On the Extremum Principle of Natural Selection with Inbreeding[1]

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SUMMARY

The extremum principle in the genetical theory of natural selection has been discussed when the population undergoes inbreeding at a constant value of the inbreeding coefficient with constant fitness of the three genotypes possible with two alleles at a given locus. The Fundamental Theorem of Natural Selection in such a case loses its predictive value in that the mean fitness of the population may decrease. This however can be restored by defining a new fitness function appropriately. It is shown that both the maximum as well as the minimum principles for such a mean fitness hold good in exactly the same manner as for true mean fitness in random mating populations incorporating dominance effects of genes. With no dominance, however, there is no need to invoke new mean fitness function and the optimality principle holds for an arbitrary mating system.

Key words : Natural selection, Evolution, Mean fitness of population, Optimisation, Extremum principle with inbreeding.

1. Introduction

In a recent communication (Narain [3]), an extremum principle of natural selection was enunciated when the exact increase in mean fitness so as to include the dominance effects of the genes in considered. However, the treatment was restricted to random mating system only. In this paper, the issue is taken up when the population is undergoing inbreeding with a constant value of the inbreeding coefficient which may be positive or negative and when there are two alleles at a given locus.

2. Increase in Mean Fitness

With two alleles A_1 and A_2 with respective frequencies p_1 and $p_2 = (1 - p_1)$ in an inbred population with inbreeding coefficient F, the genotypic

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1   This paper is dedicated to the memory of Professor Motoo Kimura who is best known as the founder and principle architect of the neutral theory of molecular evolution based on the mathematical theory of population genetics, which he had been developing using diffusion equation method since 1955. In his sad demise on November 13, 1994, the world lost one of the pioneers of the science of statistical genetics.

frequencies P_{11}, P_{12} and P_{22} of $A_1 A_1$, $A_1 A_2$ and $A_2 A_2$ respectively would be

$$\left.\begin{array}{l} P_{11} = p_1^2 (1 - F) + Fp_1 \\ P_{12} = 2 (1 - F) p_1 p_2 \\ P_{22} = p_2^2 (1 - F) + Fp_2 \end{array}\right] \tag{1}$$

Let the relative fitnesses of these genotypes be respectively, W_{11}, W_{12} and W_{22} with $W_{21} = W_{12}$. The mean fitness of such a population, denoted by $\overline{W}_F$, is

$$\overline{W}_F = p_1 W_{11} + p_2 W_{22} + 2 (1 - F) p_1 p_2 d_{12}$$
$$= \overline{W}_R - 2F p_1 p_2 d_{12} \tag{2}$$

where $\overline{W}_R$ is the mean fitness with $F = 0$ i.e., when the population is in Hardy-Weinberg equilibrium and

$$d_{12} = [W_{12} - (W_{11} + W_{22}) / 2] \tag{3}$$

expresses the degree of dominance on the arithmetic scale. The marginal fitness of alleles in the inbred population, denoted by w_{1F} and w_{2F} for A_1 and A_2 respectively are given by

$$\left.\begin{array}{l} w_{1F} = w_{1R} + p_2 F (W_{11} - W_{12}) \\ w_{2F} = w_{2R} + p_1 F (W_{22} - W_{12}) \end{array}\right] \tag{4}$$

where w_{1R} and w_{2R} are the respective marginal fitnesses with $F = 0$. $\overline{W}_F$ can alternately be expressed as

$$\overline{W}_F = p_1 w_{1F} + p_2 w_{2F} \tag{5}$$

which leads to (2). In an entirely inbred population, $F = 1$ and if $\overline{W}_I$ denotes the mean fitness of such a population consisting of homozygous genotypes $A_1 A_1$ and $A_2 A_2$ only, we have

$$\overline{W}_I = p_1 W_{11} + p_2 W_{22} \tag{6}$$

which follows from (2) also,

The three mean fitnesses $\overline{W}_F$, $\overline{W}_R$ and $\overline{W}_I$ are related as

$$\overline{W}_F = (1 - F) \overline{W}_R + F \overline{W}_I \tag{7}$$

It may be noted that

$$\overline{W}_F = \overline{W}_I + 2(1-F)p_1 p_2 d_{12} \tag{8}$$

and

$$\overline{W}_R = \overline{W}_I + 2p_1 p_2 d_{12} \tag{9}$$

so that if $d_{12} = 0$. all the three mean fitnesses are equivalent even if F is neither 1 nor 0.

