THE BASIC THEOREMS OF NATURAL SELECTION : A NAÏVE APPROACH

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1. INTRODUCTION

RECENTLY both Fisher's "fundamental theorem of natural selection" (that the mean fitness of a population tends always to increase, subject to the restraints of overpopulation and change of environment) (Fisher, 1930) and Wright's "adaptive topography" (a graph of mean fitness in which the tendency for mean fitness to maximise is used to predict equilibria and so on) (see for example Lewontin and White, 1958; Li, 1955*a*) have been much criticised. The fundamental theorem is true only with random mating and with constant selection which is the same in both sexes, and is even then only an approximation if there is dominance (Li, 1967*a*, *c*; Turner, 1967*b*). It is in general untrue if there is more than one locus (Moran, 1964; Turner, 1967*b*). The adaptive topography is more robust, as a more complex version may be used for pairs of loci with epistasis (Turner, 1967*a*) and one can devise parameters, more elaborate than mean fitness, which will maximise under many systems of selection and mating (see for example, Wright, 1955; Li, 1955*a*, 1967*b*). However, their complexity and lack of physical meaning makes these parameters inelegant; one feels that there must be a basic theorem embracing them all. This paper attempts such a theorem. The parameter used is comparatively simple, and the theorem must be known already in some form to almost every population geneticist; but so far it has been little used, except in relation to heritability in quantitative genetics (Falconer, 1961).

First the theorem will be expounded for selection, the same in both sexes, on single autosomal loci, in diploids. Then some special cases will be derived, and finally the theorem will be extended to some less restricted cases.

2. THE THEOREM

If q_i is the frequency of the i th allele, f_{ij} the frequency of the genotype formed by the combination of the i th and j th alleles, and W_{ij} the "fitness" (probability of survival) of that genotype, then

$$W_i = (\sum_j f_{ij} W_{ij}) / q_i \quad (1)$$

is the mean fitness of the allele,

$$\bar{W} = \sum_i q_i W_i = \sum_{ij} f_{ij} W_{ij} \quad (2)$$

is the mean fitness of the population, and

$$V_H = \sum_i q_i (W_i - \bar{W})^2 \quad (3)$$

may be called the haploid variance in fitness. The W_{ij} may be frequency-dependent and W_i and $\bar{W}$ may contain the inbreeding coefficient; some systems of assortative mating might also be included.

The condition for equilibrium is that

$$V_H = 0 \quad (4)$$

That this gives equilibrium is easily seen when we remember that (Wright 1949)

$$\Delta q_i = q_i(W_i - \bar{W})/\bar{W} \quad (5)$$

or that (4) implies $W_i = \bar{W}$ and hence

$$W_i = W_j \quad (6)$$

for all i, j . Under random mating V_H is half the additive genetic variance determined from breeding values, and this special case of (4) is widely known.

A general adaptive topography with equilibria at its zero points can thus be drawn by plotting V_H against allele frequencies. Like the $\bar{W}$ topography

FIG. 1.—Haploid variance (thick line), dominance and variance (thin line) for two alleles, against gene frequency. Fitnesses are $W_{00} = 1$, $W_{01} = 4$, $W_{11} = 3$. The equilibria (E) are at the zero points of the haploid variance, and the central one is stable, the arrow indicating the direction of change in the population at gene frequency $\frac{1}{2}$.

it is most easily formed by an electronic computer. Like the $\bar{W}$ topography the graph is extremely difficult to draw when there are more than four alleles; with four alleles one can plot V_H (or $\bar{W}$) inside a topologically distorted tetrahedron (Turner, 1967a). Fig. 1 shows the simplest case, two alleles with random mating.

In the $\bar{W}$ topography stable equilibria are at maxima, unstable at minima; the V_H topography says nothing about stability, so that in addition to (4) we need the equation for the change in V_H . In general this is a polynomial, but the first (linear) term is sufficient for our needs. This is a special case of equation (A17) in the appendix:

$$\Delta V_H = \{MO(W)^3\}/\bar{W} + 2\Sigma_i q_i^2 (W_i - \bar{W})^2 (\partial W_i / \partial q_i - \partial \bar{W} / \partial q_i) / \bar{W} \quad (7)$$

where

$$\{MO(W)^3\} = \Sigma_i q_i (W_i - \bar{W})^3 \quad (8)$$

is the third moment of fitness about the mean. The nature of the second term is most easily seen by reducing (7) to the equation for two alleles and

constant selection when it becomes

$$\Delta V_H = V_H \{ (q_1 - q_0)(W_0 - W_1) - 4q_0q_1d_w \} / \bar{W} \quad (9)$$

where d_w is the dominance in fitness

$$d_w = W_{01} - \frac{1}{2}(W_{00} + W_{11}), \quad (10)$$

q_0, q_1 are the gene frequencies, and the meaning of the other subscripts is obvious. Equations similar to (7) and (9) are given by Kimura (1958) and Nei (1963).

