Additive variance and average effect with partial selfing

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Summary

The covariance of an ancestor and the average of its descendants in generation t (C_{Pt}) is formulated for a breeding system which is a mixture of selfing and outcrossing. This covariance is partitioned into least squares additive ($\sigma_{A.At}$) and non-additive ($\sigma_{D.Dt}$) components summed over individual loci, and the combined inbreeding effects of all loci (H'), such that $C_{Pt} = \sigma_{A.At} + (s/2)^t[\sigma_{D.D0} + H']$. For the mth locus the covariance $_m\sigma_{A.At} = 2(1+F)\sum_i p_i\alpha_{(0)i}\alpha_{(t)i}$, in which p_i is the frequency of the ith allele whose additive effect ($\alpha_{(t)}$) depends on the generation for which it is defined. For distant descendants $\alpha_{(\infty)}$ is equal to half of the derivative of the population mean with respect to the frequency of the allele. The covariance $C_{P\infty} = \sigma_{A.A\infty}$ thus relates directly to permanent selection response measured in the equilibrium population, any additional responses observed in earlier generations being due to temporary disturbances in population genotypic structure. It is only for these distant descendants that the least squares additive component has any direct interpretation in terms of selection response. The definitions of $\alpha_{(0)}$ and $\alpha_{(\infty)}$ lead to two distinct definitions of the average effect of an allele substitution for a model with two alleles (Fisher, 1941), and to a clarification of their significance for this breeding system.

1. Introduction

The concept of the average effect of an allele substitution in a two-allele model was introduced by Fisher (1930) as an aid to the description of the relationship between additive genetic variance and population response to selection under a system of random outcrossing. Later he generalised the concept to include partial self-fertilization (Fisher, 1941), but showed that in this case response is not in general a function of the variance of the effects defined for this population. More recently Falconer (1986) has examined some of the properties of average effect and additive variance.

A general expression for the covariance of relatives for an arbitrary number of non-interacting loci, each with an arbitrary number of alleles, was given by Weir & Cockerham (1977), and used to derive some covariances among relatives descended from a population in equilibrium with respect to self and random mating by Cockerham & Weir (1984). They also gave a partition of the genotypic variance into least squares additive and non-additive components. Wright & Cockerham (1985) showed that the covariance of an ancestor and a descendant in the tth

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generation (C_{Pt}) depends on t, and that C_{Pt} evolves in a regular manner towards an asymptotic value for the distant descendants.

The purpose of this paper is to derive a general expression for C_{Pt} and to show that this can be partitioned into least squares additive ($\sigma_{A.At}$) and non-additive ($\sigma_{D.Dt}$) components. This highlights the importance of the distinction between the additive variance of population members and their additive covariance with distant descendants, and clarifies the definition and role of the average effect of an allele substitution.

2. The covariance of relatives

The covariance of diploid relatives under a general mating system can be formulated using the methods of Weir & Cockerham (1977). The basic model for the genotype of an individual with alleles i and j at one locus is

$$x_{ij} = \mu_0 + a_i + a_j + d_{ij},$$

in which the mean μ_0 is for an outbred reference population, the a terms are additive effects, and d is the dominance effect. An arbitrary number of alleles and loci are allowed, but absence of epistasis and linkage is assumed. In addition to the additive and