The total genetic variance in fitness ($\sigma^2_{w_F}$) for such a population is given by

$$\sigma^2_{w_F} = P_{11}(W_{11} - \overline{W}_F)^2 + P_{12}(W_{12} - \overline{W}_F)^2 + P_{22}(W_{22} - \overline{W}_F)^2$$

$$= (P_{11} W^2_{11} + P_{12} W^2_{12} + P_{22} W^2_{22}) - (\overline{W}_F)^2 \tag{10}$$

The variation in the marginal fitnesses of the alleles (σ^2_w), would be

$$\sigma^2_w = p_1(w_{1F} - \overline{W}_F)^2 + p_2(w_{2F} - \overline{W}_F)^2$$

$$= (p_1 w^2_{1F} + p_2 w^2_{2F}) - (\overline{W}_F)^2 \tag{11}$$

The change in gene frequency of A_1 after selection and inbreeding is given by

$$(\Delta p_1)_F = p_1(w_{1F} - \overline{W}_F)/\overline{W}_F \tag{12}$$

This relation can be expressed in several ways. One way is

$$(\Delta p_1)_F = [(\Delta p_1)_R/(1 - 2Fp_1 p_2 d_{12}/\overline{W}_R)]$$

$$+ F p_1 p_2 (W_{11} - W_{12} + 2p_1 d_{12})/\overline{W}_F \tag{12a}$$

where

$$(\Delta p_1)_R = p_1(w_{1R} - \overline{W}_R)/\overline{W}_R \tag{13}$$

The other way is to introduce the differential

$$\partial \overline{W}_F/\partial p_1 = (W_{11} - W_{22}) + 2(1-F)(1-2p_1)d_{12}$$

$$= 2(w_{1R} - w_{2R}) - 2F(1-2p_1)d_{12} \tag{14}$$

Then

$$(\Delta p_1)_F = (p_1 p_2 / \overline{W}_F) \ [\ (1-F)(w_{1R} - w_{2R}) + F(W_{11} - W_{22})]$$

$$= (p_1 p_2 / \overline{W}_F) \ [\ (1+F)/2 \ (\partial \overline{W}_F / \partial p_1) - F(1-F)(1-2p_1) d_{12} \ ]$$

$$= p_1 p_2 \, a / \overline{W}_F \hspace{4cm} (12b)$$

where

$$a = (w_{1F} - w_{2F})$$

$$= [(1+F)/2] (\partial \overline{W}_F / \partial p_1) - F(1-F)(1-2p_1) d_{12} \hspace{1.5cm} (15)$$

When $F = 0$, we get

$$(\Delta p_1)_R = (p_1 p_2 / 2 \overline{W}_R) \ (d\overline{W}_R / dp_1)$$

the famous expression given by Wright [6].

When $F = 1$, we get

$$(\Delta p_1)_1 = (p_1 p_2 / \overline{W}_1) \ (d\overline{W}_1 / dp_1)$$

an expression given in Turner [5].