Thus to determine the stability of the equilibria in the variance topography one need only determine the sign of (7) at a limited number of points in the topography; these will imply the direction of movement over the whole topography. For example, in fig. 1, the change of V_H at gene frequencies 0.5, 0.5 has from (9) a sign opposite to that of d_w , so that if dominance is positive V_H decreases and the non-trivial equilibrium (E) is stable. (This, plus the fact that the graph of V_H on q gives a non-trivial minimum only if the fitness of the heterozygote lies outside the range of the homozygotes, gives the well-known condition that heterozygotes must be fittest.) For multiple alleles with inbreeding the term within the last bracket of (7) is

$$(1 - F) \{ \Sigma_j W_{ij} (\partial q_j / \partial q_i) - \Sigma_{ij} W_{ij} [q_i (\partial q_j / \partial q_i) + q_j] \} - F \Sigma_j W_{jj} (\partial q_j / \partial q_i) \quad (11)$$

where $i \geq j$, $ij \neq ji$, and the derivatives are defined in the appendix. This will serve as an example of the more complex cases; frequency-dependence is similarly expressed in the derivatives.

3. SPECIAL CASES

Any parameter $\mathcal{T}$, such that V_H can be expressed as a function of a simple polynomial, with zero constant term, of $\partial \mathcal{T} / \partial q_i$ for all i , will maximise or minimise at equilibrium, and for a subset of such parameters this will be sufficient. Thus, for example, with two alleles under random mating and constant selection

$$V_H = \frac{1}{4} q_0 q_1 (d\bar{W}/dq_0)^2 \quad (12)$$

whence $\bar{W}$ maximises or minimises. Therefore, an important aspect of the "fundamental theorem" can be derived from the theorem of decreasing variance. Likewise some of the various parameters which maximise under more complex systems turn out to be consequences of the variance theorem.

The simplest and, usually, quickest way of solving explicitly the non-trivial equilibria is also a special case. Equation (6) says that at equilibrium the rate of transmission of any one allele into the next generation must equal the rate of transmission of any other allele. Alternatively, we may say that the rate of removal of the allele, as a fraction of its total frequency, equals the same fraction for any other allele. Formally if δq represents the rate of removal, then

$$(\delta q_i)/q_i = (\delta q_j)/q_j \quad (13)$$

For two alleles, with genotypes A_0A_0 , A_0A_1 , A_1A_1 , with fitnesses $1 - s_0$, 1 , $1 - s_1$ this gives immediately, for equilibrium

$$-s_0 q_0^2 / q_0 = -s_1 q_1^2 / q_1 \quad (14)$$

$$\hat{q}_0 / \hat{q}_1 = s_1 / s_0 \quad (15)$$

which is the well-known solution. Stability is tested by increasing the frequency of the allele on one side of (13); if that side becomes the larger the equilibrium is stable. Thus (14) becomes

$$s_0(\hat{q}_0 + \Delta q)^2 / (\hat{q}_0 + \Delta q) : s_1(\hat{q}_1 - \Delta q)^2 / (\hat{q}_1 - \Delta q) \quad (16)$$

which reduces to

$$s_0 \Delta q : -s_1 \Delta q. \quad (17)$$

The LHS is greater and the equilibrium stable if both s_i are positive.

