (Foster 1999; see also Hill 1994; Ptacek & Travis 1996; Márquez & Bosch 1997; Martins et al. 1998; Petrie & Kempenaers 1998; Dale et al. 1999; Griffith et al. 1999; Pfennig 2000; Kwiatkowski & Sullivan 2002; Safran & McGraw 2004). In particular, there is a growing body of evidence demonstrating a significant variation in male traits and female preferences between populations. Examples cover a wide range of taxa including insects, amphibians, fishes and birds (reviewed in Jennions & Petrie 1997). Endler & Houde (1995) examined the preferences of female guppies, *Poecilia reticulata*, among 11 populations in Trinidad and showed that mate preferences varied in intensity, direction and the number of traits used. In this species, females also differ in the relative importance that they place on male orange coloration or iridescence (Rodd et al. 2002).

Regardless of methodological differences (as suggested by Gil et al. 2001) or small sample sizes (as suggested by Espmark & Lampe 1993), heterogeneity between populations can arise by several mechanisms. Populations might differ in the amount of genetic variation for the trait of interest because of a founder effect and/or a genetic drift. Geographical variation in selection pressures can also produce genetic structuring among populations (e.g. Endler & Houde 1995; Brooks 2002). As mentioned above, such

genetic differences may account for the differences of pattern obtained by Takahashi et al. (2008). Furthermore, the cost of trait expression may vary with environmental conditions such as climate, predation risk, pathogen prevalence, conspecific density and sex ratio (e.g. Baird et al. 1997). A given trait within one environment may not reliably indicate mate quality in another environment (e.g. Klappert et al. 2007). Therefore, adaptive plasticity in female mate choice is thought to result from spatial and temporal variation in environmental conditions (e.g. Shine et al. 2006; Chaine & Lyon 2008), in addition to female phenotype (Jennions & Petrie 1997; Coleman et al. 2004). A spectacular illustration of the concept of adaptive plasticity in female mate choice has been recently reported by Chaine & Lyon (2008). In the lark bunting, *Calamospiza melanocorys*, sexual selection on male traits can vary dramatically across years and even show reversals in the direction of a single trait. Importantly, in a given year, these changes usually favour male traits that correlate with the highest reproductive success (Chaine & Lyon 2008). This shows unambiguously that a seemingly inconsistent female mate choice across years in fact targets the male phenotype that within each year provides the best reproductive output. Even though different selection mechanisms may arise for temporal and spatial variation, this example illustrates that, if temporal differences can be found within a given population, it is not surprising to find differences between geographically distinct populations. Finally, variation in male traits and female preferences can account for learning and cultural transmission. Indeed, male bowerbirds may copy peers when building bowers and this would explain interpopulation differences in bower designs (Madden 2006). Male song dialects in brown-headed cowbirds, *Molothrus ater*, are a consequence of complex interactions between male learning and population differences in female preferences (reviewed in Foster 1999; Freeberg 2000). Moreover, social influences such as sexual imprinting and mate choice copying can induce variation in female preferences (Freeberg 2000; Danchin et al. 2004). Preferences for male song can be influenced by social experience in female zebra finches, *Taeniopygia guttata*, and canaries, *Serinus canaria* (reviewed in Freeberg 2000).

Taken together, these examples highlight the fact that great caution is required when generalizing results from a single population to the whole set of populations of a given species, as already pointed out by Madden (2006) and Forstmeier et al. (2006). In the light of previous work by three independent groups on three independent populations of peafowl (Petrie et al. 1991; Yasmin & Yahya 1996; Loyau et al. 2005a) showing an influence of train elaboration in mate choice, it is thus rather surprising that, in their conclusion, Takahashi et al. (2008, page 1216) proposed that 'the peacock's train is an obsolete signal for which female preference has already been lost or weakened'.

Takahashi et al. (2008) also challenged the idea that the peacock's train might be an indicator of good genes, despite strong evidence supporting that hypothesis (Petrie 1992; Møller & Petrie 2002; Loyau et al. 2005b;

Petrie et al. in press). They asserted that since the peafowl is a galliform bird, the train is likely to develop in the absence of oestrogen and consequently is unlikely to be an indicator of male quality (Hagelin & Ligon 2001). Therefore, they expected females to discard this trait in mate choice. According to Takahashi et al. (2008) the female preference for the male's train is supposed to have been 'lost or weakened'. If so, it implies that this preference existed at some point and thus may still exist. Eyespots have independently evolved in several taxa (birds and butterflies) and it is likely that such a trait originally evolved through the exploitation of a sensory bias (Ryan 1990) which would also account for the 'hypnotic effect' of the train on peahens described by Ridley et al. (1984). The coexistence of the heritability of female preference (through the sensory bias) and the heritability of the train's development (Petrie et al. in press) provides strong support for the idea that the train evolved through Fisher's runaway process (Fisher 1930). At some point, as the train became an extreme trait, it presumably crossed a threshold and started to impose costs on the bearer, with only the better quality males being able to grow and display the more ornamented trains. Some results already support this last point (Møller & Petrie 2002; Loyau et al. 2005b). According to this scenario, the train has evolved as a Fisherian trait and is maintained as a good genes indicator, whatever the hormonal control. In other galliform species the development of the train may never have reached the threshold, leading to a loss of ornamental traits and associated display behaviours (Kimball et al. 2001). Therefore, we do not see why the form of hormonal control of train expression negates previous findings and know of no evidence to suggest why it should. The peahens may 'appear to be quite exceptional if they indeed select mates based on the male train' (Takahashi et al. 2008, page 1215). However, the existence of secondary sexual ornaments and display behaviours as complex and extravagant as the peacock's train and display is itself already exceptional.