The change in the mean fitness after one round of inbreeding can be determined by expressing the mean fitness, which is a function of p_1 and F, around its previous value by Taylor's expansion as

$$\overline{W}_F = \overline{W}_{F0} + (\partial \overline{W}_F / \partial p_1)(\Delta p_1)_F + (\partial^2 \overline{W}_F / \partial p_1^2)(\Delta p_1)_F^2 / 2!$$

$$+ (\partial \overline{W}_F / \partial F)(\Delta F) + (\partial^2 \overline{W}_F / \partial p_1 \partial F) \ 2 (\Delta p_1)_F (\Delta F) / 2!$$

$$+ (\partial^3 \overline{W}_F / \partial p_1^2 \partial F) \ 3 \ (\Delta p_1)_F^2 (\Delta F) / 3! \hspace{2cm} (16)$$

where

$$(\partial \overline{W}_F / \partial p_1) = (W_{11} - W_{22}) + 2(1-F)(1-2p_1) d_{12}$$

$$(\partial^2 \overline{W}_F / \partial p_1^2) = -4(1-F) d_{12}$$

$$(\partial \overline{W}_F / \partial F) = -2 p_1 p_2 d_{12} \hspace{3cm} (17)$$

$$(\partial^2 \overline{W}_F / \partial p_1 \partial F) = -2(1-2p_1) d_{12}$$

$$(\partial^3 \overline{W}_F / \partial p_1^2 \partial F) = 4 d_{12}$$

This leads to

$$\Delta \overline{W}_F = \alpha (\Delta p_1) + \beta (\Delta p_1)^2 + \gamma (\Delta F) + \delta (\Delta p_1)(\Delta F) + \varepsilon (\Delta p_1)^2 \Delta F \qquad (18)$$

where

$$\alpha = (W_{11} - W_{22}) + 2(1 - F)(1 - 2p_1) d_{12}$$

$$= \partial \overline{W}_F / \partial p_1 \text{ in view of (14)}$$

$$\beta = -2(1 - F) d_{12} \qquad (19)$$

$$\gamma = -2 p_1 p_2 d_{12}$$

$$\delta = -2(1 - 2p_1) d_{12}$$

$$\varepsilon = 2 d_{12}$$

and ΔF is the change (not increment) in inbreeding. With constant value of F, however, ΔF terms drop out and we get

$$\Delta \overline{W}_F = \alpha (\Delta p_1) + \beta (\Delta p_1)^2 \qquad (20)$$

Using (12b), (18), and (19)

$$\Delta \overline{W}_F = (\partial \overline{W}_F / \partial p_1)(p_1 p_2 a / \overline{W}_F) - 2(1 - F) d_{12} (p_1 p_2 a / \overline{W}_F)^2 \qquad (21)$$

Since from (15), one can express

$$\partial \overline{W}_F / \partial p_1 = 2 [a + F(1 - F)(1 - 2p_1) d_{12}] / (1 + F)$$

We have

$$\Delta \overline{W}_F = (2p_1 p_2 a^2 / \overline{W}_F) [1/(1 + F) - (1 - F) d_{12} p_1 p_2 / \overline{W}_F]$$

$$+ 2F(1 - F) p_1 p_2 (1 - 2p_1) a d_{12} / (1 + F) \overline{W}_F$$

$$= (2\sigma_{HF}^2 / \overline{W}_F) [\{ \overline{W}_F - (1 - F) d_{12} p_1 p_2 \} / \overline{W}_F - F / (1 + F)]$$

$$+ 2F(1 - F) p_1 p_2 (1 - 2p_1) a d_{12} - (1 + F) \overline{W}_F$$

$$= (\sigma_{HF}^2 / \overline{W}_F) [\{ 2 \overline{W}_F - (\overline{W}_F - \overline{W}_I) \} / \overline{W}_F - 2F / (1 + F)]$$

$$+ 2F(1 - F) p_1 p_2 (1 - 2p_1) a d_{12} / (1 + F) \overline{W}_F , \text{ using (8)}$$

$$= (\sigma_{HF}^2 / \overline{W}_F) [(\overline{W}_F + \overline{W}_I) / \overline{W}_F] - 2 F\sigma_{HF}^2 / (1 + F) \overline{W}_F$$

$$+ 2F(1 - F) p_1 p_2 (1 - 2p_1) a d_{12} / (1 + F) \overline{W}_F \qquad (22)$$

where

$$\sigma_{HF}^2 = p_1 p_2 a^2 \tag{23}$$

is the haploid genetic variance or the variance of the excess of gene substitution in an inbred population. Since, from (14), (15) and (19),

$$W_{11} - W_{22} = [2a - 2(1 - F)(1 - 2p_1) d_{12}] / (1 + F)$$

$$w_{1F} - w_{2F} = a$$

the expression in the third term on the right-hand side of (22) viz.

