Permanency of response to selection for quantitative characters in finite populations

(dominance and additive by additive effects/conservation of variance/drift)

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ABSTRACT To study the permanency of response to selection for a quantitative character in finite populations and the nature of the genetic effects that contribute to this response, we have used the covariance between ancestors and descendants within populations. Effects and variances are defined for an initial equilibrium random mating monoeuous population that gives rise to replicate finite populations. After a prescribed history of restricted population size, the replicate populations are expanded, and the covariance between ancestors and descendants is quantified in terms of descent measures and genetic components in the initial population as a means of determining the additive variance within populations. Several dominance components including joint dominance effects of loci contribute to the additive variance, some of which can be negative. There is always a positive contribution of additive by additive variance to the additive variance within populations, which can be large. With the new definitions of components of genetic variance within populations, selection response is formulated in the same manner as for the initial random mating population, but the components have been modified considerably by the restricted population size.

The permanency of immediate response to selection for a quantitative character is important for the evolutionist as well as the animal and plant breeder. It has long been known that dominance effects are not transmitted from ancestor to descendant in outbred populations, although there can be some immediate response from dominance, full-sib selection, for example. Griffing (1) also showed that the additive by additive (\(a^2a^2\)) variance (and other all additive types of epistatic variance), which contributed to the initial response to selection in an outbred population, dissipated with continued random mating. This was confirmed (2) by considering the covariance of descendants over time with their ancestors. These results lead to the general conjecture that only additive effects and variance are involved in permanent response to selection in large outbred populations.

The situation is very different in inbreeding. With selffertilization (3), dominance and \(a^2a^2\) effects as well as additive effects contribute to immediate, intermediate, and final response to selection in a complex manner. The same is true for mass selection (4) and family selection (5) with partial selfing.

In an analysis of the covariances of half- and full-sibs in finite populations with drift, it was found that portions of the components involving dominance behaved as additive variance, suggesting that they also would contribute to permanent response to selection within populations (6).

Within finite populations Goodnight (7) found that the \(a^2a^2\) genetic variance increased for some time with restricted population size—in contrast to the additive genetic variance, for which there is a linear decrease with inbreeding, an observation also made in ref. 8. Also, Goodnight (9) found part of the \(a^2a^2\) variance within populations to behave as additive genetic variance.

The objective of this study is to formulate the covariance between ancestors in finite populations and their descendents over time for additive, dominance, and \(a^2a^2\) effects. The argument is that permanent response to selection within populations is proportional to the final cumulative covariance (3–5), which is also referred to as the variance that is conserved with continued mating.

For simplicity we consider only random mating monoeuous populations (6). The initial population is in linkage and Hardy–Weinberg equilibrium and gives rise to replicate finite populations of size \(N\) each generation. At some generation in time the replicate populations are expanded, \(N = \infty\). It is these initial expanded populations that are the ancestral populations, and random mating is continued with \(N = \infty\).

We consider a single locus for additive and dominance effects and a pair of loci for joint dominance and \(a^2a^2\) effects. The genetic components for additive and dominance effects are defined for the initial equilibrium population (6), \(\sigma^2_a\) is the additive variance, \(\sigma^2_d\) is the dominance variance, \(d_{ij}\) is covariance between additive and homozygous dominance effects, \(d_{y}\) is variance of homozygous dominance effects, and \(h\) is the inbreeding depression. For a pair of loci we consider joint dominance effects, \(2hh'\), involving the two inbreeding depressions and the \(a^2a^2\) variance, \(\sigma^2_{a^2}\), where \(\sigma^2_{a^2} = 4\sigma^2_{a^2}\) in ref. 2. The total genetic variance in the initial population is given by \(\sigma^2_a + \sigma^2_d + \sigma^2_{a^2}\) summed over loci. The other components for dominance are required to express the variances and covariances of individuals within finite populations with drift (6).

The covariance of individuals is facilitated by descent measures, which are presented in Table 1. Several of the distinctions made in Table 1 disappear in random mating finite monoeuous populations: \(F_X = \theta_{XY} = \theta, \gamma_{XY} = \gamma_{XY} = \gamma, \Delta_{XY} = \Delta_{XY} = \Delta, F_X = \theta_{XY} = \theta, \gamma_{XY} = \gamma_{XY} = \gamma, \Delta_{XY} = \Delta_{XY} = \Delta\). Consequently, the descent measures for the population of ancestors are \(\theta, \gamma, \Delta\), and \(\delta\) for one locus and \(\theta, \gamma, \Delta\) for two loci. An average of the two-locus measure is useful, \(\bar{\Gamma} = (\theta + 2\gamma + \Delta)/4\). Explicit formulas for the one-locus measures and transition equations from which the two-locus measures can be obtained are given in appendix A of ref. 6. All results are to be formulated in terms of these measures for the ancestors. The more elaborate definitions of the descent measures in Table 1 are useful in developing the covariance between ancestors and descendents.