Crow, who invented this method (Crow, 1958) did not extend it, but it does work very well for more elaborate cases. For example, three alleles, with selection coefficients against A_0A_0 , A_0A_2 being s_{00} , s_{02} and so on (no genotype with unit fitness), the simultaneous equations

$$(\delta q_0)/q_0 = (\delta q_1)/q_1 = (\delta q_2)/q_2 \quad (18)$$

$$q_0 + q_1 + q_2 = 1 \quad (19)$$

solve by determinants to give

$$\mathcal{J}\hat{q}_0 = s_{11}s_{22} + s_{12}(s_{01} + s_{02} - s_{12}) - s_{11}s_{02} - s_{22}s_{01} \quad (20)$$

and so symmetrically for the other alleles, where $\mathcal{J}$ is the sum of the RHS of the three equations. This is the same as the usual determinantal solution (Li, 1955a), though not as elegant as that based on matrix algebra (Li, 1967c). With inbreeding

$$s_0\{(1-F)q_0^2 + Fq_0\}/q_0 = s_1\{(1-F)q_1^2 + Fq_1\}/q_1 \quad (21)$$

yields

$$\hat{q}_0/\hat{q}_1 = (s_1 - s_0F)/(s_0 - s_1F). \quad (22)$$

Equilibrium between a mutation rate μ from A_0 to its recessive allele A_1 (fitness of $A_1A_1 = 1 - s_1$) is approximately

$$-\mu q_0/q_0 = (\mu q_0 - s_1 q_1^2)/q_1$$

or

$$\hat{q}_1^2 = \mu/s_1. \quad (23)$$

With gametic selection (heterozygotes segregating $(1-m)$ A_0 gametes and $m A_1$ gametes) and random union of gametes, (δq) is best treated as survival. Then

$$\{(1-s_0)q_0^2 + 2q_0q_1(1-m)\}/q_0 = \{(1-s_1)q_1^2 + 2q_0q_1m\}/q_1 \quad (24)$$

whence

$$\hat{q}_0/\hat{q}_1 = (s_1 + 1 - 2m)/(s_0 - 1 + 2m). \quad (25)$$

The above solutions, all known from other derivations, show that the (δq) method is usually simpler and more direct than the use of Δq equations or the use of "weights" (U method) (Lewontin, 1958).

4. COMPLEX CASES

If the population has two phases, with a common gene frequency, say males and females, then

$$\Delta q_i = \frac{1}{2} q_i \{W_{iM} - \bar{W}_M\}/\bar{W}_M + (W_{iF} - \bar{W}_F)/\bar{W}_F \quad (26)$$

and equilibrium is given by

$$\frac{1}{2}\Sigma_i q_i \{ (W_{iM} - \bar{W}_M) / \bar{W}_M + (W_{iF} - \bar{W}_F) / \bar{W}_F \}^2 = 0. \quad (27)$$

Similarly, when selection acts alternately on diploids and haploids and when zygosis is by random union of gametes (as in most plants) we have

$$\Delta q_i = q_i (W_{id} - \bar{W}_d) / \bar{W}_d + q_i W_{id} (W_{ih} - \bar{W}_h) / \bar{W}_d \bar{W}_h \quad (28)$$

and equilibrium when

$$\Sigma_i q_i \{ W_{id} - \bar{W}_d + W_{id} (W_{ih} - \bar{W}_h) / \bar{W}_h \}^2 = 0, \quad (29)$$

d and h indicating diploid and haploid.

Two loci with recombination is an example of a case in which the stable genotype distribution is not reached by one round of mating. There are two ways to solve this case: we may determine the equilibria which would occur if there was no recombination (by solving for four alleles at one locus) and examine qualitatively the way recombination moves the equilibria (Turner, 1967*a*, *b*); or we may determine the equilibria exactly from the zero points of

$$\Sigma_i \{ q_i (W_i - \bar{W}) + k(i) R D W_h \}^2$$

where $i = 0, 1, 2, 3$ are the gametes ab , aB , Ab , AB , R is the recombination fraction, W_h is the fitness of double heterozygotes, the gametic excess is

$$D = q_0 q_3 - q_1 q_2$$

and

$$k(i) = -1 \text{ if } i = 0, 3$$

$$k(i) = 1 \text{ if } i = 1, 2.$$

This method uses the variance in fitness of the smallest unit taking part in the mating system—not an allele nor a chromosome, but a length of chromosome partly broken by recombination.

No doubt a similar method could be devised for autopolyploids (see Li, 1967*c*).

Stability is probably best determined by finding the change in variance at selected gene frequencies by means of a simulated round of selection.

