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INTERACTION BETWEEN SELECTION AND SEGREGATION RATIOS WITH REDEFINED CONCEPT OF FITNESS DIFFERENTIALS

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ABSTRACT. Taking into account the redefined concept of fitness differentials among the genotypes, natures of equilibria of models of differential selection in the two sexes under random mating with Mendelian segregation as well as with segregation distortion have been analyzed. Two cases of real interest, where different genes are favored in the two sexes and where overdominance is involved, have been investigated. It has been illustrated through graphical representation that the degree of dominance over the sexes (mainly comparing the heterozygous fitnesses in males and females) is a function of equilibrium region. The considered framework of the one locus model unveils most important result that, generally, above the value of Mendelian segregation, prone to arising of single stable polymorphic equilibrium increases.

Keywords: Fitness differential, Mendelian segregation, segregation distortion, Equilibrium region.

AMS Subject Classification: 92-02, 92D10

1. INTRODUCTION

In most cases, population genetic models are developed under a number of simplifying assumptions, e. g. consideration of the random mating, the fitnesses to be fixed constant, the population effectively being the infinite and so on. Like the problems relating to the other mathematical fields, it is quite impossible to consider the effect of relaxing them all. Perhaps the most important assumption is that the distinct generation can be recognized in such a way that mating occurs only between individuals of the same generation, and these individuals do not participate in further mating once the daughter generation is formed.

Mendel demonstrates that a hybrid between two different varieties possesses both types of parental factors in the gametes (principle of segregation) and the two individual genes in a particular gene pair (alleles) are equally represented in its gametes. However, it is the lethality among zygotes which results in the absence of certain classes and the distortion of expected Mendelian ratios. The phenomenon associated with segregation distortion of such ratios has been termed meiotic drive in which one or more classes of gametes are either

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lethal or unable to conjugate according to the usual meiotic segregation pattern. Meiotic drive is defined by Ganetzky [1] as “any alteration of meiosis or gametogenesis that results in preferential transmission of a particular allele or chromosome”. For example, certain *Drosophila* males of the genotype $cn\ bw/cn^+ bw^+$ (where cn and bw represent recessive genes cinnabar and brown, each causing a modified eye colour but interacting to produce white eyes when homozygous in the same fly) when mated to white eyed $cn\ bw/cn\ bw$ females, produce offspring in ratios of about 25 wild (normal) type ($cn^+ bw^+/cn\ bw$) to 1 white eye ($cn\ bw/cn\ bw$) instead of the expected 1 : 1 [2]. Generally meiotic drive associated with segregation distortion differs between the sexes. Much evidence has been cited by Úbeda and Haig [3] for demonstrating this statement.

Models of differential selection in the two sexes have been studied by a number of authors [4, 5, 6]. In order to analyse the differential selection in the two sexes, Owen [6] constructed a general mathematical framework which showed more than a single stable equilibrium under certain considered situation. Bodmer [4] took into account the fertility effect along with viability selection, and observed qualitatively different results when selective effects are opposed in the two sexes. It had been reported that only model of selection constituted by overdominance in one sex coupled with underdominance in the other sex could yield three equilibria. The equilibrium structure of models of differential selection has been analysed by Kidwell et al. [5] under the assumption of discrete generation along with random mating among selected adults. It has been shown that opposing additive selection leads to stable polymorphic equilibria, and illustrated the dependence of the equilibrium region on the average degree of dominance over the sexes.

In many mathematical models have frequently been assumed identical segregation ratios in males and females [7] as well as in many cases have also been formulated a general model of segregation distortion with identical viability parameters in males and females but otherwise, unconstrained [8, 9]. Úbeda and Haig [3] extended the Wright's [9] model and completed the analysis of Hartl's [8] results by considering the interaction between genomic imprinting (parent-of-origin-specific gene expression) and the segregation distortion. They provided an analytical and numerical analysis of the equilibria, finding examples of parameter set with three polymorphic equilibria (two stable). Using the concept of genomic imprinting, the interaction between mutation and selection has been analysed by Spencer [10] at autosomal loci, and recently, based upon the same concept, Van Cleve and Feldman [11] have presented a two-locus modifier model.

From analysis of works regarding various models of differential selection in the two sexes by a number of authors, it is quite obvious that there will be no internal equilibrium if selection favours the same allele in both males and females [12]. Thus, in the present paper, we analyse the two cases of real interest, first that different genes are favoured in the two sexes relating case and second that overdominance is involved relating case. The conservation of opposing forces strongly influences all the mechanisms, which maintain genetic variability. Such opposing forces may be the result of opposing mutation pressures, opposing viability nature, opposing mating success, opposing fertility capacity, or overdominance case where an allele is favoured in heterozygotes but is at a disadvantage in homozygotes. In the present analysis, we follow the similar structure which has been built up by Kidwell et al.[5] and extend the analysis with Mendelian segregation and with segregation distortion under construction of the redefined concept of fitness differentials among the genotypes.

2. BASIC CONCEPT AND THE MODEL

In order to redefine the concept of fitness differentials among the genotypes, we take into account a given gene locus at which two alleles may occur, namely A_1 and A_2 . For the moment, we consider a case of random-mating of monoecious population, which is so large that changes of genotypic frequency may be treated as deterministic. If small probability of mutation is ignored and there are no fitness differentials among genotypes, then according to Hardy-Weinberg law, we may state that a population having genotypic frequencies X (of A_1A_1), $2Y$ (of A_1A_2) and Z (of A_2A_2) possesses, after one generation of random mating stable genotypic frequencies x^2 , $2x(1-x)$, $(1-x)^2$, where $x = X + Y$ and $1-x = Y + Z$. If the initial frequencies X , $2Y$, Z also assume values of the form x^2 , $2x(1-x)$, $(1-x)^2$, then frequencies are stable for all generations. In that circumstances, we observe that the frequency $x = X + Y$ of the allele A_1 (in other words, frequency $1-x = Y + Z$ of the allele A_2) does not change in the following generations.

Normally mutation rates are so small that for certain specific problem we may ignore mutation events. Also, in order to avoid complexity in the present analysis we disregard the case of fertility.

