

## NEWS AND VIEWS

# Female mate choice and runaway sexual selection

from Paul H. Harvey and Stevan J. Arnold

In *The Descent of Man and Selection in Relation to Sex*<sup>1</sup>, Darwin explained how various traits usually found in only one sex — such as the peacock's tail or the deer's antlers — might have evolved. He thought that such traits resulted from one of two selective processes that favour access to mates: either selection for weapons used in combat between males, or selection for adornments used to attract females (Figs 1, 2). Darwin observed that the adornments are most clearly seen in males of species, for example, birds of paradise, where females choose from a group of displaying males. But Darwin was aware of a difficulty in his theory that has never been fully resolved: the characters favoured by females often appear to hinder the survival of males. Why should females choose to mate with those males least likely to be favoured by natural selection? Recent analytical work formalizes a model suggested by R.A. Fisher and shows how selection can favour female mating preferences for characters that actually lower male viability, even to the point of driving a population to extinction.

Fisher<sup>2</sup> described a simple model for female choice which had a surprising outcome — male characters which impair survival could be selected for and maintained in a population simply as a consequence of female choice. He considered species with heritable variation for both a male character, say tail size, and female preference for choosing mates on the basis of tail size. If environmental change led natural selection to favour an increase (or decrease) in male tail size, then, over the generations, male tail size would change. However, so would female preferences. The important idea here is that males with longer tails would tend to be mated by females who prefer longer-tailed males. The male offspring of those females will not only inherit their fathers' long tails and be favoured by natural selection but will also inherit their mothers' preference genes and pass them on to their daughters, thus causing an increase in the frequency of those preference genes. This genetic covariance or linkage disequilibrium is a result (not an assumption) of Fisher's model. Modification of male tail size will,

therefore, proceed under the influences of both natural selection and sexual selection.

Ultimately a balance between the forces of natural and sexual selection might be expected to lead to an equilibrium male tail size, but Fisher<sup>2</sup> argued that "as long as there is a net advantage in favour of further plumage development, there will also be a net advantage in favour of giving to it a more decided preference". Fisher termed this process 'runaway selection' and went on to assert that in the absence of "severe counterselection . . . it is easy to see that the speed of development will . . . increase with time exponentially, or in geometric progression" (our italics). He suggested that the process might only be checked when males had tails so long that they would be extremely unlikely to survive and females preferring to mate with them would be left without a mate.

Fisher never published a formal population genetic model of the runaway process and, since his writing style was never lucid, later workers have often chosen to add assumptions to the model. One common variant<sup>3,4</sup> claims that the runaway process is a consequence of females choosing males on relative rather than absolute criteria — for example, from one extreme of the distribution of observed male tail

Fig. 1 (right) *Strepsiceros* Kudu. One category of sexually selected characters confers a direct advantage in male-male combat over access to mates. Darwin was aware of numerous examples and had no difficulty in explaining them. Male weaponry is often more markedly developed among polygynous species. Fig. 2 (below) A second category of sexually selected characters is particularly evident in males of lek species, such as the bird of paradise, where females choose from among a group of displaying males. The males play no part in defending the nest or feeding the young. But why do females appear to choose to mate with males whose plumage must be disadvantageous in terms of natural selection?



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evolution of mating systems in terms Darwin himself might have used<sup>15</sup> and not all his claims are validated in O'Donald's population genetic treatment of his model — the runaway process does not increase at a geometric rate.

Working with a haploid two-locus analytical model and diploid two-locus simulations, the recent treatments by Kirkpatrick<sup>6</sup> also demonstrate the runaway process. But it is evident from Kirkpatrick's treatment that both Fisher and O'Donald were wrong to conclude that "preferences start to evolve only if females prefer those male phenotypes that are advantageous in natural selection"<sup>15</sup>. Indeed, female preference genes that favour more viable males do not necessarily spread through the population, and neither do the more viable males! Why should this be so? The key to the answer lies with Kirkpatrick's finding that when the male trait gene frequency is plotted against female choice gene frequency then there is a line of genetic equilibria: for every frequency of preference there is a frequency of the male trait at which the system is in equilibrium. There is not a single equilibrium point because any viability loss experienced by long-tailed males can, with some female preference, be exactly balanced by a mating advantage. When females preferring long-tailed males are common in the population then sexual selection will maintain a high frequency of the long-tailed males. When the preference gene is not at fixation, however, a low frequency of shorter-tailed males may be maintained in the population to service those females who prefer mating with them. The process is clearly frequency dependent.

What this means is that when the same male fitness and female choice functions are used while initial trait and preference frequencies are varied then different points on the line of equilibria are reached. Once populations reach the line there is a prospect for additional indeterminate evolution — genetic drift can carry small populations along the line of equilibria. Finally, it is clear from the models that females need not choose males on relative rather than absolute criteria (see above and ref. 7) for the male's tail to evolve to a maladaptive size.