The genotypic covariance between two individuals \(X\) and \(Y\) may be formulated as

\[
\begin{align*}
\epsilon_{XY} &= 2\theta_{XY}\sigma^2_a + 2(\Delta_{XY} - \delta_{XY})\sigma^2_d + 2(\gamma_{XY} + \gamma_{XY})d_1 + \delta_{XY}d_2 + (\delta_{XY} - F_XF_Y)h^2 + (\delta_{XY} - F_XF_Y)2hh' + (\theta_{XY} + \gamma_{XY} + \gamma_{XY} + \Delta_{XY})\sigma^2_{a^2}.
\end{align*}
\]

Abbreviation: \(a^2a^2\), additive by additive.

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Table 1. Identity by descent (ibd) measures for one- and two-locus states

<table>
<thead>
<tr>
<th>ibd</th>
<th>States</th>
<th>One-locus</th>
</tr>
</thead>
<tbody>
<tr>
<td>$F_X$</td>
<td>$a = b$</td>
<td></td>
</tr>
<tr>
<td>$\theta_{XY}$</td>
<td>$(a = c) = (b = c) = (b = d)$</td>
<td></td>
</tr>
<tr>
<td>$\gamma_X$</td>
<td>$(c = b) = (b = c) = (a = b)$</td>
<td></td>
</tr>
<tr>
<td>$\delta_X + \gamma$</td>
<td>$(a = c, b = d) = (a = d, b = c)$</td>
<td></td>
</tr>
<tr>
<td>$\delta_X \gamma$</td>
<td>$(a = b, c = d)$</td>
<td></td>
</tr>
</tbody>
</table>

| $F_X$ | $(a = b, e = f)$                                                       |           |
| $\theta_{XY}$ | $(a = c, e = g) = (a = d, e = h) = (b = c, f = g) = (b = d, f = h)$ |           |
| $\gamma_X$ | $(c = e, h = (a = d, e = g) = (b = c, h = f = g)$                   |           |
| $\delta_X \gamma$ | $(a = c, f = h) = (a = d, f = g) = (c = e) = (b = d, e = g)$        |           |
| $\delta_X$ | $(a = b, g = h) = (c = d, e = f)$                                    |           |

Two-locus

$F_X$ | $(a = b, e = f)$                                                       |           |
| $\theta_{XY}$ | $(a = c, e = g) = (a = d, e = h) = (b = c, f = g) = (b = d, f = h)$ |           |
| $\gamma_X$ | $(c = e, h = (a = d, e = g) = (b = c, h = f = g)$                   |           |
| $\delta_X \gamma$ | $(a = c, f = h) = (a = d, f = g) = (c = e) = (b = d, e = g)$        |           |
| $\delta_X$ | $(a = b, g = h) = (c = d, e = f)$                                    |           |

Representation of genes for $X$ and $Y$:

<table>
<thead>
<tr>
<th>Locus A</th>
<th>$a$</th>
<th>$b$</th>
<th>$c$</th>
<th>$d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Locus B</th>
<th>$e$</th>
<th>$f$</th>
<th>$g$</th>
<th>$h$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Genes connected by a line are on the same gamete. = denotes that genes are identical by descent. More than one state descent measure is the average of the probabilities for each state in parentheses. The one-locus states are for the $A$ locus. An overbar, for example, $\bar{X}$, denotes that the genes are on separate gametes. Symmetrical measures $\gamma_X$ and $\gamma_Y$ are omitted.

Details for the coefficient of $\sigma_{\theta A}^2$ are given in ref. 2 and for the other coefficients in ref. 10. As an example, for two random members of the population of ancestors, $\epsilon_{XY} = 2\sigma_{\theta A}^2 + 2(\Delta - \delta)\sigma_{\theta A}^2 + 4\epsilon_{12} + 4\epsilon_{12}^2 + (\Delta - \delta^2)h^2 + (\Delta - \delta^2)h^2 + 4\epsilon_{\bar{A}}^2$.