Let us consider the fitnesses and the frequencies of the three genotypes A_1A_1 , A_1A_2 and A_2A_2 at a considering locus A of the following forms:

genotype	A_1A_1	A_1A_2	A_2A_2
fitness	w_{11}	w_{12}	w_{22}
frequency	x^2	$2x(1-x)$	$(1-x)^2$

At this stage it is quite normal to arise question that what is the frequency of the allele A_1 in the following generation under this considered natural selection? In order to answer this question, we define mean effect on allele A_1 as $\mu_{A_1} = w_{11}x + w_{12}(1-x)$ and mean effect on A_2 as $\mu_{A_2} = w_{22}(1-x) + w_{12}x$. Thus the ratio of mean effect in per unit (since in the smooth fitness environment is $(\frac{\mu_{A_1}}{\mu_{A_2}})_{w_{11}=w_{12}=w_{22}=1} = 1$) is defined as

$$\frac{\mu_{A_1}}{\mu_{A_2}} = \left(\frac{w_{11}x + w_{12}(1-x)}{w_{22}(1-x) + w_{12}x} \right).$$

Hence, if x' be the new frequency of A_1 in the following generation, then we have

$$\frac{x'}{1-x'} = \left(\frac{w_{11}x + w_{12}(1-x)}{w_{22}(1-x) + w_{12}x} \right) \left(\frac{x}{1-x} \right),$$

i.e.,

$$\frac{x'}{1-x'} = \frac{w_{11}x^2 + w_{12}x(1-x)}{w_{22}(1-x)^2 + w_{12}x(1-x)}, \tag{1a}$$

or, equivalently,

$$x' - x = \frac{x(1-x)\{w_{11}x + w_{12}(1-2x) - w_{22}(1-x)\}}{w_{11}x^2 + 2w_{12}x(1-x) + w_{22}(1-x)^2}. \tag{1b}$$

Thus, using the recurrence relation (1b) we could obtain successive values taken by the frequency of A_1 , although indeed simple explicit expressions for these frequencies are not always available. Based upon the expression (1b), Ewens [12] states (which is accepted in genetic literature) that as x' depends on the ratios of the fitness w_{ij} other than the absolute values, x' remains unchanged if we multiply each w_{ij} by any convenient scaling constant, i.e. we can use convenient scale for each w_{ij} in the particular problem. Because of that

Ewens [12] introduced the following forms of fitness values for analysis the expression (1b):

genotype	A_1A_1	A_1A_2	A_2A_2
fitness	w_{11}	w_{12}	w_{22}
	$1 + s$	$1 + sh$	1
	$1 - s_1$	1	$1 - s_2$

in which the fitness differentials s , sh , s_1 and s_2 are of same signs in the particular problem. But expression (1a) clearly suggests that while fitness value of homozygote A_1A_1 is increasing, fitness value of other homozygote A_2A_2 must be decreasing, and interchanging the roles of homozygotes in the above statement we can arrive at the converse conclusion (since $x' = \kappa(w_{11}x^2 + w_{12}x(1-x))$ and $1-x' = \kappa(w_{22}(1-x)^2 + w_{12}x(1-x))$ simultaneously hold, κ being constant). Thus, Ewens' [12] assumption does not tend to realistically unaltered mean fitness environment and fitness values must, here, be reasonably in the following forms:

genotype	A_1A_1	A_1A_2	A_2A_2
fitness	w_{11}	w_{12}	w_{22}
	$1 + s$	$1 + sh$	$1 - s$
	$1 - s_1$	1	$1 + s_2$

We now consider the case of random mating of dioecious population (admitting two sexes) where the assumptions of the foregoing discussions are maintained. At this step it can be possible to show that Hardy-Weinberg law also holds in random mating of dioecious population in such a way that if we represent males and females' frequencies in vector forms as $\mathbf{P}_M = (X_M, 2Y_M, Z_M)$ and $\mathbf{P}_F = (X_F, 2Y_F, Z_F)$ and use the three fundamental genetic matrices, denoting by A, B, C (for details see Kapur [13]), then the frequency vector for both males and females in the first generation is given by

$$X_F \mathbf{P}_M A + 2Y_F \mathbf{P}_M B + Z_F \mathbf{P}_M C = (X_M + Y_M)(X_F + Y_F), (X_M + Y_M)(Y_F + Z_F) + (X_F + Y_F)(X_M + Y_M), (Y_M + Z_M)(Y_F + Z_F),$$

and, therefore, using this frequency vector for both males and females, we get the frequency vector for the second generation in a similar way as

$$(x^2, 2x(1-x), (1-x)^2),$$

which is nothing but Hardy-Weinberg law where $x = \frac{1}{2}(X_M + X_F + Y_M + Y_F)$.

Hence, we have now reached to our main platform where we take into account the genotypic fitness values to be different in males and females, and try to analyse the nature of equilibria along with the regions of stable equilibria under our redefined fitness differentials concept. In order to analyse the stability we follow the path which was constructed by Kidwell et al.[5] and the analysis is to be reformulated and extended with Mendelian segregation and with segregation distortion. According to our previous assumptions, we neglect the fertility selection ; the relative fitnesses of the genotypes A_1A_1 , A_1A_2 , A_2A_2 in males are designated as w_{11} , w_{12} , and w_{22} , with corresponding values v_{11} , v_{12} , v_{22} in females. In given generation frequency of allele A_1 in males and females in the mating pool are denoted by x and y respectively, thus frequency of allele A_2 in males and females are $1 - x$ and $1 - y$ respectively. As we now consider genotypic frequencies immediately after the formation of zygotes, so at the time of conception of the zygotes in the daughter generation in both sexes the genotypic frequencies are :

genotype	A_1A_1	A_1A_2	A_2A_2
frequency	xy	$x(1-y) + y(1-x)$	$(1-x)(1-y)$

With the age of maturity these frequencies will have been altering by differential viability and after selection, genotypic frequencies are:

genotype	A_1A_1	A_1A_2	A_2A_2
males	$\frac{w_{11}xy}{\bar{w}}$	$\frac{w_{12}\{x(1-y)+y(1-x)\}}{\bar{w}}$	$\frac{w_{22}(1-x)(1-y)}{\bar{w}}$
females	$\frac{v_{11}xy}{\bar{v}}$	$\frac{v_{12}\{x(1-y)+y(1-x)\}}{\bar{v}}$	$\frac{v_{22}(1-x)(1-y)}{\bar{v}}$

where

$$\begin{aligned}\bar{w} &= w_{11}xy + w_{12}\{x(1-y) + y(1-x)\} + w_{22}(1-x)(1-y), \\ \bar{v} &= v_{11}xy + v_{12}\{x(1-y) + y(1-x)\} + v_{22}(1-x)(1-y).\end{aligned}$$