$$2 p_1 p_2 (1 - F)(1 - 2p_1) a d_{12}$$

becomes

$$p_1 p_2 a [2a - (1 + F)(W_{11} - W_{22})]$$

$$= 2\sigma_{HF}^2 - (1 + F) p_1 p_2 (w_{1F} - w_{2F})(W_{11} - W_{22})$$

This makes (22) as

$$\Delta \overline{W}_F = (\sigma_{HF}^2 / \overline{W}_F)(\overline{W}_F + \overline{W}_I) / \overline{W}_F - 2F \sigma_{HF}^2 / (1 + F) \overline{W}_F$$

$$+ F [2\sigma_{HF}^2 - (1 + F) p_1 p_2 (w_{1F} - w_{2F})(W_{11} - W_{22})] / (1 + F) \overline{W}_F$$

$$= (\sigma_{HF}^2 / \overline{W}_F)(\overline{W}_F + \overline{W}_I) / \overline{W}_F$$

$$- (F / \overline{W}_F) [p_1 p_2 (w_{1F} - w_{2F})(W_{11} - W_{22})] \tag{22a}$$

Turner [5] defines covariance between genic and genotypic fitnesses as

$$COV (w_H, W_G) = p_1 p_2 (w_{1F} - w_{2F})(W_{11} - W_{22}) \tag{24}$$

This gives

$$\Delta \overline{W}_F = (\sigma_{HF}^2 / \overline{W}_F) [(\overline{W}_F + \overline{W}_I) / \overline{W}_F] - F \ COV (w_H, W_G) / \overline{W}_F \tag{25}$$

which is the same as expression (72) of Turner's paper with $\Delta F = 0$. However, one can also express the covariance term as

$$COV (\dot{w}_H, W_G) = [2 / (1 + F)] \ [\sigma_{HF}^2 - (1-F) p_1 p_2 (1 - 2p_1) a d_{12}] \tag{26}$$

With no dominance, therefore, the covariance term becomes twice the haploid variance divided by (1+F) and we get

$$\Delta \overline{W}_F = 2\,\sigma_{HF}^2 \,/\, (1+F)\,\overline{W}_F$$

$$\doteq \sigma_{AF}^2 \,/\, \overline{W}_F \tag{27}$$

where

$$\sigma_{AF}^2 = 2\sigma_{HF}^2 /(1+F) \tag{28}$$

is the additive genetic variance in an inbred population. On the other hand, with no inbreeding.

$$\Delta \overline{W}_R = (2\sigma_{HR}^2 / \overline{W}_R)\,(1 - p_1\,p_2\,d_{12}/\overline{W}_R)$$

$$= (\sigma_{AR}^2 / \overline{W}_R)\,(1 - p_1\,p_2\,d_{12}/\overline{W}_R) \tag{29}$$

as is already known (Narain [3]). Interestingly, for completely inbred population the dominance terms in the covariance expression drops out, $\overline{W}_F = \overline{W}_I$ and

$$\Delta \overline{W}_I = \sigma_A^2 / \overline{W}_I \,. \tag{30}$$

It is apparent from the above that it is the presence of dominance which is crucial for the change in mean fitness in inbred populations to follow a different pattern than the well known one based on additive genetic variance - a situation similar to the one obtained in Narain [3] for random mating populations.

