

LETTER TO THE EDITOR

Sexual Selection, Additive Genetic Variance and the “Phenotypic Handicap”

Fisher (1958) proposed “runaway” sexual selection to explain female preference for males bearing exaggerated, seemingly deleterious traits, such as bright coloration or otherwise useless ornamentation. In Fisher’s model, females selecting males bearing extreme traits gain an advantage because they produce attractive sons which are, in turn, preferred by females. Zahavi’s (1975) counterproposal, the Handicap principle, stirred considerable controversy (Bell, 1978; Eshel, 1977; Maynard Smith, 1976; Davis & O’Donald, 1976; Zahavi, 1977) by suggesting that the deleterious aspects of sexually selected traits were themselves critically important, and served to test the quality of males bearing such traits. Although largely overlooked in the ensuing discussion, the relative importance of either Fisher’s or Zahavi’s hypothesis depends on the nature of the observed variation in sexually selected traits. Fisher’s model requires some of the variation in the male trait to be heritable, and works best with highly heritable traits, while Zahavi’s model works best with traits with low (or no) heritability. The purpose of this letter is not to demonstrate that either Fisher’s or Zahavi’s model is wholly or even partially correct, but to show that there is a potential for interaction between the two models which will depend on the degree of heritability of particular traits. Until empirical evidence concerning the heritabilities of sexually selected traits is available, Zahavi’s model should not be rejected outright based on genetic models which assume continuously heritable variation. Below I briefly review Fisher’s and Zahavi’s arguments and then show how their explanatory value changes according to the degree of heritability of the male trait. Finally, I discuss two potential criticisms of Zahavi’s model as presented in this letter, and the degree of heritability to be expected of sexually selected traits.

1. Fisher’s Runaway Process

As proposed by Fisher (1958), the runaway process begins with a male trait that has an initial advantage not due to female preference. Since both having the characteristic (for males) and selecting males with the charac-

teristic (for females) would be selectively advantageous, the incidence of both the attractive character and females preferring the character would increase in the population. Eventually, as the frequencies of the trait and the preference increased, females which selected males without the favored characteristic would be disadvantaged simply because their sons would fail to have the characteristic, and would thus tend to fail in attracting females. A male trait could thus continue to develop due to the advantage conferred by female preference, even when it had lost its initial advantage—that is, even when so exaggerated that it was disadvantageous under natural selection.

Fisher argued that the rate at which females gained the preference and the rate of exaggeration of the male character would increase geometrically with time because of the development of a genetic correlation between extreme female preference and extreme expression of the male character. He termed this process “runaway” sexual selection, and hypothesized very rapid evolution of such sexually selected traits until eventually countered by strong natural selection against further development of the trait. Using specific genetic models and widely different assumptions about the particular genetic system, several investigators have confirmed and extended the essential features of Fisher’s model (O’Donald, 1980; Lande, 1981; Kirkpatrick, 1982).

An underlying assumption of Fisher’s model is that the male trait must be heritable, that is there must be additive genetic variance for the male trait, and thus a correlation between male parental phenotype and male offspring phenotype. If this correlation is absent, then a female selecting an extreme male will be no more likely to produce extreme sons than a female mating at random. Since the phenotypes of a female’s sons will not correspond to the male parental phenotype, there will be no advantage to female preference for extreme males in terms of offspring phenotype and likely some disadvantage, such as the time, energy, and other costs associated with selecting. At this point, female preference should become extinguished. Maynard Smith (1978, p. 172) clearly points out this difficulty with Fisher’s argument.

Although Fisher’s theory of runaway sexual selection depends on additive genetic variance in the male characteristic, conventional quantitative genetics predicts a reduction and eventual loss of the additive genetic variance of a trait exposed to continued directional selection (Falconer, 1960). This loss in additive genetic variance can occur due to fixation of favorable alleles or, in the case of overdominance at a locus, through the production of a stable polymorphism in which females mating at random have an equivalent distribution of male offspring phenotypes as females

(who do not assortively mate based on their own genotypes) selecting either homozygote, or the heterozygote genotype preferentially.

The predicted loss in the heritability of strongly selected traits may not occur (see the discussion below), but in cases in which Fisher's runaway process did reduce the additive genetic variance of the male trait, the progress of exaggeration of the trait would slow in proportion to the decrease in additive genetic variance, and stop when the variance was depleted, even in the absence of counterselection on the trait. The slowing and eventual halt of Fisher's process would occur in such a case both because the effect of female preference (selection) on further exaggeration of the male trait would be reduced, and because female preference itself should be relaxed. With little or no additive genetic variance in the male trait, females which tend towards random mating would likely be favored because female choice will bear little or no relationship to male offspring phenotype and yet there should be costs associated with selecting certain males.