If we let the segregation ratio of A_1 be k_m in male meiosis and k_f in female meiosis while the corresponding ratios for A_2 are $1 - k_m$ and $1 - k_f$ ($0 < k_m, k_f < 1$), then in the mating pool for the following generation, frequency of the allele A_1 in males and females (cf. Úbeda and Haig [3]) in the case of Mendelian segregation and in the case of segregation distortion are respectively

$$\bar{w}' = w_{11}xy + \frac{1}{2}w_{12}\{x(1-y) + y(1-x)\}, \quad (2a)$$

$$\bar{v}' = v_{11}xy + \frac{1}{2}v_{12}\{x(1-y) + y(1-x)\}, \quad (2b)$$

and

$$\bar{w}' = w_{11}xy + k_m w_{12}\{x(1-y) + y(1-x)\}, \quad (3a)$$

$$\bar{v}' = v_{11}xy + k_f v_{12}\{x(1-y) + y(1-x)\}. \quad (3b)$$

Now, the changes in gene frequencies are

$$\bar{w}\Delta x = w_{11}xy + \frac{1}{2}w_{12}\{x(1-y) + y(1-x)\} - \bar{w}x, \quad (4a)$$

$$\bar{v}\Delta y = v_{11}xy + \frac{1}{2}v_{12}\{x(1-y) + y(1-x)\} - \bar{v}y, \quad (4b)$$

and

$$\bar{w}\Delta x = \frac{\partial w_{11}}{\partial x}x(1-x) - (1 - k_m)w_{12}x(1-y) + k_m w_{12}y(1-x), \quad (5a)$$

$$\bar{v}\Delta y = \frac{\partial v_{11}}{\partial y}y(1-y) - (1 - k_f)v_{12}x(1-y) + k_f v_{12}y(1-x). \quad (5b)$$

Since at the equilibrium state $\Delta x = \Delta y = 0$, so at that point we have after some simple calculations

$$x = \frac{2(v_{12}-v_{22})y^2 + (2v_{22}-v_{12})y}{(4v_{12}-2v_{11}-2v_{22})y^2 + (2v_{11}-4v_{12}+2v_{22})y + v_{12}}, \quad (6a)$$

$$y = \frac{2(w_{12}-w_{22})x^2 + (2w_{22}-w_{12})x}{(4w_{12}-2w_{11}-2w_{22})x^2 + (2w_{11}-4w_{12}+2w_{22})x + w_{12}}, \quad (6b)$$

and

$$x = \frac{(v_{12}-v_{22})y^2 + (v_{22}-k_f v_{12})y}{(2v_{12}-v_{11}-v_{22})y^2 + (v_{11} - (2k_f + 1)v_{12} + v_{22})y + k_f v_{12}}, \quad (7a)$$

$$y = \frac{(w_{12}-w_{22})x^2 + (w_{22}-k_m w_{12})x}{(2w_{12}-w_{11}-w_{22})x^2 + (w_{11} - (2k_m + 1)w_{12} + w_{22})x + k_m w_{12}}. \quad (7b)$$

Each of the frequency terms is the ratio of polynomials of other frequency term and if we denote them by $x = f(y)$ and $y = g(x)$ then by substitution we obtain $x = f[g(x)]$, a quintic equation of x which can be reduced to a cubic by factoring out the trivial roots zero and one in which either A_1 or A_2 is absent. Thus, there exist at most three polymorphic equilibria. As the recurrence relations (2a) and (2b) or (3a) and (3b) can not be solved explicitly, we try to draw some certain important properties concerning their equilibrium points. Also, since the resulting cubic equation is very difficult to analyse directly and there is no internal equilibrium if selection favours the same allele in both males and females, so keeping in mind the redefined concept of fitness differential, here, in the models of opposing selection we consider the following cases.

2.1. opposing additive selection.

Mendelian segregation: The selection acts in opposite directions in two sexes in such a way that A_1 is favoured in males and A_2 is favoured in females. Thus we write the fitnesses in the following forms :

genotype	A_1A_1	A_1A_2	A_2A_2
fitness, males	$1 + h_m s_m$	$1 - h_m s_m$	$1 - 3h_m s_m$
fitness, females	$1 - 3h_f s_f$	$1 - h_f s_f$	$1 + h_f s_f$

where, $h_m, h_f \leq 0.33$ and $s_m, s_f \in (0, 1)$. Substituting the above values into (6a) and (6b), and simplifying, we have

$$x = \frac{-4h_f s_f y^2 + (1 + 3h_f s_f)y}{1 - h_f s_f}, \quad (8a)$$

$$y = \frac{4h_m s_m x^2 + (1 - 5h_m s_m)x}{1 - h_m s_m}. \quad (8b)$$

By factoring out the trivial roots zero and one, the resulting quartic equilibrium equation can easily be converted to a quadratic equation, and the only possible equilibrium is

$$x = \frac{3h_m s_m - 1}{4h_m s_m} + \frac{1}{2} \sqrt{\frac{5h_m s_m h_f s_f - h_m s_m - h_f s_f + 1}{4h_m s_m h_f s_f}},$$

in which the first term on the right hand side is always negative and the term under the radical is always positive as $h_m, h_f \leq 0.33$ and $s_m, s_f \in (0, 1)$.

