Evolution

Contentious issues in sexual selection

from Linda Partridge and Paul Harvey

WHY do peacocks have large decorative tails? The answer is probably that females use the tails as cues in mate choice. But why do females prefer to mate with such males? We do not know despite advances in our understanding that have come from population genetic models[1–4], field experiments[5] and breeding studies[6]. It is far from clear that research is progressing efficiently, or that any consensus on the basic issues is being reached. A recent conference on sexual selection* forced participants to confront these issues.

It could be that the elaborate and species-specific ornaments of many birds have evolved to prevent individuals from mating with members of the wrong species. Although perhaps part of the truth, that view is not fashionable. Much contemporary research is concerned with distinguishing between two other ideas. The first is that females choose mates by their ornaments because these indicate viability in other respects which will be transmitted to offspring. In other words, females get 'good' genes by mating with males that have ornaments. The second possibility is that the male ornaments impair survival, having evolved simply because females happen to prefer mating with adorned males. This was the view of Darwin who thought male ornaments required a special evolutionary explanation because they seemed detrimental to survival[7]. Two related issues must be resolved before deciding between these interpretations.

The first argument concerns fitness heritability. Until very recently, population geneticists have emphasized the theoretical prediction that populations at equilibrium under constant natural selection are not expected to exhibit heritability of total fitness[8,9]. Taken at face value, this implies that mate choice could not result in fitter progeny. However, contemporary theory suggests that some fitness heritability can be maintained by temporally varying (particularly cycling) selection pressures or by the interaction of selection with other processes such as mutation and migration (ref. 10 and B. Charlesworth, personal communication). Such fitness heritability could be maintained in natural populations, but is it? There is general agreement that measurements of fitness heritability are urgently required, and also that the practical problems of collecting data are formidable, especially in natural populations.

The second issue concerns the assumptions, outcomes and biological relevance of particular genetic models. If a male trait is of advantage under natural selection, then female preference for it can evolve while there is genetic variability in the male trait. The reason is that females with the preference mate disproportionately with males bearing the trait, and produce fitter sons (because they bear the trait) who also carry the preference alleles which increase in frequency as a result of the association. Once such a preference reaches a sufficient frequency in the population, females gain an extra advantage by choosing males with the trait because of the attractiveness of their sons. At this point, the male ornament can become further exaggerated to a level where it becomes disadvantageous to the male's viability, Fisher's celebrated runaway process[11]. Actually, for the runaway process to get off the ground, the male trait need not even be initially advantageous so long as some degree of female preference for it exists in the population beforehand[2,3]. In whatever way the process starts, at equilibrium there will be a negative genetic correlation between male mating success and male viability, in contradiction to the 'good genes' view.

A new wave of models explores the consequences of including a third character (together with the deleterious male trait and the female preference) that causes variation in male viability[12–14]. This can interact in various ways with the costly male trait so that, for instance, the trait is only expressed fully in the most viable males. J. Maynard Smith (Sussex University) presented a review of such models and concluded that female preference and the deleterious male trait (now an indicator of viability) can become established once mating preference alleles rise above a certain frequency.

Why are such models important and how do they relate to the notion of fitness heritability? An example is provided by Hamilton and Zuk's argument[15] that bright coloration (deleterious trait) among birds may have evolved through mate choice (preference) because bright coloration is an indicator of the extent to which an individual is resistant to parasites (viability). The important point is that Hamilton and Zuk envisage that genetic variance for resistance against parasites is maintained in the population by temporally cycling selection pressures on the resistance genes of the birds. Recent genetic models of this process by Kirkpatrick and Pomiankowski demonstrate different evolutionary dynamics from those found in the basic two-character models, or the three-character models in which additive genetic variance (heritability) of viability is not maintained in the population. The relevance of such models to the real world is the subject of continued debate. If these models are important, costly sexually-selected male ornaments provide the means by which females can assess the viability of their

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1. O'Donald, P. *Genetic Models of Sexual Selection*. (Cambridge University Press, 1980).
2. Kirkpatrick, M. *Evolution* **36**, 1 (1982).
3. Lande, R. *Proc. natn. Acad. Sci. U.S.A.* **78**, 3721 (1981).
4. Seger, J. *Evolution* **39**, 1185 (1985).
5. Andersson, M. *Nature* **299** 818 (1982).
6. Majerus, M.E.N., O'Donald, P., Kearns, P.W.E. & Ireland, H. *Nature* **321**, 164 (1986).
7. Darwin, C. *The Descent of Man and Selection in Relation to Sex*. (Murray, London, 1871).
8. Williams, G.C. *Sex and Evolution* (Princeton University Press, 1975).
9. Maynard Smith, J. *The Evolution of Sex* (Cambridge University Press, 1976).
10. Partridge, L. in *Mate Choice* (ed. Bateson, P.) 227 (Cambridge University Press, 1983).
11. Fisher, R.A. *The Genetical Theory of Natural Selection* (Clarendon, Oxford, 1930).
12. Andersson, M. *Biol. J. Linn. Soc.* **17**, 375 (1982).
13. Dominey, W.J. *J. theor. Biol.* **101**, 495 (1983).
14. Andersson, M. *Evolution* **40**, 804 (1986).
15. Hamilton, W.D. & Zuk, M. *Science* **218**, 384 (1982).
16. Huxley, J. *Evolution, the Modern Synthesis* (Allen & Unwin, London, 1942).
17. Dobzhansky, Th. *Genetics and the Origin of Species* 3rd edn. (Columbia University Press, 1951).
18. Mayr, E. *Systematics and the Origin of Species* (Columbia University Press, 1942).
19. Barton, N.H. & Hewitt, G.M. *A. rev. Ecol. Syst.* **16**, 113 (1985).
20. Levin, D.A. *Evolution* **39**, 1275 (1985).
21. Armbruster, W.S. *Evolution* **39**, 733 (1985).

100 years ago

THE NEW ELEMENT, GERMANIUM

SOME months ago Dr Clemens Winkler announced the discovery of a new element which he named germanium, a preliminary account of which has already appeared in these columns. Dr Winkler has since been able to make a more systematic examination of the subject.

The following is the best method for separating the germanium. The finely-powdered mineral is intimately mixed with an equal weight of soda and sulphur, and the whole submitted to the action of a moderate red heat in a Hessian crucible. The product is powdered whilst still warm, and repeatedly boiled with water; the aqueous extract is slightly acidulated with sulphuric acid, and the precipitated sulphides of arsenic and antimony allowed to settle. On then adding a considerable excess of hydrochloric acid, the germanium sulphide is thrown down as a white voluminous precipitate; this is gently roasted, then heated with concentrated nitric acid, and finally ignited. The germanium oxide obtained may be reduced by ignition in hydrogen.

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