2. Zahavi's Handicap Principle

Zahavi (1975) proposed that females choose extreme males precisely because such males possess a deleterious character or "handicap". He argued that such characters would serve to "test" the average fitness of the remainder of a male's genome. Thus, only males which were fitter than average would survive to reproduce when carrying the handicap while males without the handicap remain untested, perhaps with the balance of their genome being substantially inferior. Zahavi's model depends upon the existence of heritable and testable variation in the remainder of a male's genome, but not on heritable variation in the male trait.

Zahavi's hypothesis was criticized by Maynard Smith (1976) and Davis & O'Donald (1976) based on simple genetic models which showed that it was extremely unlikely that females would gain an advantage by mating with handicapped males when the handicap itself was heritable, even in the case of a sex-limited handicap. The loss in fitness to a female's sons due to inheriting the handicap would nearly always negate the potential gain in fitness to male and female offspring due to inheriting the superior, tested components of their father's genome. Although in special cases (Bell, 1978; Eshel, 1977; West-Eberhard, 1979), the handicap principle could work, it has been largely rejected on the grounds that the heritability of the handicap (and hence the decrease in fitness to a female's male offspring) is likely to be much higher than the heritability of testable fitness components.

But what about cases in which Fisher's runaway process has severely reduced or eliminated the additive genetic variance for the handicap trait, and where some heritable variation in testable fitness components exists? As pointed out by Maynard Smith (1978), "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". He did not regard this case as very important because he was considering the evolution of female preference of a handicap from its initial appearance, when the variation in the handicap is likely to show a higher heritability than the variation in testable fitness components, and not for a handicap at an endpoint in Fisher's process when the additive genetic variance may be severely reduced or eliminated. Likewise Bell (1979) cogently noted that Zahavi's handicap would work if there was no additive genetic variance for the handicap, but chose perhaps the least likely example of when the heritability would be low, namely a rare trait just appearing, rather than a trait at an endpoint of Fisher's runaway process.

3. Conclusion

Fisher's model explains the origin of sexual preference for particular male traits, and the runaway selection phase during which the male characteristic may lose its additive genetic variance. In cases in which the additive genetic variance in the male trait is lost, females selecting males with exaggerated traits would no longer increase the probability that their sons would have exaggerated traits, but would still incur the costs associated with selecting extreme males. At this point, female preference should be relaxed. During the course of evolution from some slight expression of a characteristic to its "runaway" exaggerated form, the additive genetic variance might be severely reduced or depleted many times to be slowly replenished by new mutations. During these periods of reduced or zero additive genetic variance, the handicap principle could account for the maintenance of female preference for extreme forms until the underlying additive genetic variance was restored. The relative importance of Fisher's and Zahavi's arguments will depend upon the degree to which the additive genetic variance of the trait in question is actually lost (see the discussion below).

As an example, imagine a population of males somewhat phenotypically variable for brightness of coloration, due to gene-environment interaction, but which had lost the additive genetic variance for brightness due to strong directional selection during the runaway process. At this point, the color-

ation trait would be inherited, but the variation in the trait (the intensity of the brightness) would be environmentally produced. According to the handicap principle females should choose the brightest males because these males have undergone the most severe test, surviving while being the most conspicuous, and thus on average should pass to their offspring superior fitness qualities. The heritable superior fitness qualities could be better foraging efficiency, disease resistance, predator avoidance tactics, or almost any heritable advantage which could provide individuals with strength, health, or other capabilities useful in avoiding predators. Because the intensity of brightness itself is not heritable, brightness is a "phenotypic handicap" only. With a phenotypic handicap there is no disadvantage of producing brighter than normal sons associated with selection of the brightest males as mates. The advantages of female choice for extreme males could be seen as fluctuating between Fisher's "second cause" (the advantage due to female preference), and Zahavi's handicap principle, according to the amount of additive genetic variance of the male trait. Runaway selection would work best when the heritability of the male trait was high while Zahavi's principle would work best when the heritability of the male trait was low.