Now, using the fact that $0 < x < 1$, we can determine the region of admissible equilibria in the following form where boundaries are functions of h_m :

$$\frac{h_m s_m}{h_f(1 + 4h_m s_m)} < s_f < \frac{h_m s_m}{h_f(1 - 4h_m s_m)}.$$

The equilibrium regions, bounded by these boundaries, are shown in Fig.1(a). From bounded portions of figures, we can immediately conclude that the area of bounded portion increases with decrease of fitness of heterozygote as well as of homozygote of weaker selection. Using these regions, we can easily compute equilibrium gene frequencies, where one can find out three important points, viz. (i) the equilibrium frequencies in the two sexes can be widely divergent with increase of strength of opposing selection, (ii) the average gene frequency ($\bar{p} = \frac{x+y}{2}$) is moved towards the intermediate ($0.25 \leq \bar{p} \leq 0.75$) portion of equilibrium region with increase of strength of opposing selection (cf. Kidwell et al. [5]) and (iii) areas of equilibrium regions are restricted by allele ranges of weaker selection (in respect of opposite gender) upto values where allele of weaker selection remains dominant than the other allele range of stronger selection (i.e., in the equilibrium region, the constraint $h_m s_m < h_f s_f$ always holds). The analysis of this section clearly reveals that polymorphic equilibria are always stable under such type of opposing additive selection. It is, therefore, of interest to extend the analysis in a more general context.

segregation distortion: In this section we consider only the sex independent segregation distortion, i.e. $k_m = k_f = k$ and fitness relations are parameterized as

genotype	A_1A_1	A_1A_2	A_2A_2
fitness, males	$1 + s$	1	$1 - s$
fitness, females	$1 - s$	1	$1 + s$

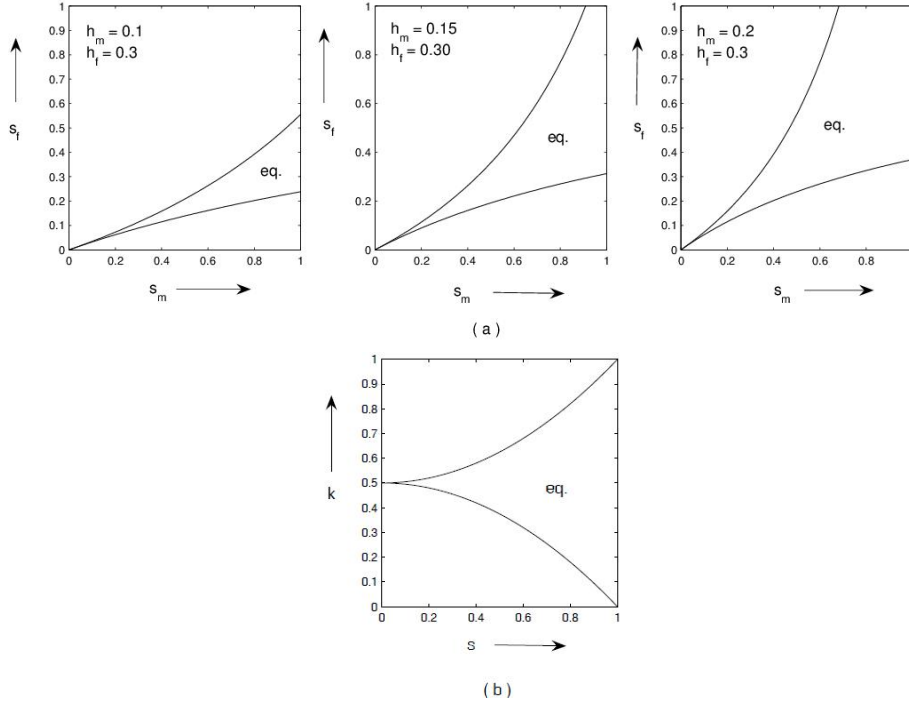


Fig 1. (a) Regions of admissible equilibria in the parameter space of the fitness differentials in males (h_m, s_m) and females (h_f, s_f) for opposing additive selection where yielding internal equilibria are stable. (b) Region of admissible equilibria in the parameter space (s, k) for opposing additive selection where yielding internal equilibrium is stable.

where, $0 < s, k < 1$.

At the point of equilibrium, substitution and simplifying the equations (5a) and (5b) yield

$$s \left(\frac{1-x}{1-y} \right) + k \left(\frac{y}{x} \right) \left(\frac{1-x}{1-y} \right) - (1-k) = 0, \tag{9a}$$

$$s \left(\frac{1-y}{1-x} \right) - k \left(\frac{x}{y} \right) \left(\frac{1-y}{1-x} \right) + (1-k) = 0. \tag{9b}$$

From (9a) and (9b), we can write quadratics of $\left(\frac{y}{x}\right)$, $\left(\frac{1-x}{1-y}\right)$, and solving those equations we have only

$$\left(\frac{y}{x}\right) = \frac{(k^2 - (1-k)^2 - s^2) + \sqrt{(k^2 - (1-k)^2 - s^2)^2 + 4s^2k^2}}{2sk} = \eta(\text{say}), \tag{10a}$$

$$\left(\frac{1-x}{1-y}\right) = \frac{((1-k)^2 - k^2 - s^2) + \sqrt{((1-k)^2 - k^2 - s^2)^2 + 4s^2(1-k)^2}}{2s(1-k)} = \xi(\text{say}). \tag{10b}$$

Thus, the equilibrium point (x, y) is given by

$$\left(\frac{1-\xi}{1-\eta\xi}, \frac{\eta(1-\xi)}{1-\eta\xi} \right).$$

Now using the fact that $0 < x < 1$, we must have $\xi, \eta < 1$; thus, the region of admissible equilibria can be written as function of s as

$$\frac{1-s^2}{2} < k < \frac{1+s^2}{2}.$$

The equilibrium region for values of s and k is depicted in Fig.1(b). For each point of (s, k) plane, we can determine gene frequencies and infer that (i) similar to previous, equilibrium frequencies of opposite sexes can be widely divergent, (ii) average gene frequencies ($\bar{p} = \frac{x+y}{2}$) are rightmediate ($0.5 \leq \bar{p} \leq 1$) throughout most of the equilibrium region; and from this point we can draw the most interesting conclusion that since above and below the Mendelian segregation, prone of arising stable polymorphic equilibrium is equal, so in this case fitness differential is more influential factor than segregation distortion.

2.2. opposing selection with arbitrary dominance.

