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The Cost of Honesty

(Further Remarks on the Handicap Principle)

The handicap principle has been suggested (Zahavi, 1975) as a mechanism which guards against cheating in the communication between mates. The theory has been further extended to include reliability components in communication systems in general (Zahavi, in press). The essence of the theory was that the reliability of communication (or advertisement) is increased in relation to the investment in the advertisement. The model of the handicap principle has been disputed by Maynard Smith (1976) and Davis & O'Donald (1976). They claimed on the basis of mathematical models that the handicap principle cannot operate under normal conditions. I believe that in natural populations the need to advertise on the one hand and the need to check the reliability of the advertisement on the other hand result in the evolution of much more sophisticated mechanisms than the simple mathematical models investigated by Maynard Smith and Davis & O'Donald. In the following I shall point to some general considerations which were overlooked in their models. These may be just some of the conditions which allow for the widespread use of handicaps in nature (Zahavi, in press).

1. The Handicap as a Test for the Phenotype

When the phenotype may affect the reproductive potential, it may be useful to test individuals for their phenotypic fitness and not only for their genotype. Under such circumstances, if handicaps act as tests, they may be useful characters even in a population at its optimal fitness among individuals which are similar to one another in their genetic constitution.

2. The Cost of the Handicap

Davis & O'Donald and Maynard Smith assume a simple additive value to the handicap and the tested quality. But the relationship between quality and the handicap may be more sophisticated. Assume that the handicap (the sexually attracting character) is present among all the members of a population. That is probably the case in most sexually attracting characters. Assume also that the phenotypic manifestation of the handicap is adjusted

to correlate to the phenotypic quality of the individual. When this correlation is kept, advertisement is honest and its cost is low, but when owing to mutations or recombinations an individual develops its handicap larger than it should be, that individual is selected out because of the increase of the handicap and consequently its cost. Since the main objection of Davis & O'Donald to the handicap was the high cost required by their model, any marked reduction of the cost rules out their objection. With the above model it is reasonable to expect a population in its optimal fitness to benefit from a handicap.

Most sexually attractive characters seem to behave in a way which fits this model. Antlers of deer, nuptial plumage of birds or their breeding displays, all of which are handicaps to survival, do not develop as a simple function of the genotype. They are usually correlated to the phenotypic quality of the individual. Young, weak or non-breeding individuals often do not develop their handicaps at all or develop them less than breeding individuals. Further, it is reasonable to assume that high quality phenotypes and experienced individuals pay less for the cost of the same sized handicap than low quality phenotypes. Hence, if there is a mechanism by which individuals may have their handicaps in relation to their current phenotypic quality, the cost of maintaining handicaps in a population need not be high. So long as the offspring of the selecting individual, which is attracted to a sexual marker, stays honest and does not deviate to grow its handicap larger than it could afford, the handicap as a marker of honest advertisement (communication) may have its adaptive value with a very small cost.

3. Genetic Models for the Handicap Principle

Although the precise mathematical model of Maynard Smith and Davis & O'Donald seems not to be favourable for the evolution of handicaps, it is not difficult to build precise genetic models which will favour it. The following is the premise for such a model.

Assume that Aa is of a better quality than AA and aa are inferior to both of them. aa can survive to mate but it is not successful in its reproduction. Hence an individual which mates with aa damages its own reproduction as well. Potential mates should be interested to distinguish between Aa, AA and aa individuals. Assume a marker M which when together with aa kills but lowers slightly the survival of Aa or AA individuals. Such a marker, which is a handicap to Aa and AA individuals, is also a good advertisement for them since it ensures to potential mates that they are not of the aa genotype. It is obvious that this model can operate in a population which is in a stable

genetic equilibrium. Generally, any genetic system in which the low quality individuals are continuously produced from the high quality ones may benefit from the use of handicaps.

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