5. DISCUSSION

Evolution by natural selection has been described as the “survival of the fittest”; this perhaps accounts for the popularity among population geneticists of maximisation theorems, seeming to be a mathematical expression of this idea (although the only author who has stated this explicitly is Blakley (1967)). But evolution by natural selection is not simply the survival of the fittest. It was well for evolutionists to emphasise the ability of selection to perfect the organism when they were battling with those who, following the vogue set by John Ray (1701), saw such perfection as evidence of Divine Love; this argument settled, we can see from such phenomena as hospitals and genetic loads that organisms are not perfect. (See Cain, 1964 for a most interesting review of the history of this idea.) Genetically speaking the fittest survive only until the end of the generation, when their genotypes are broken down in the mating system. Only an odd property of random mating tricks us into thinking the rule extends across the generations. The survival

of the fittest is not a fundamental fact of evolution by natural selection and it is not surprising that it is difficult to formulate a fundamental theorem corresponding with this idea. The theorem proposed here, that variance minimises, is based on the simple idea that populations go on evolving until all the bits of genetic material which take part in the mating system are being handed on in equal proportions. I submit that it is more profitable to regard *intra*-population evolution in this almost too obvious way than to search for physically meaningful parameters which maximise.

This is not to say that if fitness is defined in a wider sense (utilisation of energy, ability to cope with a fluctuating environment), it will not be possible to formulate a maximisation law. Even within populations we might expect the breeding system to change in such a way as to maximise the more restricted "fitness"; that is, inbreeding should change to outbreeding, outbreeding to apomixis and loose linkage to tight linkage; but as, on the whole, this does not happen we must be cautious.

Nor need we denigrate the usefulness of the various maximising parameters for prediction in individual cases. Even the controversial case of two loci under random mating is very amenable to treatment by the maximisation of $\bar{W}$. In reply to Moran's criticisms of the $\bar{W}$ topography in this case (Moran, 1964), Wright has countered that the strictures make little difference to his shifting balance theory (Wright, 1965), and that most loci are unlinked and do not interact, so that as Kimura (1965) has shown, the $\bar{W}$ topography is an adequate approximation. But many loci are closely linked, and a fair proportion of these must interact in such a way as to invalidate the $\bar{W}$ topography; as Li (1967*c*) says, an approximation valid for some cases does not excuse us from finding the general case. Kimura's (1966) demonstration that $\bar{W}$ is always maximal in a plane of constant cross-product-ratio, only provides a general theorem if the population remains in that plane. But if the $\bar{W}$ topography is extended into another dimension, and an appropriate allowance made for the effects of recombination, we have a model which describes in general the equilibria in a two-locus polymorphism, adds a new factor to the shifting-balance theory, and predicts the evolution of close linkage (a theory which Fisher (1930) first propounded in the same book as his fundamental theorem, although both cannot in general be true simultaneously) (Turner, 1967*a, b*). The extended $\bar{W}$ model also describes, by relating the variation of population path (with varying recombination) to the formation of the $\bar{W}$ hypersurface, the failure of a new allele to spread unless it is closely linked to another (Turner, unpublished). Such a model does not of course replace explicit equations (for the most recent study see Bodmer and Felsenstein, 1967) but merely gives us a framework for understanding them, and allows us to see whether or not the conclusions drawn from the equations are general (the equations can be solved only in special cases).

6. SUMMARY

1. Evolution, if the mating system is taken into account, is not simply the "survival of the fittest" and the "fundamental theorem of natural selection" (that mean fitness increases) is therefore bound to run into difficulties.

2. A basic theorem is that the haploid variance in fitness decreases to zero under selection (the decrease is not monotonic). Most selection

theorems are special cases of this theorem, as is a very simple method for finding the non-trivial equilibria.

3. An "adaptive topography" based on the theorem will predict the course of evolution even in quite complex cases, and is not restricted, as is the mean fitness topography, to the simplest conditions.

4. Equations are given for the change of mean and variance of metric characters (including fitness as a special case) under selection.

