POPULATION GENETICS OF "SEX-RATIO" (SR) IN *DROSOPHILA PSEUDOOBSCURA*

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1. INTRODUCTION

In 1957 the author set down the necessary and sufficient conditions for the existence and stability of a selectively balanced polymorphism between two alleles at a locus in the X-chromosome. These conditions depend on the selective differences in both sexes and it is neither necessary nor sufficient for the heterozygote in the homogametic sex to be at a selective advantage over both homozygotes. When these results were applied to the data recorded by Wallace (1948) for the sex-ratio condition (SR) in the X-chromosome of *Drosophila pseudoobscura* it was found that each of the given set of overall selective values corresponded with a stable polymorphic situation and the expectations for the equilibrium frequencies differed considerably from the observations. In two of the populations, for instance, Wallace found that SR was eliminated whereas, according to the overall selective values which he gave, it should have been present with an appreciable frequency. For this reason, the manner in which Wallace had arrived at overall selective values was brought seriously into question (see Bennett, 1958).

In an article published recently in *Heredity*, A. F. W. Edwards (1961) has recorded his view that the methods which I used are inapplicable to this problem and that the results I gave are wrong. However, Dr Edwards' criticisms of this analysis do not stand examination, as I hope to show in this note.

2. THEORY

The approach and terminology used previously by the author are as follows (Bennett, 1957, 1958). If p_f and q_f ($p_f + q_f = 1$) are the relative frequencies of the genes A and a in the gametic output of female members of a given generation, and p_m , q_m ($p_m + q_m = 1$) are the corresponding frequencies for males, then with random mating, the genotypes will appear in the next generation with the following relative frequencies within each sex:

$$\begin{array}{llll} \text{females} & p_f p_m AA & (p_f q_m + q_f p_m) Aa & q_f q_m aa \\ \text{males} & p_f A & & q_f a \end{array}$$

If now the selective values of the male genotypes A and a are in the ratio $t_A : 1$, (where t_A may be taken to be greater than or equal to

unity), and the selective values of female genotypes AA , Aa , aa are in the ratio $S_{AA} : 1 : S_{aa}$, the relative frequencies of the genotypes in each sex after selection will be

$$\begin{array}{lcl} \text{females} & S_{AA}p_f p_m AA & (p_f q_m + q_f p_m Aa \quad S_{aa} q_f q_m aa \\ \text{males} & t_A p_f A & q_f a \end{array}$$

These are taken to be the frequencies with which the different genotypes in each sex contribute to the gametic output of this generation. When equilibrium is attained, the gametic output of females and males will show characteristic values for the gene ratio and these values will then be maintained throughout subsequent generations. The equilibrium values of the gene ratios in the gametic output of females and males are given by

$$u_f = \frac{p_f}{q_f} = \frac{1 + t_A - 2S_{aa}}{1 + t_A - 2t_A \cdot S_{AA}}$$

and

$$u_m = \frac{p_m}{q_m} = t_A u_f.$$

It is then not a difficult matter to prove mathematically that the gene ratios can have stable equilibrium values, other than zero or infinity, if and only if both numerator and denominator of the expression for u_f are positive, *i.e.* S_{aa} must be less than $(1 + t_A)/2$ and S_{AA} must be less than $(1 + t_A)/2t_A$. Putting $t_A = 1 + h$ ($h \geq 0$), the conditions for stability

are $S_{aa} < 1 + \frac{1}{2}h$ and $S_{AA} < 1 - \frac{h}{2(1+h)}$; in this form, it can readily be

seen that if h is not zero, it is neither a necessary nor a sufficient condition for stability for the heterozygote to be at a selective advantage over both homozygotes.

It should perhaps be noted that exactly the same conditions were later expressed in a different form by Mandel (1959). He showed that it was possible to choose certain functions of the selective values which could be associated with the genotypes of the homogametic sex so that the requirement for stability was that the function associated with the heterozygote must be greater than either of those for the homozygotes.

3. APPLICATION OF THEORY TO WALLACE'S DATA ON SEX-RATIO

Wallace's data refer to selection acting on sex-ratio (SR) and the normal X-chromosome (ST) in four experimental populations of *D. pseudoobscura*, two maintained at 16.5°C . and two at 25°C . In all cases the SR chromosome declined in frequency from its initial high values; it was quickly eliminated from the populations kept at 25°C . but in those at 16.5°C . its frequency was reduced only to about 6 per cent., where, it seemed, equilibrium existed. Wallace gave

estimates of the "adaptive values" for various phases of the life cycle and by multiplying these together he arrived at "overall selective values" (see table 1). For the sexual activity of males as well as for the fecundity of females, two estimates of adaptive value were obtained by different methods of computation; taking account of these, Wallace obtained the maximum and minimum overall selective values shown in the table. (Several of the overall selective values given by Wallace are not equal to the products of the corresponding adaptive values. In these cases, the correct product values are shown in brackets in table 1. The differences, though not altogether negligible, are of little consequence for our present discussion. For ease of comparison we shall therefore continue to use the overall selective values given by Wallace.)