Table 1. *Quadratic components and identity measures*

For one locus	Sum over loci	Coefficient
$_m\sigma_A^2 = 2\sum_k p_k a_k^2$	$\sigma_A^2 = \sum_m {}_m\sigma_A^2$	$2\theta_{xy} = [P_{(i-k)} + P_{(i-l)} \\ \qquad + P_{(j-k)} + P_{(j-l)}]/2$
$_m\sigma_D^2 = \sum_k \sum_l p_k p_l (d_{kl})^2$	$\sigma_D^2 = \sum_m {}_m\sigma_D^2$	$2\delta_{\bar{x}+\bar{y}} = P_{(i-k \text{ and } j-l)} \\ \qquad + P_{(i-l \text{ and } k-l)} - 2P_{(i-j-k-l)}$
$_m D_1 = \sum_k p_k a_k d_{kk}$	$D_1 = \sum_m {}_m D_1$	$2\gamma_{\bar{x}y} + 2\gamma_{x\bar{y}} = [P_{(i-j-k)} + P_{(i-j-l)}] \\ \qquad + [P_{(i-k-l)} + P_{(j-k-l)}]$
$_m D_2^* = \sum_k p_k (d_{kk})^2 \\ \qquad - (\sum_k p_k d_{kk})^2$	$D_2^* = \sum_m {}_m D_2^*$	$\delta_{\bar{x}\bar{y}} = P_{(i-j-k-l)}$
$_m H^* = (\sum_k p_k d_{kk})^2$	$H^* = \sum_m {}_m H^*$	$\Delta_{\bar{x}.\bar{y}} - F_x F_y = P_{(i-j \text{ and } k-l)} \\ \qquad - P_{(i-j)} P_{(k-l)}$
—	$H^2 - H^* = (\sum_m \sum_k p_k d_{kk})^2 \\ \qquad - \sum_m (\sum_k p_k d_{kk})^2$	$\tilde{\Delta}_{xy} - F_x F_y$

[a] p_k is the frequency of the kth allele at the mth locus, a_k is its least squares additive effect, and d_{kl} is the dominance interaction of the kth and lth alleles in the non-inbred population.

[b] $\tilde{\Delta}_{xy}$ is the probability that the two genes at one locus in x and a second locus in y are equivalent by descent.

dominance variances usual with random outcrossing (σ_A^2 and σ_D^2), the variance of homozygous dominance effects (D_2^*) and their covariance with the additive effects of the same allele (D_1) are needed. There are further contributions due to the sum of the squared inbreeding depression effects of individual loci (H^*) and the square of the joint inbreeding effect of all loci (H^2). The coefficients of the components are measures of the probability of identity by descent of various combinations of alleles within and between genotypes. The components and their coefficients in the covariance of relatives x and y carrying alleles i, j and k, l are given in Table 1.

The covariance of any specific pair of relatives is then obtained by substitution of the appropriate identity measures in the general formula given by Weir & Cockerham (1977)

$$C_{xy} = 2\theta_{xy}\sigma_A^2 + 2\delta_{\bar{x}+\bar{y}}\sigma_D^2 + 2(\gamma_{\bar{x}y} + \gamma_{x\bar{y}})D_1 + \delta_{\bar{x}\bar{y}}D_2^*$$
$$+ (\Delta_{\bar{x}.\bar{y}} - F_x F_y)H^* + (\tilde{\Delta}_{xy} - F_x F_y)(H^2 - H^*).$$

3. Partial selfing

In a breeding system in which reproduction of all individuals takes place with a probability s of selfing and $(1-s)$ of random outcrossing, two distinct types of covariance between ancestor and descendant can be envisaged. In the first case, only the maternally derived offspring are considered, the contribution of outcrossing male gametes being ignored, so that the descendants are defined strictly through the maternal

line. This type of covariance is appropriate for the prediction of the response to selection which maintains no control over the male gametes, such as with naturally produced maternal families (Wright & Cockerham, 1985, 1986). For most other applications it is appropriate to define a covariance for all the descendant genotypes, including those produced at each generation by the outcrossing male gametes. This is equivalent to the doubling of parent–offspring covariances when there is complete outcrossing. Covariances of this type can be extended over an arbitrary number of generations, and are appropriate for the case when parental selection is carried out prior to reproduction, and also to follow the long term results of earlier selection over subsequent cycles of population reproduction without selection (Wright & Cockerham, 1985).

