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Response to Selection Under Non-Random Mating
II. Prediction

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Summary

A general expression for response to selection appropriate for both random and non-random mating situations is derived and illustrated with full-sibbing.

Key words: Response to selection; Non-random mating; Transmittability coefficient.

1. Introduction

In the earlier paper MURALIDHARAN and JAIN (1991) described the characterization of genotypic value for any breeding population in terms of transmittable and residual genetic values and the break-up of genetic variance into redefined components. This paper develops the general theory for predicting response to selection utilising these concepts.

2. Theory

Consider an arbitrary "foundation" population $P_{11}A_1A_1+2P_{12}A_1A_2+P_{22}A_2A_2$, with values of three genotypes as a, d and $-a$ and gene frequencies of A_1 and A_2 as p and q respectively. Denoting $(P_{11}P_{22}-P_{12}^2)/pq$ by λ, the index measuring the deviation of actual from the Hardy-Weinberg equilibrium genotypic frequencies, the genotypic array of the foundation population becomes $(p^2+\lambda pq)\ A_1A_1+2pq(1-\lambda)\ A_1A_2+(q^2+\lambda pq)\ A_2A_2$.

Let selection be made in the foundation population with phenotypic selection differential S. The immediate effect of selection is that it causes a change in gene frequency (Δp), which is proportional to the average excess of A_1 allele substitution, $e_{(\lambda)}$ (FALCONER, 1985):

$$\Delta p = pq e_{(\lambda)} S/\sigma_P^2 \tag{1}$$

where σ_P^2 is the phenotypic variance of the quantitative character.

By specifying the mating system by the coefficient, δ of deviation from random mating as proposed by JACQUARD (1975) the progeny mean of the selected parents, m_1 is

$$m_1 = (p-q)\,a + 2pq(1-\delta)\,d + 2[a + (1-\delta)\,(q-p)\,d]\,\Delta p$$

obtained by replacing p and q by $p+\Delta p$ and $q-\Delta p$ in Eq. (2) of the earlier paper (MURALIDHARAN and JAIN, 1991). The contribution of terms involving $(\Delta p)^2$ is assumed negligible. Also note that the progeny mean in the absence of selection is

$$m_1^* = (p-q)\,a + 2pq(1-\delta)\,d.$$

The response to selection, R is then $m_1 - m_1^*$:

$$R = 2[a + (1-\delta)\,(q-p)\,d]\,\Delta p.$$

Expressing

$$a + (1-\delta)\,(q-p)\,d = \left[a + \frac{1-\delta}{1+\delta}\,(q-p)\,d\right] + (1-\delta)\left[1 - \frac{1}{1+\delta}\right](q-p)\,d$$

$$= \frac{e_{(\delta)}}{1+\delta} + \delta\left[\frac{1-\delta}{1+\delta}\right](q-p)\,d\,\Delta p$$

we write, response to selection, after substituting for Δp from (1) as

$$R = \frac{2pq e_{(\lambda)}\, e_{(\delta)}\, S}{(1+\delta)\,\sigma_P^2} + 2\delta\left[\frac{1-\delta}{1+\delta}\right](q-p)\,d\,\Delta p$$

where $e_{(\delta)} = (1+\delta)\,a + (1-\delta)\,(q-p)\,d$ is the "expected average excess" of A_1 allele substitution.

Since from Eq. (9) of MURALIDHARAN and JAIN (1991), the regression of offspring on parent is

$$b_{OP} = \frac{\mathrm{Cov}(O, P)}{\sigma_P^2} = \frac{pq e_{(\lambda)}\, e_{(\delta)}}{\sigma_P^2} = \frac{\sigma_t^2 + \sigma_{tu}}{\sigma_P^2}$$

we get

$$R = \frac{2}{1+\delta}\, b_{OP}\, S + 2\delta\left[\frac{1-\delta}{1+\delta}\right](q-p)\,d\,\Delta p$$

Only the term involving "b_{OP}" is predictable in this equation. The contribution of the other term is expected to be negligible as it involves quantities of small magnitude and furthermore, d, on summing over all loci may also be ngligible. Thus for all practical purposes, we write response to selection as

$$R=\frac{2}{1+\delta} b_{OP} S \tag{2}$$

When the matings are at random (i.e. $\delta=0$), for an equilibrium population, the expression for response to selection reduces to the well known expression

$$R=2 b_{OP} S=2(\tfrac{1}{2}) h^2 S=h^2 S$$

where h^2 is the coefficient of heritability.

We note that b_{OP} in Eq. (2) is the ratio of the redefined components of variance $(\sigma_t^2+\sigma_{tu})$ to σ_P^2, that is the regression of transmittable genetic values on phenotypic values. Hence it may be referred to as the "transmittability coefficient". For a random mating population, transmittability coefficient reduces to half the heritability coefficient.

The response to selection will not be constant from generation to generation in a non-random mating population. Since the response depends on transmittability coefficient and the coefficient of deviation from random mating, the response in later generations can be predicted by determining these quantities in each generation.