Wallace's maximum and minimum overall selective values, when tested in the manner indicated above, are found to correspond with stable non-trivial equilibria. The equilibrium values of the genotypic frequencies which can be calculated from these selective values are shown in table 2 set out as in Bennett (1958). Two points may be emphasised. Firstly, the frequencies "before selection" refer to the relative frequencies with which the different genotypes arise in each sex. Secondly, as explained in the previous section and in Bennett (1958), the frequencies "after selection" are those with which the different genotypes contribute to the gametic output, *i.e.* they are the effective genotypic frequencies at procreation. The differences between these two sets of frequencies are determined by the overall selective values which take account of all the selective forces acting.

The equilibrium and its stability can be considered in terms of overall selective values—despite Dr Edwards' view to the contrary. When overall selective values were introduced into this problem by Wallace (*loc. cit.*, p. 212), he described them as "estimates of the various degrees to which the composition of successive gene pools is influenced by flies of different chromosomal constitution". When this is considered along with table 1, it is clear that Wallace's overall selective values take account of gametic and zygotic selection and that they refer to a complete generation interval. Dr Edwards does not acknowledge this fact but instead complains (*loc. cit.*, p. 301) that because I did indeed treat Wallace's values just as overall selective values, I therefore "confounded gametic and zygotic selection, an erroneous procedure in this case"! The first part of this statement is unreasonable in view of what has been said about Wallace's introduction of these overall values, and the second part is incorrect. The two forms of analysis, one using overall and the other separate gametic and zygotic selective values, must lead to the same equilibrium values for the relative frequencies with which the different genotypes arise in each sex. Dr Edwards repeats the values I had given for these frequencies but he has attempted to go further by calculating expectations for the genotypic frequencies at maturity and also for the sex-ratio

of the population. However, in considering Wallace's population data, the frequencies at maturity are of no use whatsoever and the sex-ratio of the population is not of basic genetical interest. Furthermore, Dr Edwards has based his calculation of the expectations for the sex-ratio of the population on assumptions which are not justified.

TABLE 1

"Adaptive values" for various phases of the life cycle as given by Wallace (1948) for his populations of D. pseudoobscura polymorphic for sex-ratio (SR)

	Males		Females		
	SR	ST	SR/SR	SR/ST	ST/ST
16½° C.					
Larval competition . . .	0.740	1	0.622	1	0.940
Longevity w/food . . .	1.113	1	0.819	1	1.000
Fecundity * . . .	—	—	0.545	1	0.903
Fecundity ** . . .	—	—	0.552	1	0.781
Sexual activity † . . .	0.878	1	—	—	—
Sexual activity †† . . .	0.846	1	—	—	—
"sex-ratio" . . .	2.000	1	—	—	—
Egg hatchability . . .	—	—	1.000	1	1.000
Overall selective value . . .					
Maximum . . .	1.452 (1.446)	1	0.343 (0.281)	1	0.849
Minimum . . .	1.393	1	0.278	1	0.734
25° C.					
Larval competition . . .	0.407	1	0.152	1	0.847
Longevity w/food . . .	1.086	1	0.645	1	1.000
Fecundity * . . .	—	—	0.627	1	0.615
Fecundity ** . . .	—	—	0.580	1	0.543
Sexual activity † . . .	0.820	1	—	—	—
Sexual activity †† . . .	0.788	1	—	—	—
"sex-ratio" . . .	2.000	1	—	—	—
Egg hatchability . . .	—	—	0.234	1	0.603
Overall selective value . . .					
Maximum . . .	0.724	1	0.021 (0.014)	1	0.314
Minimum . . .	0.696	1	0.014 (0.013)	1	0.277

* Eggs/female (average of all counts).

** Total eggs/original number females.

† Using fraction of females inseminated.

†† Using number of females inseminated.

The genotypes with which we are concerned are determined directly from a cytological examination of the salivary glands of larvæ. Wallace arrived at his population frequencies by taking samples of eggs from the population cages and determining the genotypes of the larvæ. Clearly then, it is the relative frequencies of the genotypes at appearance (*i.e.* "before selection" in my terminology) with which we must be primarily concerned in the analysis. Dr Edwards seems to think that the population frequencies of the genotypes "at maturity" are of importance in this problem. Not only are there no observed values for such frequencies but also their expectations can only be calculated if the selection is broken up into gametic and zygotic components.