Mendelian segregation : In order to extend the previous analysis under more general scenario, we use the following fitness values in males and females:

genotype	A_1A_1	A_1A_2	A_2A_2
fitness, males	$1 + s_m$	$1 - h_m s_m$	$1 - s_m$
fitness, females	$1 - s_f$	$1 - h_f s_f$	$1 + s_f$

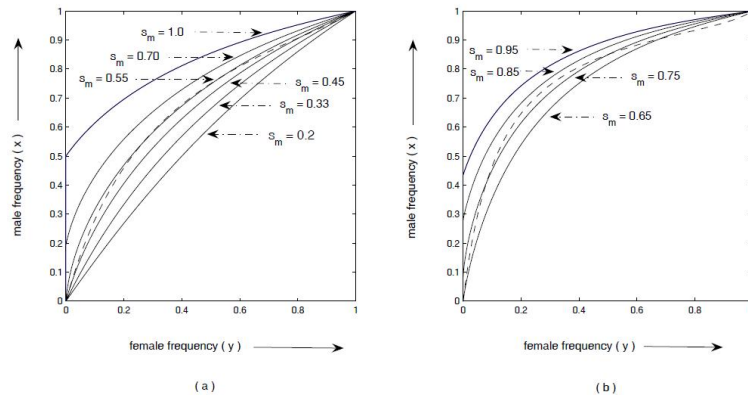


Fig. 2. Graphs of equations (6a) and (6b). Dashed lines are the graphs of equation (6a).
 (a) Equilibrium gene frequency as a function of s_m , where male heterozygote's fitness is relatively favourable than female heterozygote's fitness. $h_f = 0.7, s_f = 0.5, h_m = 0.3$. $s_m = 0.2$: there is no internal equilibrium. $s_m = 0.33$: there is no internal equilibrium and the graph of equation (6b) is tangent to that of equation (6a) in the vicinity of (1,1). $s_m = 0.45$: the graph of equation (6b) is tangent to the dashed line of equation (6a) in the vicinity of (0,0) and there exists an internal equilibrium point. $s_m = 0.55$: in such type of fitness values female drives out A_1 gene and there exist two internal equilibrium points. $s_m = 0.70$ and $s_m = 1.0$: there exists no equilibrium point and in female gene A_1 has been eliminated. As equilibrium points are the coordinates of meeting points of solid line of equation (6b) and dashed line of equation (6a), we can say that internal equilibrium point moves towards the middle point $(\frac{1}{2}, \frac{1}{2})$ with increase of s_m .
 (b) Equilibrium gene frequency as a function of s_m in case of lower values of heterozygotes, where male heterozygote's fitness is relatively favourable than female heterozygote's fitness. $h_f = 0.9, s_f = 0.7, h_m = 0.6$. $s_m = 0.65$: there is an internal equilibrium and the graph of equation (6b) has become tangent to that of equation (6a) in the vicinity of (0,0). $s_m = 0.75$: in such type of selection the female derives out the A_1 gene and there exist two internal equilibrium points, one stable and other unstable. $s_m = 0.85$ and $s_m = 0.95$: there is no internal equilibrium point and A_1 gene is to be eliminated, i.e. only stable trivial equilibrium is (1,1). If male heterozygote starts with relatively high selection frequency the polymorphism will be maintained, otherwise it will be eliminated.

Figs.2(a)-2(d) are drawn on the basis of comparing heterozygous fitness values in males and females, where graphs of equations (6a) and (6b) are depicted for selective values, and equilibria are being the intersecting and/or touching points of the graphs. All graphs are

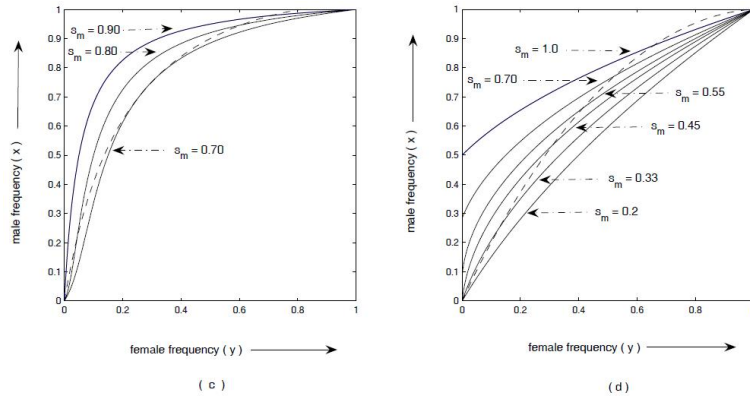


Fig. 2. (c) Equilibrium gene frequency as a function of s_m , where female heterozygote's fitness is relatively favourable than male heterozygote's fitness. $h_f = 0.6, s_f = 0.8, h_m = 0.9$. $s_m = 0.70$: there is a single unstable equilibrium and in male A_2 will be lost. $s_m = 0.80$: there are two internal equilibria, one stable and other unstable. At $s_m = 0.80 + \epsilon_0$ (very small number) the unstable equilibrium, where A_1 is relatively rare will be moved to coincide with the trivial equilibrium at $(0,0)$. $s_m = 0.90$: the unstable internal equilibrium is disappeared. For any values of initial gene frequencies the polymorphism will be always preserved.

(d) Equilibrium gene frequency as a function of s_m in case of a stable internal equilibrium, where both male and female heterozygotes' fitnesses are strongly favourable. $h_f = 0.1, s_f = 0.5, h_m = 0.009$. $s_m = 0.2$: there is no internal equilibrium. $s_m = 0.33$ and $s_m = 0.45$: there exists a stable internal equilibrium. $s_m = 0.55, s_m = 0.70$, and $s_m = 1.0$: the selection in the female derives out the A_1 gene and stable internal equilibrium point moves towards the trivial equilibrium point $(1,1)$.

shown in respect of female frequency and varying values of male fitness differential s_m , i.e. only the graph of equation (6b) changes and the equilibrium point moves along the fixed graph of equation (6a) in the (y, x) space. How the degrees of dominance influence on the equilibria are explained throughout the Figs.2(a)-2(d), and it has been demonstrated that polymorphism will only be preserved under certain circumstances. All results are arranged in Table 1. In fact, in order to understand the way how the system behaves, observation of the equilibrium appearing and disappearing is an important task.