We work with two covariances: $\epsilon_{AD}$, the covariance between the ancestor, $A$, and a descendet, $D$, in the $n$th generation after expansion and $\epsilon_{AU}$, the covariance between the ancestor and an unrelated individual, $U$, in the $n$th generation, unrelated except for that brought on by the finite population history. The covariance of interest is $\epsilon_{*AD} = \epsilon_{AD} - \epsilon_{AU}$; i.e., corrected for the general relationship among individuals.

Algorithms are given in ref. 11 for formulating the single-locus descent coefficients. Those involving $U$ do not change with $\tau$: $F_{\lambda} = F_{\lambda_0} = \theta_{AU} = \theta$, $\gamma_{AU} = \gamma_{AU_0} = \gamma$, $\Delta_{X + U} = \Delta$, and $\Delta_{X_0}$ for the descendet, $F_D$, $\theta$ remains the same and using the algorithms,

$\theta_{AD} = (1 - \theta)2^{-\tau - 1} + \theta$,

$\gamma_{AD} = \gamma_{AD} = (\theta - \gamma)2^{-\tau + \gamma}$,

$\Delta_{X + D} = (\theta + \gamma - 2\Delta)2^{-\tau + \Delta}$, and

$\Delta_{X_0} = (\gamma - \Delta)2^{-\tau + \Delta}$, and

$\delta_{AD} = (\gamma - \delta)2^{-\tau + \delta}$.

The descent measures for two loci are considerably more cumbersome. Most of the arguments involved in their evaluation are given in ref. 2, and some of the arguments will be sketched. We take account of linkage measured by $\lambda$ where $(1 - \lambda)/2$ is the recombination fraction. Letting $\alpha = (1 + \lambda)/2$, $\alpha$ is the probability that a parental gamete was parental in the previous generation and $1 - \alpha$ is the probability that it was a recombinant (on two gametes) in the previous generation. Consequently, for $\theta_{AU}$, which involves a random parental gamete of $A$ and of $U$, $\theta_{AU} = \alpha\theta_{AU_0} + (1 - \alpha)\gamma$ because $\gamma_{AU_0} = \gamma$, being the probability for a parental gamete in the ancestral population and any recombinant gamete. Carrying the argument back to the ancestral generation $\theta_{AU} = \alpha\theta + (1 - \alpha)\gamma = (\theta - \gamma)\alpha^2 + \gamma$. By the same argument $\gamma_{AXU} = \alpha\gamma_{AXU_0} + (1 - \alpha)\Delta = (\gamma - \Delta)\alpha^2 + \Delta$ because $\Delta_{XU_0} = \Delta$ between two recombinant gametes does not change with $\tau$. In summary,

$4\theta_{AU} = \theta_{AU} + \gamma_{AXU} + \gamma_{AXU} + \Delta_{XU} = (\theta - \Delta)\alpha^2 + 2(\gamma + \Delta)$.

The descent measure $\theta_{AU}$ involves genes on four gametes and does not change with $\tau$.

In arguing the parental gametes for $D_{x_{+1}}$ back to $A$ we have to take into account the gametes received from each parent, $D$, and $U$. Consequently,

$\theta_{AD_{x_{+1}}} = \alpha(\theta_{AD_1} + \alpha(\theta - \gamma))2^{-\tau - 1} + (1 - \alpha)(\theta - \gamma)2^{-\tau - 1} + (2 - \alpha)\gamma2^{-\tau - 1}$.

This transition equation is for $\tau > 1$. When $\tau = 1$, the ancestor and descendet are parent and offspring for which $\theta_{AD_1} = \alpha(1 + \theta)2^{-2} + (1 - \alpha)(\theta + \gamma)2^{-1}$. With this initial condition a solution is found,

$\theta_{AD_2} = \alpha(1 - \theta + \Delta)2^{-1} + \alpha(\theta - \gamma)2^{-\tau - 1}$.

The transition equation for $\gamma_{AD_2}$ follows the same pattern,

$\gamma_{AD_2} = \alpha(\gamma_{AD_1} + \gamma_{AD_2})2^{-2} + (1 - \alpha)(\theta + \gamma)2^{-1} + (2 - \alpha)\gamma2^{-\tau - 1}$.

This initial value for ancestor and offspring is $\gamma_{AD_1} = (1 - \alpha)(1 + \theta + 2\Delta)2^{-2} + (1 - \alpha)(\theta + \gamma)2^{-1}$, which leads to the solution,

$\gamma_{AD_2} = \alpha(1 - \alpha)2^{-2} + (1 - \alpha)(\theta + \gamma)2^{-1} + (2 - \alpha)\gamma2^{-\tau - 1}$.

