A FURTHER PARADOX OF THE TWO-LOCUS MODEL*

By M. A. B. Deakin†

Abstract

The standard two-locus model of mathematical genetics leads to a number of paradoxical results. This paper derives another. At equilibrium, the gametotype with the highest mean fitness cannot be the most frequent.

Moran (1964) has pointed out three paradoxes associated with the standard two-locus model in population genetics. The present note demonstrates another which appears to have been so far overlooked. It may be stated as follows:

> "Under the conditions of the standard two-locus problem, the gametotype with the highest mean fitness at equilibrium can never be the most frequent."

The proof is as follows. The equilibrium situation may be expressed as

$$x_i(w_i - \bar{w}) = \pm RD \qquad (1 \leqslant i \leqslant 4), \tag{1}$$

where x_i is the frequency and w_i the mean fitness of the ith of the four gametotypes AB, Ab, aB, ab taken in that order, $\bar{w}$ is the mean fitness of the population as a whole, R is the frequency of recombination, and $D = x_1x_4 - x_2x_3$. The plus sign is used if $i = 1$ or 4, the minus sign otherwise. $\bar{w}$ is a weighted mean of the quantities w_i. These equations are derived by (*inter alia*) Lewontin and Kojima (1960).

We suppose for definiteness that AB is the fittest gametotype, i.e.

$$w_1 = \max_{1 \leqslant i \leqslant 4} w_i. \tag{2}$$

It thus follows that

$$w_1 > \bar{w} \tag{3}$$

and thus, by equation (1), that

$$D > 0. \tag{4}$$

Again, by means of equation (1), we thus find

$$w_4 > \bar{w}. \tag{5}$$

We now have

$$w_1 - \bar{w} > w_4 - \bar{w} > 0. \tag{6}$$

But, by equation (1),

$$x_1(w_1 - \bar{w}) = x_4(w_4 - \bar{w}) = RD. \tag{7}$$

It now follows from (6) and (7) that

$$x_4 > x_1. \tag{8}$$

* Manuscript received 3 July 1973.

† Department of Mathematics, Monash University, Clayton, Vic. 3168.

This analysis says nothing of the relative frequencies of the other gametotypes Ab, aB, but does show that ab is more common that AB.

In Ewens' (1969) non-epistatic (additive fitness) model, $w_i = \bar{w}$ at equilibrium and the paradox is avoided. This situation can arise in other cases, but is necessarily rare as it depends on the satisfaction of precise numerical equalities (Deakin 1973).

I am indebted to Professor J. F. Crow who pointed out a simplification of the argument I had originally used.

References

Deakin, M. A. B. (1973).—The effect of epistasis in the standard two-locus model. *Aust. J. biol. Sci.* **26**, 181–8.

Ewens, W. J. (1969).—Mean fitness increases when fitnesses are additive. *Nature, Lond.* **221**, 1076.

Lewontin, R. C., and Kojima, K.-I.—The evolutionary dynamics of complex polymorphisms. *Evolution* **14**, 458–72.

Moran, P. A. P. (1964).—On the nonexistence of adaptive topographies. *Ann. Human Genet.* **27**, 383–93.