Table 1. Obtained results of Mendelian segregation (opposing selection with arbitrary dominance)

characteristic	Nature of trivial equilibrium(0,0)	Nature of trivial equilibrium(1,1)	Nature of polymorphic equilibrium (or equilibria)
male $A_1 A_2$ favorable than female $A_1 A_2$ (stronger selection)	stable equilibrium unstable equilibrium	stable equilibrium unstable equilibrium stable equilibrium stable equilibrium	— one stable equilibrium two stable equilibria —
male $A_1 A_2$ favorable than female $A_1 A_2$ (weaker selection)	unstable equilibrium —	stable equilibrium stable equilibrium stable equilibrium	one stable equilibrium two stable equilibria —
female $A_1 A_2$ favorable than male $A_1 A_2$ (general selection)	stable equilibrium stable equilibrium	— —	unstable equilibrium one stable equilibrium and one unstable one stable equilibrium
stronger selection of both $A_1 A_2$	stable equilibrium unstable equilibrium —	stable equilibrium stable equilibrium stable equilibrium	— one stable equilibrium one stable equilibrium

Table explains the equilibrium nature in row wise where at the point — we can not take/make any conclusion. Here, an equilibrium point is unstable in the sense that in every neighbourhood (however small) of that point always exists at least another one equilibrium point of the system.

It is quite clear that when graphs of equations (6a) and (6b) are tangent to one another, then the possibility of creating an instability may arise. Thus, in regard to stable and unstable equilibrium concept, tangent condition plays a crucial role.

Taking $a_f = 2\frac{v_{11}}{v_{12}} - 1$ and $b_f = 2\frac{v_{22}}{v_{12}} - 1$ (as well as introducing similar compact parameters in male fitness values [5, 6]) and using these compact parameters into (6a) and (6b), we have

$$x = f(y; a_f, b_f) \text{ and } y = f(x; a_m, b_m)$$

respectively, where $f(y; a, b) = \frac{(1-b)y^2 + by}{1+y(1-y)(a+b-2)}$. Thus the required condition for the tangents of equations (6a) and (6b) to coincide at (0,0) is

$$f^{(1)}(0; a_f, b_f) \cdot \frac{1}{f^{(1)}(0; a_m, b_m)} = 1,$$

i.e. $b_m b_f = 1$ and for coincidence at (1,1), the required condition is $a_m a_f = 1$, where superscript 1 within first bracket indicates first order derivative.

Again, if we introduce the function $g(r, s; a, b) = \frac{(a+1)rs + r(1-s) + s(1-r)}{(a+1)rs + r(1-s) + s(1-r) + (b+1)(1-r)(1-s)}$, then equations (2a) and (2b) can respectively be written as

$$x' = g(x, y; a_m, b_m) \text{ and } y' = g(y, x; a_f, b_f).$$

Consequently, the 1st order approximation of the system evaluated in the proximity of equilibrium (x_e, y_e) is

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} \frac{\partial x'}{\partial x} |_{(x_e, y_e)} & \frac{\partial x'}{\partial y} |_{(x_e, y_e)} \\ \frac{\partial y'}{\partial x} |_{(x_e, y_e)} & \frac{\partial y'}{\partial y} |_{(x_e, y_e)} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}, \text{ i.e. } \mathbf{X}' = \mathbf{GX}.$$

Hence the Jacobian matrix at (0,0) for the above set of equations is

$$\mathbf{G}_0 = \begin{pmatrix} \frac{1}{b_f + 1} & \frac{1}{b_f + 1} \\ \frac{1}{b_m + 1} & \frac{1}{b_m + 1} \end{pmatrix}$$

whose dominant eigenvalue is

$$\lambda_d = \frac{1}{b_m + 1} + \frac{1}{b_f + 1}. \quad (11a)$$

Similarly the dominant eigen value of the Jacobian matrix of the considered set of equations evaluated at (1,1) is

$$\lambda_d = \frac{1}{a_m + 1} + \frac{1}{a_f + 1}. \quad (11b)$$

If $c(\lambda) = \lambda^2 - tr(\mathbf{G}) + det(\mathbf{G})$ be the characteristic polynomial associated with the linearized system where signs have their usual meaning, then the necessary and sufficient conditions for local stability of (x_e, y_e) are $c|_{\lambda=1} > 0$ and $\frac{\partial c}{\partial \lambda} |_{\lambda=1} > 0$ (Lessard and Karlin [14]), or, equivalently $\lambda_d < 1$ (Ewens[12]); thus we can say that the trivial equilibrium at (0,0) is stable when λ_d of equation (11a) is less than 1, i.e. when $b_m b_f > 1$ and the equilibrium is unstable when $b_m b_f < 1$. Similarly the equation (11b) implies that the trivial equilibrium (1,1) is stable when $a_m a_f > 1$ and when $a_f a_m < 1$ it is unstable, i.e. each of the tangent conditions $a_f a_m = 1$ and $b_f b_m = 1$ divides the space into two parts one of which is stable and the other is unstable in respect of each trivial equilibrium.

Using Owen's equation for fixed values of h_m and h_f , the regions of one unstable and one stable equilibrium are depicted by Kidwell et al. [5] in (s_m, s_f) space. It is obvious that using the condition of the existence of a multiple root of the obtained cubic equation

from equations (6a) and (6b), one can derive the Owen equation, although we can not deny that the depicted procedure of the relations between s_f and s_m , which are obtained from Owen's equation, is quite obscure as for each value of s_m we may obtain at most four real values of s_f , i.e. in that circumstances graphical representation of function (!) like $s_f = f(s_m)$ in the (s_m, s_f) space is not possible (or realistic) in respect of biological as well as mathematical points of view (see Kidwell et al. [5]). This is the reason why we have not considered the Owen's equation in the present analysis .

Now, using the considered fitness values in males and females we see that the trivial equilibria are unstable when

$$s_f < \frac{s_m(1 - h_m)}{(1 - s_m)(1 + h_f) - s_m(1 - h_m)}, \tag{12a}$$

$$s_f > \frac{s_m(1 + h_m)}{(1 + s_m)(1 - h_f) + s_m(1 + h_m)}. \tag{12b}$$

Fig.3 represents the boundaries of regions of equilibria as a function of s_m in the (s_m, s_f) space for fixed values of h_m and h_f . Actually, the graphs of equations (12a) and (12b) divide the (s_m, s_f) space into three different characteristic regions, which are marked by different symbols. Graphical representations show that the relation $h_m + h_f = 0.109$ concerning the dominance parameters divides the equilibrium properties of this model into two classes, one is under the condition $h_m + h_f > 0.109$ in which more than a single internal equilibrium is occurred, and the second is under the condition $h_m + h_f < 0.109$ where only a single stable polymorphic equilibrium is found, i.e. the entire region bounded by the equations (12a) and (12b) is characterized by a single stable polymorphic equilibrium.