Finally, $\Delta_{AD_2} = (\gamma - \Delta)2^{-2} + \Delta$ completes the list of descent measures for evaluating the covariances.

It is the covariance between the ancestor and its descendants that relates to permanency of response to selection. Each ancestor has 2 descendents in the $n$th generation. It is the cumulative covariance that is conserved. We define the additive variance, $\sigma_{\theta A}^2$, for the ancestors to be

$\sigma_{\theta A}^2 = 2\epsilon_{\theta AD}$, as $\tau \to \infty$. 

After making the appropriate substitutions we find
\[ 2\nu_{AD} = \sigma_{\theta}^2 + 2 - \alpha - 1[1 - 2\theta - 2\gamma + 3\Delta - \lambda(\theta - \Delta)]\sigma_{\theta}^2, \]
and except for the trivial condition of \( \alpha = 1 \),
\[ \sigma_{\theta}^2 = (1 - \theta)\sigma_{\theta}^2 + 2(\theta - \gamma - 2\Delta + 2\delta)\sigma_{\theta}^2 + 4(\theta - \gamma)d_1 \]
\[ + 2(\gamma - \delta)d_1^2 + 2(\gamma - \Delta)h_2 + 2(\gamma - \Delta)hh' + 4(\theta - \Delta)\sigma_{\theta}^2. \]

In any infinite equilibrium population with continued random mating \( 2\nu_{AD} = \sigma_{\theta}^2 + 2 - \alpha - 1\sigma_{\theta}^2 \), where \( \sigma_{\theta}^2 \) and \( \sigma_{\theta}^2 \) are defined for that population (2). Consequently, \( \sigma_{\theta}^2 = (1 - 2\theta - 2\gamma + 3\Delta - \lambda(\theta - \Delta))\sigma_{\theta}^2 \) as the \( a+a \) variance within ancestral populations corresponds to \( \sigma_{\theta}^2 \) in an infinite equilibrium population. With complete linkage, \( \lambda = 1 \) and \( \alpha = 1 \), all of \( 2\nu_{AD} \), is additive variance, and the remainder of the variance involving dominance and \( a+a \) effects behaves as dominance variance representing interactions of gametes.

The covariance between ancestor and offspring is
\[ \nu_{AD} = \frac{1}{2}\sigma_{\theta}^2 + \frac{1}{4}\sigma_{\theta}^2, \]
where the coefficients 1/2 and 1/4 are those for parent and offspring in an infinite equilibrium population but are for \( \sigma_{\theta}^2 \) and \( \sigma_{\theta}^2 \) in that population.

To facilitate the analysis, we have assumed an expanded ancestral population with a finite history. Thus, we have actually investigated the potential permanency of response to selection within finite populations that are expanded. Nevertheless, several important features are clarified.

We have substantiated that various dominance components defined for the initial equilibrium population contribute in part to the additive variance in finite populations as indicated by half- and full-sib covariances (6). We have substantiated that \( a+a \) effects defined for the initial population contribute to the additive variance within populations as found by Goodnight (9) and have quantified in terms of descent measures the amount. With these new definitions of variances, selection response is formulated the same as for an infinite equilibrium population. For selection among ancestors the only difference between intermediate and permanent response involves epistasis, \( a+a \) variance in our case.

Only a cursory evaluation of the contents of \( \sigma_{\theta}^2 \) will be made. For this purpose we note that \( \theta \approx \gamma \approx \Delta \approx \delta \) and \( \theta \approx \gamma \approx \Delta \approx \theta' \). Consequently, all coefficients of the components are positive. The components are all positive, except for \( d_1 \), which is a covariance between additive and homozygous dominance effects and can be negative and \( 2hh' \), which can be negative. The sum of \( 2hh' \) over all pairs of loci is \( (\Sigma h)^2 - \Sigma h^2 \) and is not apt to be negative, and its coefficient \( 2(\gamma - \Delta) \) is always very small (6). There is a loss in additive variance with a coefficient of \( 1 - \theta \), but a gain due to \( a+a \) variance with an approximate coefficient of \( 4\theta(1 - \theta) \). Other approximations for the first few generations in finite populations with \( \theta \) small are \( \gamma \approx \Delta \approx \gamma \approx \theta' \) and \( \delta \approx \theta' \), so that important determinants of \( \sigma_{\theta}^2 \) involve \( \sigma_{\theta}^2 \), \( d_1 \), and \( \sigma_{\theta}^2 \). These and the other components are determined by gene frequencies and the genetic model in the initial population.

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