Whatever reason Dr Edwards may have had for considering frequencies at maturity, it is unreasonable to compare their values with the frequencies "after selection" given by myself and then to complain that, because they differ, my values must be wrong. (This is what he does in discussing his table 5 reproduced here as table 3.) Of course, they must differ because the frequencies "after selection" are the frequencies with which the different genotypes contribute to the gametic output and they are certainly not the same as the frequencies at maturity. Moreover, the only frequencies I have given are those included in table 2; I am not responsible for the figures which Dr

TABLE 2

Equilibrium values for the genotypic frequencies within each sex corresponding to Wallace's overall selective values given in table 1

Temp. (° C.)	Selective values	Genotypic frequencies	Males		Females		
			SR	ST	SR/SR	SR/ST	ST/ST
16.5	Maximum	Before selection	0.341	0.659	0.146	0.478	0.376
		After selection	0.429	0.571	0.059	0.564	0.377
	Minimum	Before selection	0.364	0.636	0.161	0.485	0.354
		After selection	0.443	0.557	0.057	0.614	0.329
25	Maximum	Before selection	0.393	0.607	0.125	0.461	0.413
		After selection	0.319	0.681	0.004	0.777	0.219
	Minimum	Before selection	0.405	0.595	0.130	0.466	0.404
		After selection	0.322	0.678	0.003	0.804	0.193

Edwards has published under my name as part of his table 5. It is impossible to arrive at *any* expectations for the frequencies at maturity by the method I described.

In his table 6 Dr Edwards reproduces figures I had published for the relative frequencies of genotypes within each sex "before selection" and he complains that these are not the same as the frequencies he has calculated taking account of additional assumptions affecting the sex-ratio of the population. Dr Edwards says, "the sex-ratio of the population is, on his (Bennett's) model, always one-half". Of course, the sex-ratio of the effective population at procreation (*i.e.* "after selection" in my terminology) cannot be anything but one-half. But it also needs emphasising, apparently, that although the sex-ratio of the population is not of primary importance in considering the *SR* polymorphism, my "model" which is concerned with the relative genotypic frequencies within each sex allows for *any* sex-ratio in the population. Dr Edwards suggests that the sex-ratio of the population at birth and at maturity is of basic importance in this problem and in

his concern to take account of it, he has introduced into his "model" several assumptions which he has neither justified nor even stated explicitly. Thus he has supposed that the zygotic selective values are the same for *ST* males and *ST/SR* females. He does not mention his assumption that the relative selective values within each sex (values calculated by Wallace on a different basis in males and females as may be seen in table 1) can be taken as directly comparable between sexes. The "viability" factor t , which Dr Edwards has introduced for the expected proportion of daughters born to *SR* males, was actually taken as equal to unity by Wallace in calculating his overall selective values. Following Barker (1958), Dr Edwards has gone beyond the data provided by Wallace and used a value of $t = 0.9382$ recorded by Darlington and Dobzhansky (1942) for another population of *D. pseudoobscura* maintained at 25° C. He does not consider whether it is

TABLE 3

"Equilibrium frequencies at maturity on the two models"—as given by Edwards (1961)
(Table 5, loc. cit., p. 302)

		Bennett	Edwards
females	<i>ST/ST</i>	0.149	0.172
	<i>SR/ST</i>	0.528	0.612
	<i>SR/SR</i>	0.003	0.003
males	<i>ST</i>	0.218	0.172
	<i>SR</i>	0.102	0.040
	Sex-ratio	0.320	0.212
Male gene frequency . .		0.319	0.190
Female gene frequency . .		0.393	0.393
Overall gene frequency . .		0.379	0.369

justifiable to assume that the "viability" factor t is determined solely by temperature, *i.e.* that humidity and other environmental factors as well as background genotype have no effect. Furthermore, Dr Edwards has assumed that all sons of sex-ratio males receive a Y-chromosome whereas it is known that some are XO and sterile. In view of all this, it is not surprising that Dr Edwards' "model" for Wallace's populations leads to expectations for the sex-ratio differing consistently from the values observed.

4. SUMMARY

In 1957 the author gave the necessary and sufficient conditions for the existence and stability of a selectively balanced polymorphism between two alleles at a locus in the X-chromosome and he applied these results in a study of Wallace's (1948) data on the sex-ratio (*SR*) polymorphism in *D. pseudoobscura* (Bennett, 1957, 1958). Edwards (1961), referring to this application, has stated "unfortunately it happens that his (Bennett's) results are, on the surface, reasonable and some are indeed correct" (but) "in view of the inapplicability

of Bennett's model to the present problem it seems best to disregard it in this connection". Dr Edwards' criticism of this work does not stand examination. His results are the same as those given by the author in 1958 for the equilibrium frequencies with which the different genotypes arise in each sex. In considering this *SR* polymorphism, these are the only frequencies that matter. Since Wallace's *SR* population data refer exclusively to frequencies at hatching, it is quite unnecessary to break up the overall selective values into gametic and zygotic components as Dr Edwards would have us do (to calculate expectations for the genotypic frequencies at maturity). Furthermore, Dr Edwards' calculations of the expected sex ratio for the *SR* population are based on various assumptions which do not seem to be justified.

5. REFERENCES

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