The average inbreeding coefficient in a population in equilibrium remains constant from generation to generation at $F = s/(2-s)$. The transition equations for other identity coefficients under this system are simple and these evolve in a very regular manner (Table 2). The covariance between a parent and the mean value of its descendants in any generation t is then obtained by substitution of the appropriate values of the identity coefficients into the general formula given above:

$$C_{Pt} = (1+F)\sigma_A^2 + F[3 + F + (1-F)(s/2)^t]D_1$$
$$+ F[F + (1-F)(s/2)^t]D_2^* + (s/2)^t[(1-F)\sigma_D^2$$
$$+ F(1-F)H^* + H'].$$

Table 2. *The identity coefficients necessary for the expression of the covariance of a parent and all its descendants in the tth generation,* C_{Pt}

Identity coefficient	Initial value	Transition equation	Transitory value
F	F	(Constant)	F
θ_{Pt}	$(1+F)/2$	(Constant)	$(1+F)/2$
$\gamma_{\ddot{P}t}$	F	(Constant)	F
$\gamma_{P\bar{\imath}}$	F	$s(\gamma_{P\bar{\imath}-1}+\theta_{Pt-1})/2$	$F\{(s/2)^t+(1+F)[1-(s/2)^t]/2\}$
$\delta_{\ddot{P}\bar{\imath}}$	F	$s(\delta_{\ddot{P}\bar{\imath}-1}+\gamma_{\ddot{P}t-1})/2$	$F\{(s/2)^t+F[1-(s/2)^t]\}$
$\delta_{\ddot{P}+\bar{\imath}}$	$(1-F)/2$	$s\delta_{\ddot{P}+\bar{\imath}-1}/2$	$(s/2)^t(1-F)/2$
$\Delta_{\ddot{P}\cdot\bar{\imath}}$	F	$s(\Delta_{\ddot{P}\cdot\bar{\imath}-1}+F)/2$	$F\{(s/2)^t+F[1-(s/2)^t]\}$
Δ_{Pt}	$F(1+2F)/(2+F)$	$s(\Delta_{P\cdot t-1}+F)/2$	$F[F+(s/2)^t(1-F^2)/(2+F)]$

In this expression

$$H' = (H^2 - H^*)[F(1-F^2)]/(2+F)$$

is the joint inbreeding contribution of all pairs of loci to the population variance due to their correlated genotypic distribution.

The behaviour of the identity coefficients also leads to the following relationship among the covariances which was noted by Wright & Cockerham (1985)

$$C_{Pt} = C_{P\infty} + (\sigma_G^2 - C_{P\infty})(s/2)^t,$$

in which σ_G^2 is the population genotypic variance but can be regarded as equivalent to the covariance in generation zero (C_{P0}).

4. A least squares partition of the covariance

Cockerham & Weir (1984) gave a least squares partitioning of the genotypic variance into additive and non-additive (dominance) portions. For the *m*th locus

$$_m\sigma_{AF}^2 = (1+F)_m\sigma_A^2 + 4F_mD_1 + sF_mD_2^*,$$

and

$$_m\sigma_{DF}^2 = (1-F)[_m\sigma_D^2 + (s/2)_mD_2^* + F_mH^*],$$

in which all components are defined for the single locus considered. Although this partition cannot be applied as it stands to the covariance with any later generations, it does suggest that a more general definition of an additive covariance $_m\sigma_{A \cdot At}$ may exist. This partition may be achieved by solving for values of $\alpha_{(0)i}$ and $\alpha_{(t)i}$ for one locus which minimize the residual covariance in C_{Pt}

$$_m\sigma_{D \cdot Dt} = F\sum_i p_i[x_{ii}-2\alpha_{(0)i}-\mu][y_{ii}-2\alpha_{(t)i}-\mu']$$
$$+(1-F)\sum_i\sum_j p_ip_j[x_{ij}-\alpha_{(0)i}-\alpha_{(0)j}-\mu]$$
$$\times[y_{ij}-\alpha_{(t)i}-\alpha_{(t)j}-\mu'],$$

in which y is a random descendant of x, and μ and μ' are the means of parental and descendant generations. The details of this procedure are given in the Appendix, but the results are

