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Do peahens not prefer peacocks with more elaborate trains?

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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

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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