Sexual Selection and the Handicap Principle

JOHN MAYNARD SMITH

*School of Biological Sciences, University of Sussex
Brighton, Sussex, England*

The theory that sexual selection may cause females to select males with a handicap is analysed by means of a simple model. It is concluded that the proposed mechanism does not produce the results claimed for it, even allowing for sex-limited inheritance of the handicap.

Introduction

Zahavi (1975) has recently suggested a new mechanism of sexual selection. He proposes that it will be selectively advantageous for a female to choose as a mate a male with some conspicuous characteristic which is also a handicap as far as survival is concerned. By choosing such a male, the female will acquire a mate of high "fitness" in other respects, because only a fit male can survive to breed despite the presence of the handicap.

If the handicap is not itself inherited (because it is environmentally caused, or because there is no additive genetic variance for it), there is no reason to doubt that the proposed mechanism could work. But if, as is more plausible, the handicap is itself inherited, then a female who chooses a male with a handicap has children who inherit from their father not only the genes which made him "fit", but also the genes which gave him a handicap. This fact raises doubts about whether Zahavi's proposed mechanism could work. Indeed, it might be sufficient to enable one to reject the mechanism out of hand (except in the case of a non-inherited handicap), were it not for the fact that the genes for the handicap are likely to be sex-limited. Peahens do not have long tails. Thus the daughters of the choosing female would get the advantages of their father's fitness without the handicap.

Although not part of Zahavi's original argument, sex-limited effects might save it. It seems impossible to decide the question by purely verbal arguments. The purpose of this paper is to offer a simple model which is intended to incorporate the essential features of Zahavi's proposal. It is difficult to formulate an analytically soluble model, because linkage disequilibrium is an

essential feature of the situation. The behaviour of the model has therefore been investigated on a computer. The conclusion drawn is that the proposed mechanism does not produce the result claimed for it.

The Model

Consider an infinite diploid population with three unlinked loci, with two alleles at each locus:

(i) *AA* and *Aa* are "fitter" than *aa*; that is, $\bar{A}$ individuals of both sexes are more likely to survive to breed.

(ii) *BB* and *Bb* males have a "handicap"; e.g. a long tail as in a peacock. *bb* males are more likely to survive to breed. The gene is not expressed in females.

(iii) *CC* and *Cc* females mate only with $\bar{B}$ males; *cc* females are un-selective, mating with males in the proportions in which they occur in the adult male population. The gene is not expressed in males.

The genes *A* and *B* affect the probabilities of surviving to become a breeding adult as follows:

genotype	$\bar{A}\bar{B}$	$\bar{A}bb$	$aa\bar{B}$	*aabb*
fitness of female	1	1	$1-s$	$1-s$
fitness of male	$1-t$	1	$(1-s)(1-ut)$	$1-s$

Here, *s*, *t* and *u* are all positive, and *s*, *t* and *ut* are less than one. By introducing *u* it is possible to choose any relative fitnesses of the four geno-types. The handicap, *t* (for having a "tail"), affects males only.

The assumptions about mating are incompatible with monogamy, except when *C* females are very rare. It is therefore implicit in the model that a male can mate several times, the frequency of matings being determined by female choice.

With these assumptions, the model is simple to simulate. Starting with the frequency of the 27 genotypes in the two sexes before selection in generation *O*, the genotype frequencies of $\bar{B}$ males, *bb* males, $\bar{C}$ females and *cc* females are obtained by applying the fitness values. The relative frequencies of the matings $\bar{C}♀ \times \bar{B}♂$, and *cc*♀ × any ♂, are calculated, allowing for female choice. The male and female gamete populations for the two types of mating can then be calculated, and hence the zygote frequencies in the next generation, assuming all types of mating are equally productive. It is assumed that sex is determined by a gene unlinked to the other three.

The initial zygote frequencies were constructed assuming linkage equil-ibrium, with the frequencies of allele *A* and *B* at 0·5; the initial frequency of

C was varied for reasons explained below. Later generations depart from linkage equilibrium; therefore the direction of evolutionary change was determined after the model had been run for 5 generations.

Conclusions

If the initial frequency of C is not small, it can be the case that the frequency of both choosiness in females ($\bar{C}$) and handicap in males ($\bar{B}$) increases. This is an illustration of the point made by Fisher (1930). If some females choose $\bar{B}$ males, the rest mating randomly, then $\bar{B}$ males leave on average more offspring. Therefore $\bar{C}$ females, by choosing $\bar{B}$ males, ensure that their sons will be fitter than average. This effect can be strong enough to overcome the presence of a handicap to $\bar{B}$ males. To give an example, if the initial frequency of choosy females, $\bar{C}$, is 0·2, and for $u = 1$, the frequency of $\bar{C}$ and $\bar{B}$ both increase if $t \leqslant 0·2$, but decrease if $t \geqslant 0·3$.

This increase is due to what I will call the Fisher effect. It has nothing to do with the handicap principle, since it works best if there is no handicap.

To test the handicap principle, in the absence of any Fisher effect, it is necessary to start the simulation with the initial frequency of C small. Then $\bar{B}$ males do not mate significantly more often than bb males, and the Fisher effect does not operate.

Simulations were started with an initial frequency of $\bar{C}$ of 0·001. A wide range of values of s, t and u were tried. In all cases the frequency of both genes B and C declines; males with a "handicap" are not favoured, and females which select males with a handicap are not favoured.

Discussion

It would be wrong to conclude that the handicap principle as proposed by Zahavi cannot operate. It may be that some change in the assumptions made would enable the process to work, although the model investigated in the last section was intended to incorporate Zahavi's ideas.

One modification is to suppose that the handicap is not heritable. The model of the previous section is easily modified to give this result. Thus suppose that Bb individuals have long tails and BB and bb short tails. Then, starting with a gene frequency of 0·5, there is no parent–offspring correlation for tail length. The Fisher effect does not operate in such a model, whatever the values of t or the frequency of the gene C; there is no advantage in a female choosing a male with a long tail if her sons do not resemble their father. The handicap principle can however work. If $u > 1$, then the frequency of C increases; if $u < 1$, the frequency of C decreases. In both cases the

frequency of B remains at 0·5. This dependence on u was foreseeable; if $u = 1$ then the relative frequency of $\bar{A}$ and aa is the same in $\bar{B}$ and bb males, whereas if $u > 1$, $\bar{A}$ is relatively commoner in $\bar{B}$ than in bb males.

To suggest this type of overdominant inheritance for the "handicap", while retaining additive genetic variance for "fitness", is special pleading. With additive inheritance of both handicap and fitness, the handicap principle appears not to work.

REFERENCES

FISHER, R. A. (1930). *The Genetical Theory of Natural Selection.* Oxford: Clarendon Press.
ZAHÁVI, A. (1975). *J. theor. Biol.,* 53, 205.