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7. APPENDIX: CHANGES OF MEAN AND VARIANCE OF METRIC CHARACTERS UNDER SELECTION

Here is derived, in a general form, the equation for the change of variance (7) and also several other equations of general interest which use the same proof. First note the definitions of the partial derivatives of allele frequencies (Wright, 1955)

$$\partial q_i / \partial q_i = 1, \quad \partial q_j / \partial q_i = -q_j / (1 - q_i). \quad (\text{A1})$$

The change in any population parameter, $\mathcal{Z}$, with changing gene frequency can be calculated from the infinite expansion

$$\Delta \mathcal{Z} = \sum_i (\Delta q_i) \frac{\partial \mathcal{Z}}{\partial q_i} + \sum_{ij} \frac{(\Delta q_i)(\Delta q_j)}{2!} \frac{\partial^2 \mathcal{Z}}{\partial q_i \partial q_j} + \sum_{ijk} \frac{(\Delta q_i)(\Delta q_j)(\Delta q_k)}{3!} \frac{\partial^3 \mathcal{Z}}{\partial q_i \partial q_j \partial q_k} \dots \quad (\text{A2})$$

($i \geq j \geq k$)

Take a metric character, values X_{ij} in diploids, so that the mean for an allele is

$$X_i = \sum_j f_{ij} X_{ij} / q_i \quad (\text{A3})$$

and the population mean and haploid variance are given by

$$\bar{X} = \sum_{ij} f_{ij} X_{ij} = \sum_i q_i X_i \quad (\text{A4})$$

$$V_{H(X)} = \sum_i q_i (X_i - \bar{X})^2 \quad (\text{A5})$$

having a *haploid covariance* with fitness

$$\{\text{covar}_H(W, X)\} = \sum_i q_i (W_i - \bar{W})(X_i - \bar{X}) \quad (\text{A6})$$

We first establish the rule for taking the derivatives in (A2) by determining the change in mean for two alleles under random mating and with no dominance. In this case we need use only one gene frequency in the derivative (as the other is automatically determined), so that

$$\Delta q_0 = (q_0 q_1 / 2 \bar{W})(d\bar{W} / dq_0) \quad (\text{A7})$$

and the haploid covariance with fitness is

$$\{\text{covar}_H(W, X)\} = \frac{1}{2} q_0 q_1 (d\bar{W} / dq_0)(d\bar{X} / dq_0). \quad (\text{A8})$$

Substitution of $\bar{X}$ for $\mathcal{Z}$ in (A2) yields at once

$$\Delta \bar{X} = 2\{\text{covar}_H(W, X)\} / \bar{W} \quad (\text{A9})$$

To obtain this result by summing

$$\Delta \bar{X} = (\Delta q_0)(\partial \bar{X}/\partial q_0) + (\Delta q_1)(\partial \bar{X}/\partial q_1) \quad (\text{A10})$$

using rule (A1) and equation (5) it is necessary to differentiate only that part of $\bar{X}$ which is a direct function of q_i . That is, (A10) must be written

$$\Delta \bar{X} = (\Delta q_0)\{\partial(q_0 X_0)/\partial q_0\} + (\Delta q_1)\{\partial(q_1 X_1)/\partial q_1\} \quad (\text{A11})$$

By symmetry and induction this applies to any number of alleles. Also by symmetry and induction (for details of the method, see Turner, 1967*b*, appendix III) the change in $\bar{X}$ for any number of alleles without dominance will be twice the haploid covariance with fitness (divided by $\bar{W}$), and the first term of the expansion is therefore

$$\Delta \bar{X} = \Sigma_i (\Delta q_i) \{\partial(q_i X_i)/\partial q_i\} = 2\{\text{covar}_H(W, X)\}/\bar{W} \quad (\text{A12})$$

for any number of alleles.

The same rule of differentiation applies to the variance, and to the second derivatives.

Under random mating, but including dominance, we introduce the second term of (A2), all higher terms being zero. Thus we have finally

$$\Delta \bar{X} = 2\{\text{covar}_H(W, X)\}/\bar{W} + \{\Sigma_i q_i^2 (W_i - \bar{W})^2 X_{ii} + 2\Sigma_{ij} q_i q_j (W_i - \bar{W})(W_j - \bar{W}) X_{ij}\}/\bar{W}^2 \quad (ii \neq ij) \quad (\text{A13})$$

which for two alleles reduces to

$$\Delta \bar{X} = 2[\{\text{covar}_H(W, X)\} - 2V_H q_0 q_1 d_X/\bar{W}]/\bar{W} \quad (\text{A14})$$

where

$$d_X = X_{01} - \frac{1}{2}(X_{00} + X_{11}) \quad (\text{A15})$$

is the dominance of the character and V_H is the haploid variance in *fitness*, (A14) may also be obtained directly by the method of (A7-10).