Kirkpatrick's analysis independently followed a treatment of the problem by Lande<sup>7</sup> which, more realistically, assumed that both male traits and female mate preferences are under polygenic control. Lande modelled such a system with male traits and female preferences treated as normally distributed variables. Although we might expect selection to deplete heritable variance in both traits, Lande points out that this is not necessarily so<sup>8</sup>; at some point depletion by selection will be balanced by enrichment of variation by mutation and recombination. If we assume that variances in male trait and female preference metrics remain the same

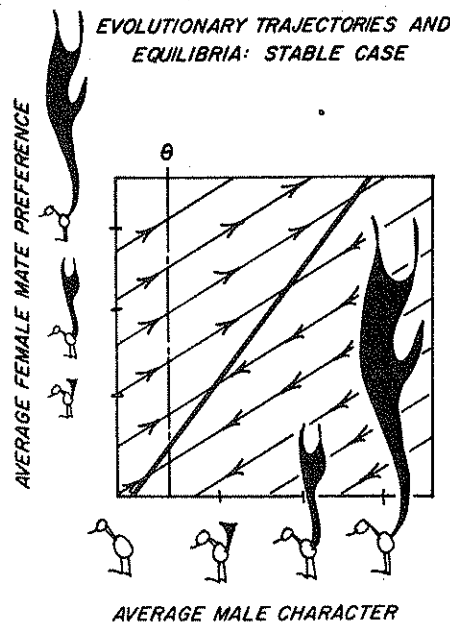
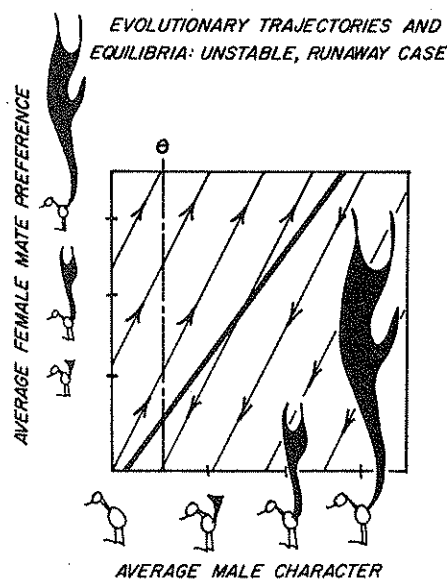


Fig. 3 Females choose mates on the basis of tail size. The light lines depict possible trajectories for the joint evolution of male tail size and female preferences, and the arrows indicate the direction taken. (The male tail size that is optimal for viability is indicated by the symbol  $\theta$ .) The heavier line connects the equilibrium states at which the males tail length and the females mating preference cease to undergo evolutionary change (other than by random drift along the line). Whether the evolutionary process leads to stable or unstable equilibria depends on genetic parameters and the strength of viability selection.



between generations, but that character averages change as consequences of natural and sexual selection, then Lande's models also reveal a line of equilibria. For any strength of female preference there is a male trait size such that the system is in equilibrium. Lande demonstrates the line of equilibria in three models assuming quite different rules of female choice. Again, there is no direct selection on female mating preferences, which evolve as a genetically correlated response to selection on males.

Lande's formulation allows a different

interpretation of what Fisher meant by runaway selection. With the two-locus models, populations perturbed slightly from the line of equilibria always return there (although not necessarily to the same point) and the runaway process ends. However, in Lande's models, evolutionary trajectories may lead away from the line of equilibria so that both male trait and female preference can evolve "away from the line at a geometrically increasing rate" (Fig. 3), as Fisher originally claimed. The qualitative conditions for the line of equilibria to be unstable are that females show much heritable variation in mate preference and that there is weak natural selection on the male character. Lande points out that his models help to explain why males of closely related species may differ in a "substantially nonadaptive and random pattern" while the females are phenotypically similar, and also that "random genetic drift may be an important factor promoting speciation by sexual isolation and the evolution of sexual dimorphism".

The similar conclusions reached by models with such dissimilar genetic assumptions underscores the generality of the conclusions. Lande's model, in particular, is general in terms of its assumptions yet clear predictions follow from it<sup>9</sup>. One other idea based on females choosing bizarre males precisely because the male traits constitute handicaps to survival<sup>10</sup> has gained questionable credence among some ethologists who seem not to understand that population geneticists have been unable to model the process successfully. O'Donald<sup>5</sup> presents a detailed analysis of the topic.

The model first sketched by Fisher 67 years ago<sup>11</sup> is only now becoming understood and its widespread implications appreciated. There is no reason why the runaway process should be restricted to plumage characters — vocalizations or pheromone production are other possible candidates. Shortly we might expect relevant parameters to be measured and the efficacy of the theory to be tested. In any event, the finding that, under a variety of circumstances, sexual selection can result in a decline of male viability and thus contribute to population extinction is an important one for evolutionary biology. □

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