To conclude, we agree with Takahashi et al. (2008) that it is important to publish negative results, and hopefully further such studies will be published so that a more meaningful meta-analysis can be carried out. However, the failure to detect evidence of mate choice in one study based on a limited array of traits does not mean that females do not prefer males with more elaborate trains. Only a very strict experimental study across several captive and wild populations could demonstrate that. To date, only one study on peafowl mate choice has been done in the wild (Yasmin & Yahya 1996) and, unfortunately, the number of eyespots was not recorded. Further studies of wild populations with natural levels of genetic variation will be particularly useful in extending our understanding of peahen mating preferences.

We thank Dirk S. Schmeller, Alexis S. Chaine, L. Morris Gosling and Jean Clobert who provided valuable comments and discussion and two anonymous referees who improved the manuscript.

References

- Baird, T. A., Fox, S. F. & McCoy, J. K. 1997. Population differences in the roles of size and coloration in intra- and intersexual selection in the collared lizard, *Crotaphytus collaris*: influence of habitat and social organization. *Behavioral Ecology*, **8**, 506–517.
- Brooks, R. 2002. Variation in female mate choice within guppy populations: population divergence, multiple ornaments and the maintenance of polymorphism. *Genetica*, **116**, 343–358.
- Chaine, A. S. & Lyon, B. E. 2008. Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. *Science*, **319**, 459–462.
- Coleman, S. W., Patricelli, G. L. & Borgia, G. 2004. Variable female preferences drive complex male displays. *Nature*, **428**, 742–745.
- Dale, S. T., Slagsvold, T., Lampe, H. M. & Sætre, G. P. 1999. Population divergence in sexual ornaments: the white forehead patch of Norwegian pied flycatchers is small and unsexy. *Evolution*, **53**, 1235–1246.
- Danchin, E., Giraldeau, L.-A., Valone, T. J. & Wagner, R. H. 2004. Public information: from nosy neighbors to cultural evolution. *Science*, **305**, 487–491.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. Princeton, New Jersey: Princeton University Press.
- Endler, J. A. & Houde, A. E. 1995. Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution*, **49**, 456–468.
- Espmark, Y. E. & Lampe, H. M. 1993. Variations in the song of the pied flycatcher within and between breeding seasons. *Bioacoustics*, **5**, 33–65.
- Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.
- Forstmeier, W., Hasselquist, D., Bensch, S. & Leisler, B. 2006. Does song reflect age and viability? A comparison between two populations of the great reed warbler *Acrocephalus arundinaceus*. *Behavioral Ecology and Sociobiology*, **59**, 634–643.
- Foster, S. A. 1999. The geography of behaviour: an evolutionary perspective. *Trends in Ecology & Evolution*, **14**, 190–195.
- Freeberg, T. M. 2000. Culture and courtship in vertebrates: a review of social learning and transmission of courtship systems and mating patterns. *Behavioural Processes*, **51**, 177–192.
- Gil, D., Cobb, J. L. S. & Slater, P. J. B. 2001. Song characteristics are age-dependent in the willow warbler, *Phylloscopus trochilus*. *Animal Behaviour*, **62**, 689–694.
- Griffith, S. C., Stewart, I. R. K., Dawson, D. A., Owens, I. P. F. & Burke, T. 1999. Contrasting levels of extra-pair paternity in mainland and island populations of the house sparrow (*Passer domesticus*): is there an 'island effect'? *Biological Journal of the Linnean Society*, **68**, 303–316.
- Hagelin, J. C. & Ligon, J. D. 2001. Female quail prefer testosterone-mediated traits, rather than the ornate plumage of males. *Animal Behaviour*, **61**, 465–476.
- Hill, G. E. 1994. Geographic variation in male ornamentation and female mate preference in the house finch: a comparative test of models of sexual selection. *Behavioral Ecology*, **5**, 64–73.
- Jaenike, J. R. 1973. A steady state model of genetic polymorphism on islands. *American Naturalist*, **107**, 793–795.
- Jennions, M. D. & Petrie, M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews*, **72**, 283–327.
- Kimball, R. T., Braun, E. L., Ligon, J. D., Lucchini, V. & Randi, E. 2001. A molecular phylogeny of the peacock-pheasants (Galliformes: *Polyplectron* spp.) indicates loss and reduction of ornamental traits and display behaviours. *Biological Journal of the Linnean Society*, **73**, 187–198.