3. Increase in Newly Defined Mean Fitness

The expressions for the change in mean fitness $\overline{W}_F$ given by (22) and (25) are not necessarily positive indicating that the average fitness may decrease (Turner ([4], [5])). Since, with no change in inbreeding,

$$\Delta \overline{W}_I = Cov\,(w_H,\,W_G)/\overline{W}_F, \tag{31}$$

the change in the function $(\overline{W}_F + F\,\overline{W}_I)$ given by

$$\Delta\,(\overline{W}_F + F\,\overline{W}_I) = (\,\sigma_{HF}^2 / \overline{W}_F)\,[\,(\overline{W}_F + \overline{W}_I)/\,\overline{W}_F\,] \tag{32}$$

is necessarily positive so that $(\overline{W}_F + F\,\overline{W}_I)$ increases to a maximum with a stable equilibrium. However, if dominance (d_{12}) is zero, from (8) and (9)

$$\overline{W}_F = \overline{W}_R = \overline{W}_I \tag{33}$$

and the function $\overline{W}_F + F\overline{W}_I$ becomes

$$\overline{W}_F + F\overline{W}_I = (1 + F)\overline{W}_F \tag{34}$$

We have, as a consequence, $\Delta\overline{W}_F$ given by (27) as necessarily positive. In such a case, $\overline{W}_F$ increases to a maximum with a stable equilibrium. The situation becomes similar to the situation discussed in Narain [3] for the case of no dominance. No new principle is involved and the optimisation leads to similar maximum and minimum principles.

The expression $(\overline{W}_F + F\overline{W}_I)$ was used by Wright [6] to give a fitness function which maximises. Here, however, the new mean fitness $\overline{W}_F^*$ is defined as

$$\overline{W}_F^* = (\overline{W}_F + F\overline{W}_I)/(1 + F)$$
$$= [(1 - F)/(1 + F)]\overline{W}_F + [2F/(1 + F)]\overline{W}_I \tag{35}$$

which always increases and has a stable equilibrium. Comparing (7) and (35) we find that the difference in $\overline{W}_F$ and $\overline{W}_F^*$ lies in different weights attached to the random mating component $\overline{W}_R$ and the inbred component $\overline{W}_I$ of the mean fitness of the population. Both sets of weights have, however, the same values when either F=0 or 1. By (14), we find that

$$\partial\overline{W}_F^*/\partial p_1 = (W_{11} - W_{22}) + 2(1 - F)(1 - 2p_1)d_{12}/(1 + F)$$
$$= 2(w_{1R} - w_{2R}) - 4F(1 - 2p_1)d_{12}/(1 + F) \tag{36}$$

Following similar derivations as in the case of $\Delta\overline{W}_F$, we get for $\Delta\overline{W}_F^*$ with a constant value of F

$$\Delta\overline{W}_F^* = \alpha^*(\Delta p_1) + \beta^*(\Delta p_1)^2 \tag{37}$$

where

$$\left.\begin{aligned}\alpha^* &= (W_{11} - W_{22}) + 2(1 - F)(1 - 2p_1)d_{12}/(1 + F)\\ &= \partial\overline{W}_F^*/\partial p_1 \text{ in view of (36)}\\ \beta^* &= -2(1 - F)d_{12}/(1 + F)\end{aligned}\right\} \tag{38}$$

Using (14), (15), (37) and (38), we get

$$\Delta\overline{W}_F^* = [2\sigma_{HF}^2/(1 + F)\overline{W}_F][\{\overline{W}_F - p_1 p_2(1 - F)d_{12}\}/\overline{W}_F]$$
$$= (\sigma_{AF}^2/\overline{W}_F)[1 - p_1 p_2(1 - F)d_{12}/\overline{W}_F] \tag{39}$$

This expression is similar to expressing (12) of Narain [3] with an extra $(1 - F)$ multiplier term in the paranthesis. It therefore becomes identical to it when $F = 0$. Also, since

$$2 (1 - F) p_1 p_2 d_{12} / \overline{W}_F = 1 - \overline{W}_I / \overline{W}_F$$

we get

$$\Delta \overline{W}_F^* = (\sigma_{AF}^2 / 2 \overline{W}_F) [(\overline{W}_F + \overline{W}_I) / \overline{W}_F] \tag{40}$$

indicating that in inbred populations the newly defined fitness $\overline{W}_F^*$ can have a maximum at a stable equilibrium.