4. Discussion

Two criticisms of the proposed interaction between the handicap principle and the runaway process will be addressed. First, the handicap may not test for any heritable advantage in testable fitness components, either because it is the wrong test, or because no heritable variation in fitness exists. Second, the additive genetic variance of the handicap trait may never be depleted as predicted by conventional quantitative genetics.

O'Donald (1980) pointed out that the handicap is testing for survivorship under a restricted set of conditions, namely possession of the handicap. If the typical offspring were to express the handicap at a reduced intensity, then the fitness qualities which had been advantageous to the extremely handicapped male parent may no longer be advantageous when expressed in the offspring. However, in populations where the handicap trait has lost its heritable variation, most males should differ in intensity of expression of the handicap only, rather than differing so substantially as to favor a different (background) fitness set, as suggested by O'Donald. Additionally, a female parent should, in an evolutionary sense, be most concerned with the survival of those offspring which most closely resemble the exaggerated male parent since these are the male offspring most likely to be successful at attracting mates.

Whether or not heritable variation in testable fitness components occurs is a more crucial difficulty because the handicap test requires heritable variation in fitness. Since the variation in the handicap is not heritable, it is the variation in "total fitness", the remaining features of the male genome, which must be testable. The difficulty here is that the heritable variation in "total fitness", like that of the male trait, will tend to be eliminated by selection (Williams, 1975; Maynard Smith, 1978). Despite this tendency, however, local variations in space and time should favor the presence of some additive genetic variance in fitness. Frequency dependent models dealing with competitive biotic cycles (Hamilton, 1980; Glesener & Tilman, 1978; Jaenike, 1978) seem to be the most promising in showing that the heritability of "total fitness" may indeed be substantial. Hamilton & Zuk (1982) have suggested that sexually selected "handicaps" might provide tests of how well a male's genetic background has dealt with temporally varying parasites or pathogens. Females selecting handicapped males would be selecting males which had proven their ability to express the handicap trait in an exaggerated form (or simply to survive while expressing the trait) in the face of local and temporal variants in parasites and pathogens.

The second major potential criticism concerns the loss of additive genetic variance for the handicap itself. To the degree that the additive genetic variance of the male trait is not eliminated by the runaway process, the handicap principle is unsatisfactory because the variation in the handicap would be heritable. Although conventional quantitative genetics theory predicts that strong directional selection will eliminate the additive genetic variance of a trait, the results of long-term selection experiments often do not conform to this expectation. Selection limits can be reached without the complete elimination of genetic variability, at least some of which is additive, perhaps due to selection for lethals, or the opposition of natural and artificial selection (Yoo, 1980). Additionally, in large populations mutations may provide a continual source of variation (Hill, 1982). The results of long-term selection experiments are often confusing (Clayton & Robertson, 1956), and in some cases (e.g. Yoo, 1980), some replicate lines lose their additive variance, while other lines remain unaffected, or even shown an increase in the additive component!

Whatever the results of artificial selection experiments, they may not indicate the fate of the additive genetic variance in sexually selected traits in natural systems. Natural and artificial conditions differ substantially as to effective population size, strength and duration of selection, and complexity of gene-environment interactions. Further, most artificial selection experiments, unlike female preference, have selected for the trait in both sexes rather than in males only. Thus, even if traits consistently lost their

additive genetic variance under artificial selection regimes, sexually selected traits in natural populations might still retain high heritabilities.

The heritabilities of traits in natural populations can be maintained by several mechanisms including pleiotropic effects of linkage disequilibria among genes with major effects on fitness (Lande, 1982), newly arising mutations in polygenic traits (Lande, 1976), or fluctuating selective pressures (Cade, 1981). In fact, heritable variation can be found in many ecologically important traits (for review, see Grant & Price, 1981), but data on the heritability of strongly sexually selected traits is needed, especially those traits believed to be under directional selection. Cade (1981) found heritable variation in how often male field crickets (*Gryllus integer*) sing which he attributed to fluctuating counterselection by an acoustically orienting parasitoid dipteran, *Euphasiopteryx ochracea*. In this case, the orientation of females to singing males also benefits the non-calling "parasitic" males, and thus the effect of female "choice" may not be one of directional selection. Also, polymorphisms in the color patterns of fishes which affect female choice can be genetically maintained and have been attributed to the opposition of natural and sexual selection (Endler, 1980). Such polymorphisms, however, may represent special cases of the maintenance of genetic variability. What are obviously needed are empirical studies aimed at detecting the additive genetic variance of nonpolymorphic, continuously varying sexually selected traits (handicaps) which are thought to be, or preferentially have been demonstrated to be, under a directional selective pressure due to female preference for extreme expression. If, for example, a trait such as the "orangeness" of male cock-of-the-rock plumage (*Rupicola rupicola*) is shown to have considerable heritable variation, then it is difficult to see how the maintenance of its exaggerated form could be attributed to the handicap principle.