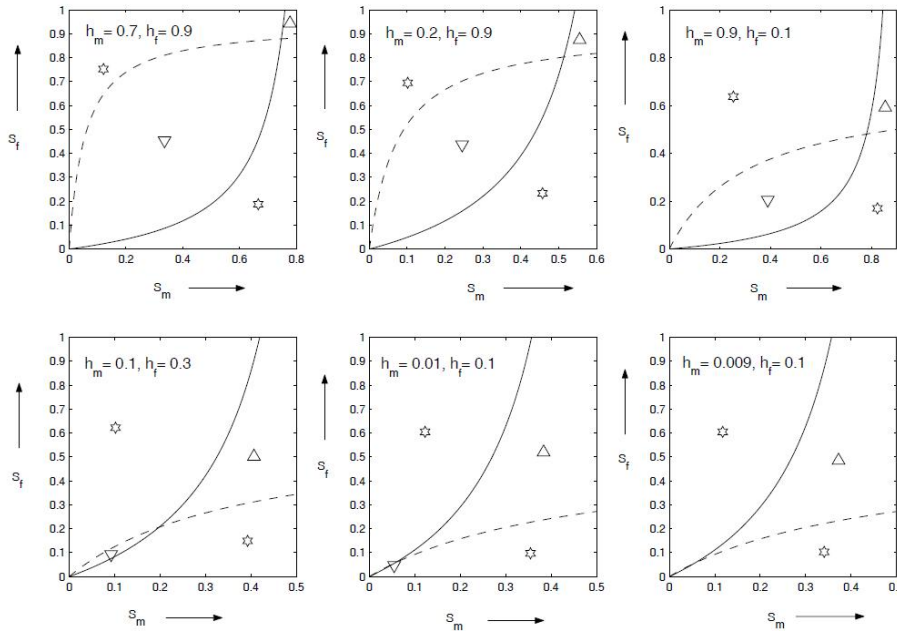


Fig. 3. Regions of equilibria in the (s_m, s_f) space for fixed values of h_m and h_f . The dashed line (- -) divides the region in the two portions, one stable and other unstable in respect of (1,1). Along the solid line (—) the trivial equilibrium (0,0) goes from stability to instability. The regions, marked by six-pointed star (☆), characterize that only one trivial equilibrium is stable between (0,0) and (1,1). The regions, marked by triangle-upward (△), contain a single stable polymorphic equilibrium and the regions, marked by triangle-downward (▽), contain a single unstable equilibrium.

Thus, we can say that when dominance parameters satisfy the relation $h_m + h_f = 0.109$, the obtained entire equilibrium region is identical to the case of opposing additive selection where heterozygous fitness values are arithmetic mean of the homozygous fitness values. Consequently, we can conclude from the above observation that each pair of curves of following forms will produce a stable polymorphic regions:

$$s_m = \frac{s_m}{(1 - s_m)(1 + h_f) - s_m}, \quad s_m = \frac{s_m}{(1 + s_m)(1 - h_f) + s_m} \quad \text{if } h_f < 0.109;$$

$$s_m = \frac{s_m(1 - h_m)}{(1 - s_m) - s_m(1 - h_m)}, \quad s_m = \frac{s_m(1 + h_m)}{(1 + s_m) + s_m(1 + h_m)} \quad \text{if } h_m < 0.109;$$

and

$$s_m = \frac{s_m}{1 - 2s_m}, \quad s_m = \frac{s_m}{1 + 2s_m}.$$

It is, therefore, clear that area of the region of a single stable polymorphic equilibrium will be increased with decrease of the degree of dominance, and in the case of more than a single internal equilibrium, region characterized by a single unstable equilibrium, increases as the degree of dominance increases.

segregation distortion: To examine the nature of an equilibrium point under opposing selection with arbitrary dominance in this arena we consider the following fitness values in males and females:

genotype	A_1A_1	A_1A_2	A_2A_2
fitness, males	$1 + s$	$1 - h_ms$	$1 - s$
fitness, females	$1 - s$	$1 - h_fs$	$1 + s$

Similar to previous section, the Fig.4 is plotted on the bases of comparing heterozygous fitness values in males and females, where two cases are examined of which one is $k_m \geq k_f$ and other is $k_f \geq k_m$. All the obtained results are summarized in the Table 2. Here, one of the significant observations is that we can get only a single stable internal equilibrium point when the difference of male and female segregation distortion is equal to 4. This clearly suggests the lack of multiple equilibrium with equal segregation distortions in the two sexes which is a quite well-known result.

Now we have, following the similar steps of the previous section, that the trivial equilibria (0,0) and (1,1) are respectively unstable when

$$\left(k_m \frac{w_{12}}{w_{22}} + k_f \frac{v_{12}}{v_{22}}\right) > 1,$$

$$\left(k_m \frac{w_{12}}{w_{11}} + k_f \frac{v_{12}}{v_{11}}\right) > 1,$$

i.e. the region characterized by a single stable internal equilibria is bounded by

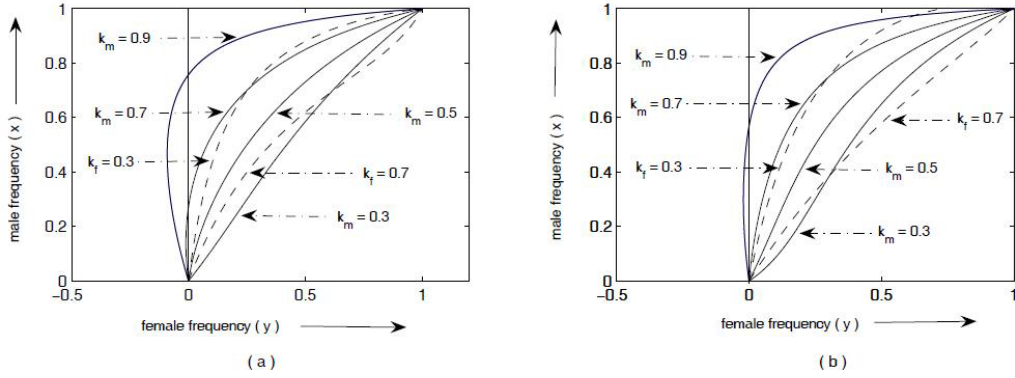


Fig. 4. Graphs of equations (7a) and (7b). Dashed lines are the graphs of equation (7a), where intersecting point of two curves represents an equilibrium point. (a) Case of male heterozygote's fitness is relatively favourable than female heterozygote's fitness for $h_f = 0.7$, $h_m = 0.3$, $s = 0.5$. Internal equilibrium point is stable. (b) Case of female heterozygote's fitness is relatively favourable than male heterozygote's fitness for $h_f = 0.3$, $h_m = 0.7$, $s = 0.5$. Internal equilibrium point is stable.