$$\alpha_{(0)i} = [(1-F)(x_{i.}-x_{..})+F(x_{ii}-x_{.})]/(1+F),$$

and

$$\alpha_{(t)i} = [2(\theta_{Pt}-\gamma_{P\bar{\imath}})(x_{i.}-x_{..})+\gamma_{P\bar{\imath}}(x_{ii}-x_{.})]/(1+F),$$

and with $\mu = \mu'$ as expected. Here $x_{i.} = \sum_j p_j x_{ij}$, $x_{..} = \sum_i\sum_j p_ip_j x_{ij}$ and $x_{.} = \sum_i p_i x_{ii}$, and the subscripts Pt refer to descent measures between parent and *t*th generation descendant (Table 2).

The terms $\alpha_{(0)i}$ and $\alpha_{(t)i}$ are the effects of allele i when measured in the parental and the descendant populations respectively. These can be expressed in terms of the genotypic model, for which

$$x_{ii} = \mu_0 + 2a_i + d_{ii} \quad \text{and} \quad x_{i.} = \mu_0 + a_i.$$

Then

$$\alpha_{(0)i} = a_i + d_{ii}F/(1+F),$$

and generally

$$\alpha_{(t)i} = a_i + d_{ii}\gamma_{P\bar{\imath}}/(1+F)$$
$$= a_i + d_{ii}F\left(\frac{1}{2}+\frac{(1-F)(s/2)^t}{2(1+F)}\right).$$

Since the one locus contribution to the mean population genotypic value can be written as

$$y = (1-F)\sum_i\sum_j p_ip_j x_{ij} + F\sum_i p_i x_{ii},$$

then

$$\delta y/\delta p_i = 2(1-F)x_{i.} + Fx_{ii} = 2a_i + Fd_{ii} = 2\alpha_{(\infty)i}.$$

Thus, by the time that sufficient generations have elapsed for the descendant alleles of any individual ancestor to be randomly distributed in the population, the average effect of any allele is equal to twice the population derivative with respect to that allele. The significance of this result will be expanded later in terms of the two-allele genotypic model.

The additive covariance for the locus is obtained as the sum of products of the values of $\alpha_{(0)i}$ and $\alpha_{(t)i}$

$$_m\sigma_{A \cdot At} = (1-F)\sum_i\sum_j p_ip_j[\alpha_{(0)i}+\alpha_{(0)j}][\alpha_{(t)i}+\alpha_{(t)j}]$$
$$+4F\sum_i p_i\alpha_{(0)i}\alpha_{(t)i}$$
$$= 2(1+F)\sum_i p_i\alpha_{(0)i}\alpha_{(t)i}$$
$$= 2\sum_i p_i(1+F)[a_i+d_{ii}F/(1+F)]$$
$$[a_i+d_{ii}\gamma_{P\bar{\imath}}/(1+F)]$$
$$= (1+F)_m\sigma_A^2 + 2[\gamma_{P\bar{\imath}}+F]_mD_1 + s\gamma_{p\bar{\imath}m}D_2^*$$

GRH 50

When $t = 0$, $\gamma_{P\ddot{u}} = F$ and this reduces to the additive variance of the parental population already given by Cockerham & Weir (1984). The residual covariance for a single locus is found by difference to be

$$_m\sigma_{D \, . \, Dt} = (s/2)^t(1-F)[_m\sigma_D^2 + (s/2)_mD_2^* + F_mH^*]$$
$$= (s/2)^t\,_m\sigma_{D \, . \, D0}.$$

It follows that the total covariance over all loci can be written as

$$C_{P\infty} = \sigma_{A \, . \, A\infty} = (1+F)_m\sigma_A^2 + F(3+F)_mD_1$$

The coefficient of the non-additive components disappears as t approaches infinity so that for the distant descendants

$$C_{P\infty} = \sigma_{A \, . \, A\infty} = (1+F)_m\sigma_A^2 + F(3+F)_mD_1$$
$$+ F^2\,_mD_2^*,$$

and has no non-additive component.