Thus the change in the mean of a metric character equals its haploid covariance with fitness (divided by $\bar{W}$) (this is *not* the directly measurable diploid covariance) minus a correction for dominance (*cf.* Falconer, 1966). The change in mean fitness itself is readily shown to be (from A14) for two alleles

$$\Delta \bar{W} = V_H/\bar{W} \times (\bar{W} + \bar{W}_I)/\bar{W} \quad (\text{A16})$$

where $\bar{W}_I = \Sigma_i q_i W_{ii}$. This is not in general true for three or more alleles (C. C. Li, personal communication) contrary to my former opinion (Turner, 1967*b*); the exact equation for $\Delta \bar{W}$ with any number of alleles is clearly (A13) with X replaced by W .

The change in the haploid variance of the character is approximately, using the same rule of differentiation as for the mean, and taking only the first term of (A2):

$$\begin{aligned} \Delta V_{H(X)} &\simeq \Sigma_i (\Delta q_i) \{\partial q_i (X_i - \bar{X})^2 / \partial q_i\} \\ &= \Sigma_i [\{q_i (W_i - \bar{W}) / \bar{W}\} \times \{(\partial q_i / \partial q_i) (X_i - \bar{X})^2 \\ &\quad + 2q_i (X_i - \bar{X}) [\partial (X_i - \bar{X}) / \partial q_i]\}] \\ &= \{\text{com}_H(W, X^2)\} / \bar{W} \\ &\quad + 2\Sigma_i q_i^2 (W_i - \bar{W}) (X_i - \bar{X}) (\partial X_i / \partial q_i - \partial \bar{X} / \partial q_i) / \bar{W} \end{aligned} \quad (\text{A17})$$

or for two alleles

$$\Delta V_{H(X)} \simeq \{\text{covar}_H(W, X)\} \{(q_1 - q_0)(X_0 - X_1) - 4q_0q_1d_X\} / \bar{W} \quad (\text{A18})$$

where

$$\{\text{como}_H(W, X^2)\} = \Sigma_i q_i (W_i - \bar{W})(X_i - \bar{X})^2. \quad (\text{A19})$$

The derivatives in (A17) follow rule (A1), and involve the whole of $\bar{X}$, not merely $q_i X_i$. (A17-18) therefore state that the change in the haploid variance of a character is approximately equal to a comoment with fitness, minus a correction for dominance; this approximation is true for any conditions of selection and mating. These equations reduce to (7) and (9) when the character considered is fitness itself.

The exact equations for the change in variance are in general very elaborate, but that for the haploid variance in fitness at two alleles under constant selection and random mating involves only the first four terms of (A2) and is

$$\begin{aligned} \Delta V_H = \frac{V_H}{\bar{W}} & \left\{ (q_1 - q_0)(W_0 - W_1) - 4q_0q_1d_w \right. \\ & + \frac{V_D - V_H - 4(q_1 - q_0)(W_0 - W_1)q_0q_1d_w}{\bar{W}} \\ & + \frac{(q_1 - q_0)(W_0 - W_1)V_D + 4V_Hq_0q_1d_w/3}{\bar{W}^2} \\ & \left. - \frac{V_Hd_w}{\bar{W}^3} \right\} \quad (\text{A20}) \end{aligned}$$

where V_D is the dominance variance in fitness, and d_w is defined in (10). The first term of this is of course equation (9). Similarly for the dominance variance:

$$\begin{aligned} \Delta V_D = \frac{V_D}{\bar{W}} & \left\{ 2(q_1 - q_0)(W_0 - W_1) + \frac{(q_0^2 + q_1^2)(W_0 - W_1)^2}{\bar{W}} + \frac{2}{3} \frac{MO(W)^3}{\bar{W}^2} \right. \\ & \left. + \frac{1}{3} \frac{V_D V_H^2}{\bar{W}^3} \right\} \quad (\text{A21}) \end{aligned}$$

(See (8) for $MO(W)^3$.) Nei (1963) gives the first terms of (A20-21). The equation given by O'Donald (1967) for the change of variance in the absence of dominance (namely $\Delta V_H = -V_H^2/\bar{W}^2$) is equal to the *second* (quadratic) term of (A20). Warburton (1967) assuming no dominance and $\bar{W} = 1$, found the first two terms of (A20). All these authors use the additive variance, so that (A20) is actually half the value which they obtain.

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