4. Optimisation of the New Mean Fitness

The expression for the $\Delta \overline{W}_F^*$ given by (39) can be used for optimisation purposes.

The divergence in the gene frequency of the two alleles between parent and offspring generations can be expressed in terms of a genetic distance squared as

$$D^2 = [(\Delta p_1)^2 / p_1 (1 + F)] + [(\Delta p_2)^2 / p_2 (1 + F)]$$

$$= (\Delta p_1)^2 / C \tag{41}$$

where

$$C = p_1 p_2 (1 + F) \tag{42}$$

4.1 Maximum principle

First maximise (37) for variations in (Δp_1) at a constant value of F subject to the constraint that D^2 given by (41) is some fixed quantity, say λ.

Using the Lagrangian

$$\alpha^* (\Delta p_1) + \beta^* (\Delta p_1)^2 - \mu [(\Delta p_1)^2 / C - \lambda]$$

differentiating it with respect to Δp_1 and equating to zero gives

$$\Delta p_1 = \alpha^* / [2 (\mu / C - \beta^*)] \tag{43}$$

Substituting from equation (43) in equation (41) for (Δp_1) gives

$$\lambda = \alpha^{*^2} / [4 (\mu / C - \beta^*)^2 C] \tag{44}$$

which gives

$$\mu = [\beta^* C + (\alpha^* / 2) (C / \lambda)^{1/2}] \tag{45}$$

This leads finally to

$$(\Delta p_1) = (\lambda\, C)^{1/2} \tag{46}$$

This result is independent of β^* or d_{12}. But β^* given by (38) is zero either when $F=1$ or when $d_{12} = 0$. Hence irrespective of the presence or absence of dominance, the optimisation gives the same results. If the equation (46) is to give the same $(\Delta\, p_1)$ as that given by equation (12b), we must have

$$\lambda = \sigma_{HF}^2 / (1 + F) (\overline{W}_F)^2 = \sigma_{AF}^2 / 2 (\overline{W}_F)^2 \tag{47}$$

The *maximum principle* in the genetical theory of natural selection in inbred populations can therefore be stated as :

> *Of all the per-generation gene frequency changes, including those that lead to the same genetic distance, [$\sigma_{AF}^2 / 2 (\overline{W}_F)^2$] between parent and daughter generation gene frequency values as the natural selection gene frequency changes in inbred populations, the natural selection values maximize the change in the newly defined mean fitness of the population ($\Delta\, W_F^*$), irrespective of the presence or absence of dominance in fitness values.*

4.2 *Minimum principle*

We next minimize (41) for variation in (Δp_1) subject to the constraint that $\Delta\, W_F^*$ given by (37) is some fixed quantity, say λ^*. Using the Lagrangian

$$Q = (\Delta\, p_1)^2 / C - \mu^* [\, \alpha^* (\Delta\, p_1) + \beta^* (\Delta\, p_1)^2 - \lambda^* \,], \tag{48}$$

differentiating it with respect to $(\Delta\, p_1)$ and equating to zero, we get

$$(\Delta\, p_1)^* = \mu^* \, \alpha^* C / [\, 2 (1 - \beta^* C \mu^*) \,] \tag{49}$$

Substituting from equation (49) in equation (37) for $(\Delta\, p_1)^*$ gives a quadratic equation in μ^*

$$\beta C^2 (\, \alpha^{*^2} + 4 \lambda^* \beta^*) \mu^{*^2} - 2C (\, \alpha^{*^2} + 4 \lambda^* \beta^*) \mu^* + 4 \lambda^* = 0$$

which gives

$$\mu^* = [\, 1 - \alpha^* / (\, \alpha^{*^2} + 4 \lambda^* \beta^*)^{1/2}] (\beta^* C)^{-1} \tag{50}$$