5. Two-allele case

When there are two alleles 1 and 2 with frequencies p and $q = (1-p)$, then from the general model, $p\alpha_1 + q\alpha_2 = 0$, so that $\alpha_1 = q\alpha$ and $\alpha_2 = -p\alpha$. Thus the two effects can both be described in terms of a single parameter α, which is the difference $\alpha = \alpha_1 - \alpha_2$. This is the average effect of an allele substitution as defined by Fisher (1930, 1941). As before this effect can be defined for any generation. Writing the genotypic values for the two allele model as $B_1B_1 = b$, $B_1B_2 = h$ and $B_2B_2 = -b$, the equivalence of the effects for the two models is

$$\mu + a_1 = q[b + h(q-p)], \quad \mu + a_2 = -p[b + h(q-p)],$$
$$d_{11} = -2q^2h,$$
and $d_{22} = -2p^2h.$

Thus, for the general case α_t, and those of most interest:

$$\alpha_t = a_1 - a_2 + (d_{11} - d_{22})\gamma_{Pi}/(1+F)$$
$$= b + h(q-p)[1 - 2\gamma_{Pi}/(1+F)]$$
$$= b + h(q-p)(1-F)[1 - (s/2)^{t+1}],$$

so that

$$\alpha_0 = b + h(q-p)(1-F)/(1+F),$$

and

$$\alpha_\infty = b + h(q-p)(1-F).$$

The additive covariance for this model is

$$_m\sigma_{A \, . \, At} = 2(1+F)\sum_i p_i\alpha_{(0)i}\alpha_{(t)i} = 2(1+F)pq\alpha_0\alpha_t.$$

Falconer (1986) has shown that α_0 is the coefficient of regression of genotypic value onto allele doseage and that the least squares additive population variance is the variance in genotypic value accounted for by the regression. Since allele doseage in diploids is equal to

twice the allele frequency, the additive variance can be written as

$$_m\sigma_{AF}^2 = 4\sigma_p^2 \, \alpha_0^2 = \sigma_p^2(b_{x/p})^2 = \sigma_x^2 b_{p/x}b_{x/p},$$

in which $\sigma_p^2(=pq[1+F]/2)$ is the variance in allele frequency and b denotes a regression coefficient. When there is random mating, the distinct paths from genotype to allele and back to genotype help to clarify the role of additive variance in the determination of selection response due to changes in allele frequency. With partial selfing, however, the response to selection is a simple function of changes in allele frequency only for the distant descendants of the selections. In this case response is a function of the additive covariance

$$_m\sigma_{A \, . \, A\infty} = 4\sigma_p^2 \, \alpha_0\alpha_\infty = \sigma_x^2 b_{p/x}b_{y/p},$$

in which y is the descendant population mean. The equivalence of α_∞ to $b_{y/p}$ has already been shown in terms of the general model as it equals one-half of the differential of the equilibrium descendant mean with respect to p, or the whole differential with respect to allele doseage.

The related quantity, average excess, was shown by Falconer (1986) to be equal to $(1+F)\alpha_0$ and is evidently the average effect adjusted to take account of the increased variance in allele frequency with inbreeding so as to relate directly to the selection differential applied to the locus. In the light of the above interpretation of the roles of α_0, α_∞ and σ_p^2, it can be considered an unnecessary and probably confusing concept.

6. Discussion

In general the response to selection with partial selfing is not a function of the additive variance in the parental population. The only selection response which relates directly to a component of variance or covariance associated with individual alleles is that measured when all changes in population genotypic structure are due only to changes in allele frequency, and with partial selfing this is the case only in distant generations when the selected population has regained its characteristic inbreeding structure. Any additional gain which may be observed in earlier generations is due to temporary alterations in the genotypic structure of the population when there is dominance, and this is gradually lost as equilibrium is regained. Although it has been possible to define and formulate least squares additive effects for all intermediate generations, and express their covariance with the parental effects, these have no direct interpretation in terms of response.