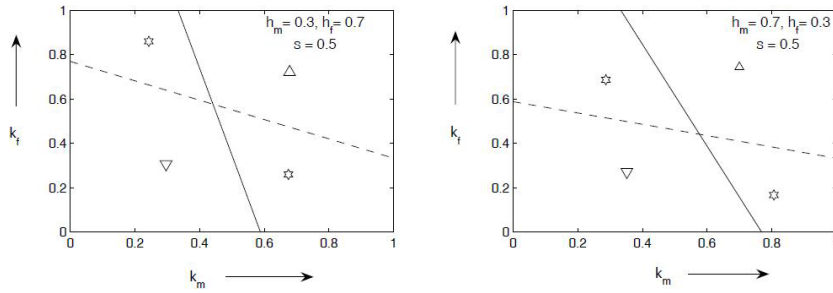


Fig. 5. Regions of equilibria in the (k_m, k_f) space, where dashed lines, solid lines and other symbols represent the same interpretations as in Fig.3.

$$k_f > \frac{(1+s)((1-s) - k_m(1-h_m s))}{(1-s)(1-h_f s)}, \quad (13a)$$

$$k_f > \frac{(1-s)((1+s) - k_m(1-h_m s))}{(1+s)(1-h_f s)}. \quad (13b)$$

Fig.5 shows the boundaries of regions of equilibria as a function of k_m in the (k_m, k_f) space for fixed values of h_m, h_f and s , where heterozygote values have been compared. Regions clearly demonstrate that above the value of Mendelian segregation, prone of arising a single stable polymorphic equilibrium increases. It is important to note here that if we interchange the values of h_m and h_f between themselves, areas of covered regions remain unchanged.

2.3. overdominance in females and directional selection in males.

Mendelian segregation : In this section, we assume the following viabilities:

genotype	$A_1 A_1$	$A_1 A_2$	$A_2 A_2$
fitness, males	$1 + s_m$	$1 - h_m s_m$	$1 - s_m$
fitness, females	$1 - s_f$	$1 + h_{2f} s_f$	$1 + h_{3f} s_f$

Table 2. Obtained results of segregation distortion (opposing selection with arbitrary dominance)

characteristic	Nature of trivial equilibrium(0, 0)	Nature of trivial equilibrium(1, 1)	Nature of polymorphic equilibrium (or equilibria)
male A_1A_2 favorable than female A_1A_2 ($k_m \geq k_f$)	stable equilibrium unstable equilibrium	stable equilibrium stable equilibrium	— —
male A_1A_2 favorable than female A_1A_2 ($k_f \geq k_m$)	stable equilibrium stable equilibrium	stable equilibrium stable equilibrium	one stable equilibrium —
female A_1A_2 favorable than male A_1A_2 ($k_m \geq k_f$)	stable equilibrium unstable equilibrium	— —	— one stable equilibrium
female A_1A_2 favorable than male A_1A_2 ($k_f \geq k_m$)	stable equilibrium unstable equilibrium	stable equilibrium stable equilibrium	stable equilibrium —

Table explains the equilibrium nature in row wise where at the point — we can not take/make any conclusion.

where $h_{2f} > h_{3f}$.

Clearly the equilibrium with A_1 absent will be unstable when $\frac{1-h_m s_m}{1-s_m} + \frac{1+h_{2f} s_f}{1+h_{3f} s_f} > 2$. Since $h_{2f} > h_{3f}$, each term on the left hand side is greater than 1, and consequently the expression is always true. On the other hand, the trivial equilibrium (1,1) will be unstable when $\frac{1-h_m s_m}{1+s_m} + \frac{1+h_{2f} s_f}{1-s_f} > 2$. Since we can consider the following inequality as

$$\frac{1 + h_{2f} s_f}{1 - s_f} - \frac{1 - h_m s_m}{1 + s_m} > \epsilon,$$

thus we have $2 \frac{(1+h_{2f} s_f)}{1-s_f} > 2 + \epsilon$, which implies that values of ϵ may be less than 1. Hence, we can conclude that the polymorphism will be maintained when the differential of female heterozygote satisfies the condition $h_{2f} s_f > \frac{\epsilon}{2}$.

segregation distortion: We omit this analysis since no framework of fitnesses of males and females here cannot reveal any additional significant observation.

3. CONCLUDING REMARKS

In the foregoing analysis, we have redefined the concept of fitness differentials among the genotypes and the concept has been applied in discussing the model of opposing selection in the two sexes with Mendelian segregation as well as with segregation distortion. In the earlier investigation of opposing selection between the sexes, Kidwell et al. [5] assumed that homozygotes of favourable gene remain unchanged throughout the life cycle, which is not justified in respect of biological implications as well as mathematical background. The present model clearly demonstrates that the degree of dominance over the sexes is a function of equilibrium region, although we cannot use the term average degree of dominance since we have obtained $h_m + h_f = 0.109$ instead of $h_m + h_f = 1$. Here, we find only one stable internal equilibrium point in segregation distortion while at most two stable equilibria have been found in Mendelian segregation, although in case of segregation distortion possibility of arising a single stable internal equilibrium is much higher than in Mendelian segregation. Farther comparison reveals that trivial equilibrium (1,1) does not exhibit unstable state in segregation distortion. Even though the model is not immediately clarify whether the wider conditions of Prout [15] – the instabilities of

both trivial equilibria are sufficient and necessary conditions to have precisely one stable polymorphic equilibrium or three polymorphic equilibria (two of them stable and the other unstable) – are also satisfied, the considered model without genomic imprinting concept partly generalize the result obtained by Úbeda and Haig [3] in the sex-specific viability sense. We do believe that our redefined concept might be helpful for better understanding the biological significance of various genetic phenomena and to consider the genomic imprinting effect and the fertility effect [16] on this model would be a challenging work.

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