NOTES AND COMMENTS

THE EVOLUTION OF DOMINANCE: HALDANE v FISHER REVISITED

J. T. MANNING

Department of Zoology, University of Liverpool, England

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SUMMARY

Fisher's model for the evolution of dominance indicates that the accumulation of dominance modifiers will be accelerated by (1) an increased frequency of the mutant heterozygote, (2) increased selection for the phenotype of the normal homozygote.

The model has been criticised by Haldane on the grounds that point (1) is not fulfilled, that is dominance appears to be more common in populations with a low frequency of mutant heterozygotes (populations of inbreeders).

In support of Fisher's model it is argued that intense selection for the wild type phenotype is more common in inbreeders than outbreeders. This situation should promote the accumulation of dominance modifiers (point (2) above).

1. INTRODUCTION

FISHER (1928, 1931) first made the suggestion that the common dominance of the wild type phenotype is an adaptation. According to this theory mutant genes tend to become recessive as the result of the selection of modifying genes. These modifiers alter the phenotype of the heterozygote until it resembles that of the homozygous wild type. Fisher argued that the following conditions would facilitate the evolution of dominance:

2. AN INCREASE IN THE FREQUENCY OF THE HETEROZYGOUS MUTANT

Mutants will first appear as heterozygotes. Modifiers of the heterozygote will increase in frequency as a response to recurrent mutation. As a result of selection for such modifiers the heterozygote will look more and more like the homozygous wild type. During this process the fitness of the heterozygote will increase and associated with this there will be an increase in heterozygote frequency. Selection for dominance modifiers can only act on heterozygotes. Therefore an increase in heterozygote frequency will accelerate the accumulation of modifiers.

3. INCREASED SELECTION FOR THE PHENOTYPE OF THE NORMAL HOMOZYGOTE

When selection pressure for the normal homozygote phenotype is low this will reduce the rate of modifier accumulation. In such cases incomplete dominance may be expected. Fisher (1931) gives several possible examples of this.

A number of authors have criticised Fisher's model (for a review see Sheppard, 1967). One such criticism was put forward by Haldane (1939).

He pointed out that if the spread of dominance modifiers is facilitated by an increasing heterozygote frequency then populations with low heterozygote frequency should commonly show incomplete dominance. Haldane argued that these latter conditions should be found in inbreeders. However, a comparison of the inbreeding *Lathyrus odoratus* and *Pisum sativum* with the recently outbred *Primula sinensis* and presently outbred *Papaver rhoeas* led him to conclude that "dominance is often commoner in inbred than outbred species".

Now inbreeders have often evolved from outbreeders but the reverse has occurred only rarely (Stebbins, 1957). Sheppard (1967) has therefore suggested that the dominance observed in inbreeders may have evolved in their outbreeding ancestors. This explanation could account for an *equal* development of dominance in outbreeders and inbreeders. However, it is not competent to explain a superior development of dominance in inbreeders (Haldane's conclusion). The purpose of this paper is to argue that the inbreeding habit is associated with frequent periods of intense selection for the wild type. Now Fisher maintained that when selection for the wild type was high the evolution of dominance would be facilitated. The heterozygous mutant phenotype is often 2 or 3 per cent less fit than the homozygous wild type (Crow and Temin, 1964). This situation is presumably the result of incomplete dominance. If a population is subject to periodic increases in selection intensity then only the extraordinary fit individuals and their offspring will consistently survive. According to Fisher's model these conditions will lead to the perfection of dominance. I now present evidence that inbreeding is associated with frequent fluctuations in selection intensity.

4. INBREEDING AND HIGH SELECTION INTENSITY

The Mediterranean type climate, as experienced in California and other areas, is subject to great annual fluctuations especially in rainfall. Stebbins (1957) has pointed out that inbreeding is very common among plants of such areas. Some species of the genus *Clarkia* are subject to a fluctuating climate which causes periodic drastic reductions in population size ("catastrophic selection"). The evolution of inbreeding has been associated with catastrophic selection in *Clarkia xantiana* (Moore and Lewis, 1965, 1966) and *Clarkia franciscana* (Lewis and Raven, 1958).

Individuals of a species are likely to encounter unfavourable conditions near the boundaries of the species range (Ford, 1971). Inbreeding also commonly arises near such boundaries. Many examples in both plant and animal groups are given by Baker (1955), Stebbins (1957) and Ford (1971). This phenomenon is so common that Stebbins has suggested it deserves recognition as Baker's law. An example may be seen in the distribution of *Limnanthes floccosa* which is an inbreeding derivative of the outbreeding *L. alba*. The former species has evolved in the north-western margin of the range of *L. alba* in Sacramento Valley, California. Drought conditions are common in this valley (Arroyo, 1973).

Inbreeding in plants is most common in annual weeds and other colonisers of newly available situations. The habitats occupied by such species are temporary. They are constantly changing their total area and their carrying capacity per unit area. Competition will therefore fluctuate considerably.

It may be argued that the effect of fluctuation in population density

will be minimised by the presence of a large reservoir of seed within the soil. However, it is maintained here that population density fluctuates regularly in inbreeders. Regular fluctuation should be effective in changing the genotypic structure of the seed reservoir. In addition the size of such a reservoir is dependent on the degree of seed dormancy. This is not invariably well developed in inbreeders (*e.g.* the eight species in the *Festuca microstachys* complex show little or no dormancy, Kannenberg and Allard, 1967).

A few direct measures of selection intensity in inbreeding populations have been made. Iman and Allard (1965) found "it is not uncommon for 90 per cent or more of seedling plants to fail to reach maturity in dense stands of wild oats". Kannenberg and Allard (1967) working with *F. microstachys* noted "it was not unusual to find 300 or more seedlings per square foot shortly after germination and as many as two dozen or more plants survive". These measures of mortality do not take into account elimination at the level of the seed.

Finally some plants that can produce both chasmogamous flowers (adapted for cross fertilisation) and cleistogamous flowers (adapted for selfing) may be mentioned. These include species of *Stipa* and *Danthonia* (Chase, 1908), *Bromus* (Harlan, 1945) and *Myosurus* (Stebbins, 1957). It has been shown that in all these species the onset of unfavourable conditions will stimulate the production of cleistogamous flowers. Such conditions include drought in *Stipa*, *Danthonia* and *Myosurus* and low light intensities (perhaps indicating overcrowding) and shallow soil in *Bromus*.

5. REFERENCES

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