- Klappert, K., Mazzi, D., Hoikkala, A. & Ritchie, M. G. 2007. Male courtship song and female preference variation between phylogeographically distinct populations of *Drosophila montana*. *Evolution*, **61**, 1481–1488.
- Kwiatkowski, M. A. & Sullivan, B. K. 2002. Geographic variation in sexual selection among populations of an iguanid lizard, *Sauromalus obesus* (= *ater*). *Evolution*, **56**, 2039–2051.
- Loyau, A., Saint Jalme, M. & Sorci, G. 2005a. Intra and inter-sexual selection for multiple traits in the peacock (*Pavo cristatus*). *Ethology*, **111**, 810–820.
- Loyau, A., Saint Jalme, M., Cagniant, C. & Sorci, G. 2005b. Multiple sexual advertisements honestly reflect health status in peacocks (*Pavo cristatus*). *Behavioral Ecology and Sociobiology*, **58**, 552–557.
- Loyau, A., Gomez, D., Moureau, B., Théry, M., Hart, N. S., Saint Jalme, M., Bennett, A. T. D. & Sorci, G. 2007a. Iridescent structurally-based coloration of eyespots correlates with mating success in the peacock. *Behavioral Ecology*, **18**, 1123–1131.
- Loyau, A., Saint Jalme, M., Maugé, R. & Sorci, G. 2007b. Male sexual attractiveness affects the investment of maternal resources into the eggs in peafowl (*Pavo cristatus*). *Behavioral Ecology and Sociobiology*, **61**, 1043–1052.
- Madden, J. R. 2006. Interpopulation differences exhibited by spotted bowerbirds *Chlamydera maculata* across a suite of male traits and female preferences. *Ibis*, **148**, 425–435.
- Márquez, R. & Bosch, J. 1997. Male advertisement call and female preference in sympatric and allopatric midwife toads. *Animal Behaviour*, **54**, 1333–1345.
- Martins, E. P., Bissell, A. N. & Morgan, K. K. 1998. Population differences in a lizard communicative display: evidence for rapid change in structure and function. *Animal Behaviour*, **56**, 1113–1119.
- Møller, A. P. & Petrie, M. 2002. Condition dependence, multiple sexual signals, and immunocompetence in peacocks. *Behavioral Ecology*, **13**, 248–253.
- Petrie, M. 1992. Peacocks with low mating success are more likely to suffer predation. *Animal Behaviour*, **44**, 585–586.
- Petrie, M. & Halliday, T. 1994. Experimental and natural changes in the peacock's (*Pavo cristatus*) train can affect mating success. *Behavioral Ecology and Sociobiology*, **35**, 213–217.
- Petrie, M. & Kempnaers, B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. *Trends in Ecology & Evolution*, **13**, 52–58.
- Petrie, M., Halliday, T. & Sanders, C. 1991. Peahens prefer peacocks with more elaborate trains. *Animal Behaviour*, **41**, 323–331.
- Petrie, M., Cotgreave, P. & Stewart, I. 1996. Variation in the train morphology of peacocks (*Pavo cristatus*). *Journal of Zoology*, **238**, 365–371.
- Petrie, M., Cotgreave, P. & Pike, T. W. In press. Variation in the peacock's train shows a genetic component. *Genetica*.
- Pfennig, K. S. 2000. Female spadefoot toads compromise on mate quality to ensure conspecific matings. *Behavioral Ecology*, **11**, 220–227.
- Ptacek, M. B. & Travis, J. 1996. Inter-population variation in male mating behaviours in the sailfin mollie, *Poecilia latipinna*. *Animal Behaviour*, **52**, 59–71.
- Ridley, M. W., Lelliott, A. D. & Rands, M. R. W. 1984. The courtship display of feral peafowl. *World Pheasant Association Journal*, **9**, 57–68.
- Rodd, F. H., Hughes, K. A., Grether, G. F. & Baril, C. T. 2002. A possible non-sexual origin of mate preference: are male guppies mimicking fruit? *Proceedings of the Royal Society of London, Series B*, **269**, 475–481.
- Ryan, M. J. 1990. Sexual selection, sensory systems and sensory exploitation. *Oxford Surveys in Evolutionary Biology*, **7**, 157–195.
- Safran, R. J. & McGraw, K. J. 2004. Plumage coloration, not length or symmetry of tail-streamers, is a sexually selected trait in North American barn swallows. *Behavioral Ecology*, **15**, 455–461.
- Shine, R., Webb, J. K., Lane, A. & Mason, R. T. 2006. Flexible mate choice: a male snake's preference for larger females is modified by

- the sizes of females encountered. *Animal Behaviour*, **71**, 203–209.
- Takahashi, M., Arita, H., Hiraiwa-Hasegawa, M. & Hasegawa, T.** 2008. Peahens do not prefer peacocks with more elaborate trains. *Animal Behaviour*, **75**, 1209–1219.
- Wiens, J. J.** 2001. Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends in Ecology & Evolution*, **16**, 517–523.
- Yasmin, S. & Yahya, H. S. A.** 1996. Correlates of mating success in Indian peafowl. *Auk*, **113**, 490–492.