Fisher (1941) and Kempthorne (1957) show that the population additive variance can predict the immediate response to selection for a single locus with two alleles only if a certain relationship among the homozygote and heterozygote frequencies is retained. In the present notation, this requires that the quantity

$F/[pq(1-F)^2]$ remains unchanged after selection and reproduction. However, while the prediction of response on the basis of additive variance in the presence of dominance has to assume that the change in frequency of individual alleles is very small, this condition requires that p undergoes a change of similar order of magnitude as does F. Equating $_m\sigma_{AF}^2$ to $_mC_{P1}$ yields no simple expressions even in terms of the two-allele model. On the other hand, the use of σ_{AF}^2 to predict the final response can be tested by comparing $\alpha_{(0)}$ and $\alpha_{(\infty)}$, showing that this would require selection to be accompanied by a permanent increase in the rate of selfing to a new value of $s' = 2s/(1+s)$.

Although he took care to refer to the offspring or descendant population, Fisher (1941) clearly thought of the average effect of an allele substitution as a regression of individual genotypes onto allele doseage, as he defined it as 'the partial regression, in the population as actually constituted, of the genotypic measurement on the numbers of genes in each genotype'. This view can now be seen to be inappropriate when attempting to predict or explain selection response, as the product of average effects defined for parents and descendants in $\sigma_{A.A\infty}$ bears out the important principle that while selection operates to discriminate among genotypes, its effects are observed on populations. It is only with random mating that the average effect is unique and can be defined as the effect of changes in allele doseage either on individual genotypic values within the population, or on the population mean itself, so that the additive variance is also unambiguous. In elaboration of Fisher's earlier definitions, the terms α_0 and α_∞ can now be referred to as the genotypic and population effects, respectively, of an allele substitution, and it may be that of all the interesting properties of random mating noted by Fisher (1930) and others, their equality is the most important and fundamental.

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Appendix

The least squares partition of the covariance of ancestor and the mean of its descendants, C_{Pt}.

For a single locus, the residual variance which is to be minimised can be written as the sum of separate contributions from the inbred and non-inbred fractions of the population:

$$_m\sigma_{D.Dt} = F\sum_i p_i[x_{ii}-2\alpha_i-\mu][y_{ii}-2\alpha_i'-\mu']$$
$$+(1-F)\sum_i\sum_j p_i p_j[x_{ij}-\alpha_i-\alpha_j-\mu][y_{ij}-\alpha_i'-\alpha_j'-\mu'],$$

in which y_{ij} is the mean genotype of the descendants of parent x_{ij} from the population with allele frequencies p_i and p_j, and solutions are required for α_i, α_i', μ and μ'. Differentiating:

$$d(_m\sigma_{D.Dt})/d\mu' = -F\sum_i p_i[x_{ii}-2\alpha_i-\mu]$$
$$-(1-F)\sum_i\sum_j p_i p_j[x_{ij}-\alpha_i-\alpha_j-\mu],$$

and

$$F[x_.-\mu]+(1-F)[x_{..}-\mu] = 0$$

when

$$\mu = Fx_. +(1-F)x_{..}$$

since $\sum_i p_i\alpha_i = 0$, and in which $x_. = \sum_i p_i x_{ii}$ and $x_{..} = \sum_i\sum_j p_i p_j x_{ij}$.

$$d(_m\sigma_{D.Dt})/d\alpha_i' = -2Fp_i[x_{ii}-2\alpha_i-\mu]$$
$$-2(1-F)\sum_j p_j[x_{ij}-\alpha_i-\alpha_j-\mu],$$

and

$$Fp_i[x_{ii}-2\alpha_i-\mu]+(1-F)[x_{i.}-\alpha_i-\mu] = 0$$

when

$$\alpha_i = [F(x_{ii}-x_.)+(1-F)(x_{i.}-x_{..})]/(1+F),$$

in which $x_{i.} = \sum_j p_j x_{ij}$.