3. Response in Successive Generations

We specify the non-random matings in the foundation population by δ_0 and the matings in the successive generations by δ_1, δ_2, etc. The transmittability coefficient corresponding to the matings in the $(t-1)$th generation is denoted by $b_{t,t-1}$. Further, for simplicity we denote $e_{(t)}$ for $e_{(\delta_t)}$ $t=0, 1, 2$, etc. and $e_{(t)}/(1+\delta_t)$ by $\alpha_{(t)}$.

The response to selection in generation t is then

$$R_{(t)}=\frac{2}{1+\delta_{t-1}} b_{t,t-1} S \tag{3}$$

For predicting $R_{(t)}$, the value of $b_{t,t-1}$ has to be known which can be obtained from its value in the preceding generation by the following approximate relationship. Considering

$$\frac{1-\delta_t}{1+\delta_t}=\frac{1-\delta_{t-1}-(\delta_t-\delta_{t-1})}{1+\delta_{t-1}+(\delta_t-\delta_{t-1})}=\frac{1-\delta_{t-1}-(\delta_t-\delta_{t-1})}{(1+\delta_{t-1})\,[1+(\delta_t-\delta_{t-1})/(1+\delta_{t-1})]}$$

we can write

$$\alpha_{(t)}=a+\frac{1-\delta_t}{1+\delta_t}(q-p)\,d=a+\frac{1-\delta_{t-1}}{1+\delta_{t-1}}(q-p)\,d=\alpha_{(t-1)}$$

assuming of course that the contribution of terms involving $(\delta_t - \delta_{t-1})/(1+\delta_{t-1})$ and d is negligible. Hence $e_{(t)}$ can be approximated as

$$e_{(t)} = (1+\delta_t)\,\alpha_{(t)} = [(1+\delta_t)/(1+\delta_{t-1})]\,e_{(t-1)}$$

Hence,

$$\frac{b_{t,t-1}}{b_{t-1,t-2}} = \frac{pq e_{(t-1)}\, e_{(t-2)}}{pq e_{(t-2)}\, e_{(t-3)}} = \frac{e_{(t-1)}}{e_{(t-3)}} = \frac{1+\delta_{t-1}}{1+\delta_{t-3}}$$

or

$$b_{t,t-1} = \frac{1+\delta_{t-1}}{1+\delta_{t-3}}\, b_{t-1,t-2}, \quad t>2 \tag{4a}$$

and

$$b_{2,1} = \frac{1+\delta_0}{1+\lambda}\, b_{1,0} \tag{4b}$$

which is the required recurrence relation between the transmittability coefficients. This can be used in predicting response to selection in successive generations.

An alternative form of expression (3) for response to selection obtained by using (4) recursively is

$$R_{(t)} = \frac{2(1+\delta_{t-2})}{(1+\delta_0)\,(1+\lambda)} \quad b_{1,0}\, S, \quad t \geqq 2 \tag{5}$$

This form is suitable for predicting response to selection in generation t, directly from the initial values of the parameters.

4. Illustration

Consider a selection experiment for abdominal bristle number in *Drosophila melanogaster* in which the matings are restricted between full-sibs. The parents are selected from a random mating population for higher bristle numbers with selection differential $S = 5.3$ bristles. To predict the response to this selection in successive generations, we first need to know the appropriate value of $b_{1,0}$. When there is no dominance, epistasis and environmental effect, the correlation between offspring and parent is

$$r_{1,0} = 2 f_{1,0} / [(1+f_1)\,(1+f_0)]^{1/2}, \quad \text{where } f_{1,0} = 3/8$$

is the coefficient of kinship between offspring and parent; and $f_1 = 1/4$ and $f_0 = 0$ are the coefficients of consanguinity of the offspring and the parent respectively so that $r_{1,0} = 0.6708$. Also covariance between offspring and parent, $C_{1,0}$ is

$$C_{1,0} = r_{1,0}\,[(1+f_1)\,(1+f_0)]^{1/2}\,\sigma_a^2 = 0.75\,\sigma_a^2$$

where σ_a^2 is the additive genetic variance defined for the random mating population. Hence $b_{1,0}$ can be approximated as

$$b_{1,0} = C_{1,0}/\sigma_p^2 = (.75)\,h^2$$

where h^2 is the heritability in the initial random mating population. For $h^2 = 0.5$ the predicted response to selection in successive generations of full-sibbing are as in Table 1.

Table 1

Response to selection in successive generations of full-sibbing

Generation (t)	δ_{t-1}	Expected response
1	1/4	3.18
2	3/8	4.37
3	8/16	4.77
4	19/32	5.07
5	43/64	5.32

The predicted response under full-sibbing is higher than the corresponding value of 2.65 obtained under random mating. Further the response increases from generation to generation. This is expected as the regression of offspring on parent increases with inbreeding.

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