I have made no attempt to determine here how much or how little additive genetic variance in a male trait can remain and still have the handicap principle contribute to the maintenance of female choice for extreme phenotypes. Clearly, Zahavi's handicap principle does not require zero additive genetic variance for the handicap trait, only weak heritability relative to the heritability of testable "total fitness" which, as argued above, may be considerable. The relative importance of the handicap principle and Fisher's runaway process at maintaining female preference for extreme males during the evolution of exaggerated male traits may ultimately depend on what actually happens to the additive genetic variance in male traits during the course of their evolution from first expression to their present exaggerated form, and the nature of heritable variation in potentially testable "total fitness".

A seminar run by M. J. West-Eberhard and W. G. Eberhard while at the University of Michigan (Spring, 1982) stimulated me to reconsider the problem of female preference for males bearing exaggerated traits. My thanks to them and to the seminar participants, especially R. Smuts. I thank S. A. Arnold, J. F. S. Barker, D. S. Falconer, M. Houck, M. Kirkpatrick, B. Lacey, L. Lee, J. Maynard Smith, G. R. Smith and an anonymous reviewer for comments on the manuscript, and W. D. Hamilton for his sponsorship of my NSF postdoctoral fellowship and for many helpful discussions and comments.

*Museum of Zoology and
Division of Biological Sciences
University of Michigan
Ann Arbor, Michigan 48109, U.S.A.*

WALLACE J. DOMINEY

(Received 13 July 1982, and in revised form 12 October 1982)

REFERENCES

- BELL, G. (1978). *Evolution* **32**, 872.
 CADE, W. H. (1981). *Science* **212**, 563.
 CLAYTON, G. A. & ROBERTSON, A. (1957). *J. Genet.* **55**, 152.
 DARWIN, C. R. (1871). *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.
 DAVIS, J. W. F. & O'DONALD, P. (1976). *J. theor. Biol.* **57**, 345.
 ENDLER, J. A. (1980). *Evolution* **34**, 76.
 ESHEL, I. (1977). *J. theor. Biol.* **70**, 245.
 FALCONER, D. S. (1960). *Introduction to Quantitative Genetics*. Edinburgh: Oliver and Boyd.
 FISHER, R. A. (1958). *The Genetical Theory of Natural Selection*. New York: Dover.
 GLESENER, R. R. & TILMAN, D. (1978). *Am. Nat.* **112**, 659.
 GRANT, P. R. & PRICE, T. D. (1981). *Am. Zool.* **21**, 795.
 HAMILTON, W. D. (1980). *Oikos* **35**, 282.
 HAMILTON, W. D. & ZUK, M. (1982). *Science* **218**, 384.
 HILL, G. W. (1982). *Proc. natn. Acad. Sci. U.S.A.* **79**, 142.
 JAENIKE, J. (1978). *Evol. Theor.* **3**, 191.
 KIRKPATRICK, M. (1982). *Evolution* **36**, 1.
 LANDE, R. (1976). *Genet. Res. Camb.* **26**, 221.
 LANDE, R. (1981). *Proc. natn. Acad. Sci. U.S.A.* **78**, 3721.
 LANDE, R. (1982). *Ecology* **63**, 607.
 MAYNARD SMITH, J. (1976). *J. theor. Biol.* **57**, 239.
 MAYNARD SMITH, J. (1978). *The Evolution of Sex*. Cambridge: Cambridge University Press.
 O'DONALD, P. (1980). *Genetic Models of Sexual Selection*. Cambridge: Cambridge University Press.
 WEST-EBERHARD, M. J. (1979). *Proc. Am. Phil. Soc.* **123**, 222.
 WILLIAMS, G. C. (1975). *Sex and Evolution*. Princeton: Princeton University Press.
 YOO, B. H. (1980). *Theor. appl. Genet.* **57**, 25.
 ZAHAVI, A. (1975). *J. theor. Biol.* **53**, 205.
 ZAHAVI, A. (1977). *J. theor. Biol.* **67**, 603.