These two solutions are complete, but for the others the descendant genotypic values y_{ij} have to be expanded in terms of the probabilities of occurrence of different genotypes expressed in terms of descent measures. These are

$$y_{ij} = \gamma_{0t}(x_{ii}-x_{jj})+2\delta_{\ddot{o}+t}x_{ij}+2\sum_k p_k(\theta_{0t}-\gamma_{0t}-\delta_{\ddot{o}+t})$$
$$\times(x_{ik}+x_{jk})+\sum_k\sum_l p_k p_l(1+4\theta_{0t}+2\gamma_{0t}+2\delta_{\ddot{o}+t})x_{kl},$$
$$= \gamma_{0t}(x_{ii}+x_{jj})+2\delta_{\ddot{o}+t}x_{ij}+2(\theta_{0t}-\gamma_{0t}-\delta_{\ddot{o}+t})$$
$$(x_{i.}+x_{j.})+(1-4\theta_{0t}+2\gamma_{0t}+2\delta_{\ddot{o}+t})x_{..}$$
$$y_{ii} = \gamma_{It}x_{ii}+2\sum_k p_k(\theta_{It}-\gamma_{It})x_{ik}+\sum_k\sum_l p_k p_l(1-2\theta_{It}$$
$$+\gamma_{It})x_{kl}$$
$$= \gamma_{It}x_{ii}+2(\theta_{It}-\gamma_{It})x_{i.}+(1-2\theta_{It}+\gamma_{It})x_{..}$$

5-2

Alleles k and l are random population alleles non-identical to i or j. The descent measures differ from those given in Table 2 since they are defined separately for inbred and non-inbred parents, as indicated by the I and 0 subscripts. It follows that

$$y_{i.} = \gamma_{0i}(x_{ii}+x_{.}) + 2(\theta_{0t}-\gamma_{0i})(x_{i.}+x_{..}) + (1-2\theta_{0t})x_{..},$$
$$y_{..} = 2\gamma_{0i}x_{.} + (1-2\gamma_{0i})x_{..} \quad \text{and}$$
$$y_{.} = \gamma_{It}x_{.} + (1-\gamma_{It})x_{...}$$

Differentiating first and then substituting for y_{ij}

$$d(_m\sigma_{D.Dt})/d\mu = -F\sum_i p_i[y_{ii}-2\alpha_i'-\mu']$$
$$-(1-F)\sum_i\sum_j p_i p_j[y_{ij}-\alpha_i'-\alpha_j'-\mu'],$$

and

$$F[y_{.}-\mu] + (1-F)[y_{..}-\mu] = 0$$

when

$$\mu' = Fy_{.} + (1-F)y_{..} = Fx_{.} + (1-F)x_{..} = \mu.$$
$$d(_m\sigma_{D.Dt})/d\alpha_i = -2Fp_i[y_{ii}-2\alpha_i'-\mu']$$
$$-2(1-F)\sum_j p_j[y_{ij}-\alpha_i'-\alpha_j'-\mu'],$$

and

$$Fp_i[y_{ii}-2\alpha_i'-\mu'] + (1-F)(y_{i.}-\alpha_i'-\mu') = 0$$

when

$$\alpha_i' = [F(y_{ii}-y_{.}) + (1-F)(y_{i.}-y_{..})]/(1+F)$$
$$= \{[F\gamma_{Ii}+(1-F)\gamma_{0i}](x_{ii}-x_{.}) + 2[F(\theta_{I0t}-\gamma_{I0i})$$
$$+(1-F)(\theta_{0t}-\gamma_{0i})](x_{i.}-x_{..})\}/(1+F),$$

and, since

$$F\theta_{It}+(1-F)\theta_{0t} = \theta_{Pt} \quad \text{and} \quad F\gamma_{Ii}+(1-F)\gamma_{0i} = \gamma_{Pi},$$
$$\alpha_i' = [\gamma_{Pi}(x_{ii}-x_{.}) + 2(\theta_{Pt}-\gamma_{Pi})(x_{i.}-x_{..})]/(1+F).$$