This leads to

$$(\Delta p_1)^* = (\alpha^* / 2\beta^*) [\, \{ 1 + 4\lambda^* \, \beta^* / \alpha^{*^2} \}^{1/2} - 1] \tag{51}$$

The result depends on whether β^* is zero or not. In other words, when $F=1$, the result depends on whether dominance is present or not. For $\beta^* = 0$, and if (51) is to give the same (Δp_1) as given by (12b), we must have

$$\lambda^* = [\, 2\sigma_{HF}^2 \,/\, (1+F)\, \overline{W}_F \,]\, [\, 1 - p_1\, p_2\, d_{12}\, (1-F)\, /\, \overline{W}_F \,]$$

$$= (\sigma_{AF}^2 \,/\, \overline{W}_F)\, [\, 1 - p_1\, p_2\, d_{12}\, (1-F)\, /\, \overline{W}_F \,] \tag{52}$$

But if $\beta^* = 0$, or dominance is absent then the minimization of (41) subject to (37) gives λ^* as

$$\lambda^* = 2\sigma_{HF}^2 \,/\, (1+F)\, \overline{W}_F$$

$$= \sigma_{AF}^2 \,/\, \overline{W}_F \tag{53}$$

In fact, the most general relation between λ and λ^* is obtained by equating the two (Δp_1)s given by (46) and (51). This is

$$\lambda^* = (\beta^*\, C)\, \lambda + [\alpha^*\, (C)^{1/2}\,]\, (\lambda)^{1/2} \tag{54}$$

Apparently, the choice of λ given by equation (47) coupled with whether β^* is zero or not i.e., whether dominance is absent or not determines λ^* as ($\sigma_{AF}^2 \,/\, \overline{W}_F$) or that given by equation (52) respectively.

The *minimum principle* in the genetical theory of natural selection in inbred populations can, therefore, be stated as :

> *Of all the per-generation gene frequency changes, including those that lead to the same change in the newly defined mean fitness of the population ($\Delta\, \overline{W}_F^*$) as the natural selection gene frequency changes, the natural selection values minimise the genetic distance between parent and daughter generation gene frequency values.*

5. Discussion

The results on the extremum principle in the genetical theory of natural selection obtained in Narain [3] for random mating populations have been extended in this paper to inbred populations. However, there is one major difference. In random mating populations, the natural selection gene frequency changes which lead to the same genetic distance between parent and daughter generations maximise the mean fitness of the population irrespective of the presence or absence of dominance in fitness values. In inbred populations, on the other hand, the mean fitness of the populations may decrease due to the covariance between the genic and genotypic fitnesses and therefore the Fundamental Theorem of Natural Selection loses its predictive value. This can, however, be restored if we define a new mean fitness function wherein the

weightages attached to the random and inbred components are respectively $(1 - F) / (1 + F)$ and $2F / (1 + F)$. For such a mean fitness, the maximum principle is found to be the same as in the random mating case holding true irrespective of the presence or absence of dominance. Not only the maximum principle but also the minimum principle holds good in that the natural selection gene frequency changes which lead to the same increase in new mean fitness of the population, minimise the genetic distance between parent and daughter generation gene frequency values. In this case, however, the results depend on the presence or absence of the dominance effects.

In the context of the optimality principle of Ewens [1], it is interesting to note that the results for the inbred populations for the mean fitness $\overline{W}_F$ hold good in exactly the same manner as for the random mating population if the dominance effects are absent. There is no necessity then to invoke new fitness function $\overline{W}_F^*$. The partial increase in the mean fitness then coincides with the increase in $\overline{W}_F$ and the generality of the optimality theorem of Ewens [1] holds for an arbitrary mating system.

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