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Gene Flow Technique for Response to Selection under Non-Random Mating

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Summary

The gene flow technique for predicting response to selection in random mating populations with overlapping generations is extended to cover any system of mating and illustrated with full-sibbing.

Key words: Response to selection; Non-random mating; Gene flow technique.

1. Introduction

HILL (1974) presented a formal method for predicting response to selection in random mating populations with overlapping generations, which is popularly known as the gene flow technique. The matings are however, not at random in many of the populations. The gene flow technique is therefore extended in this paper to incorporate non-random matings. The theory so developed has been illustrated with respect to a full-sib mating system. This, inter alia, included extending the concepts of average coefficient of consanguinity and kinship to age-structured populations.

2. The Gene Flow Technique

Consider a population that has attained a constant age structure in which males are retained for u years (or breeding seasons) and females for v years. The population then has $u+v$ sex-age classes. Both males and females are used for breeding for the first time when they are one year old so that they are expected to have their first progeny at the age of 2 years. The population is assumed sufficiently large so that the effects of genetic drift are negligible.

Let us denote the proportion of genes in individuals of sex-age class i at time t coming from individuals of sex-age class j at time $t-1$ by p_{ij} ($i, j = 1, 2, \ldots, u+v$). The matrix $P = (p_{ij})$ then describes the flow of genes between different classes of individuals in successive time periods. The elements of first and $(u+1)^{\text{th}}$ rows of P describe the passage of genes by reproduction. The off-diagonal elements, $p_{i,i-1}$; $i \neq 1, u+1$, of unity exhibit the passage of genes due to ageing. Also for $i \neq 1, u+1$ and $j \neq i-1$, $p_{ij}=0$.

In analogy to the concepts of breeding value and heritability coefficient defined for random mating populations we use the more general terms viz. "transmittable genetic value" and "transmittability coefficient" respectively which are tenable for any system of mating (MURALIDHARAN and JAIN, 1992a, b). We let

$$\tau(t)=(\tau_1(t), \tau_2(t), \ldots, \tau_{u+v}(t))'$$

be the vector of average transmittable genetic values of individuals of different sex-age classes at time t; if no individual of a particular class is a potential parent at time t, the average transmittable value of that group will be zero. (We take τ in place of t used in the earlier cited papers to avoid confusion with time);

$$B(t)=\operatorname{diag}(\beta_1(t), \beta_2(t), \ldots, \beta_{u+v}(t))$$

be the diagonal matrix of transmittability coefficients; if individuals of class j are non-reproductive at time t, $\beta_j(t)$, the regression of transmittable genetic values of the parents belong to the sex-age class j at time t on their phenotypic values, will be zero; and

$$y(t)=(y_1(t), y_2(t), \ldots, y_{u+v}(t))'$$

be the vector of mean phenotypic values of the quantitative character in different sex-age classes at time t.

From the definition of transmittable genetic values we have

$$\tau(t)=B(t)\, y(t).$$

Clearly, the expected phenotypic value of one year old males at time $t+1$ will be given by

$$y_1(t+1)=\sum_{j=1}^{u+v} p_{1j}\tau_j(t). \tag{1a}$$

Likewise the expected phenotypic value of one year old females at time $t+1$ is

$$y_{u+1}(t+1)=\sum_{j=1}^{u+v} p_{u+1,j}\tau_j(t). \tag{1b}$$

These two equations relate the performance of the progeny aged one year old at time $t+1$ to the performance of their parents.

Now assume that selection is practiced in the population at time $t=0$ and the vector of mean phenotypic values after selection is

$$y^*(t)=y(0)+s(0)$$

where $y(0)$ is the vector of mean phenotypic values for the unselected population, and $s(0)=(s_1(0), \ldots, s_{u+v}(0))'$ is the vector of the phenotypic selection differentials.

The response to selection (R) under non-random mating in populations with discrete generations is

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

where b_{OP} is the transmittability coefficient, δ is the coefficient of deviation from random mating and S is the phenotypic selection differential (MURALIDHARAN and JAIN, 1992b). In order to extend this result for a population with overlapping generations, we introduce the following matrix

$$B^*(t)=\operatorname{diag}(\beta_1^*(t), \ldots, \beta_{u+v}^*(t))$$

where

$$\beta_j^*(t)=2\,\beta_j(t)/(1+\delta_j(t)); \qquad j=1, \ldots, u+v$$

and $\delta_j(t)$ is the coefficient of deviation from random mating, defined for the parents belonging to the class j at time t. It thus follows that the increments in transmittable values due to selection at time $t=0$ is given by

$$\tau^*(0)=B^*(0)\, s(0).$$

The increments in the expected performance of the descendents of these selected individuals at time $t=1$ can be obtained by an application of Eqs. (1); which also correspond to the effect of selection from the reproduction of selected group of individuals. Thus the response vector at time $t=1$ will be given by

$$\begin{aligned} r(1) &= (P-Q)\,\tau^*(0) \\ &= (P-Q)\,B^*(0)\,s(0) \end{aligned} \tag{2a}$$

where matrix Q has the same form as that of P with the first and $(u+1)$th rows set to zeroes; Q specifies the passage of genes due to ageing alone.

Let us consider the potential parents at time $t=1$. Their transmittability coefficients are given by the elements $B(1)$. Since the increments in transmittable genetic values at time $t=1$ (i.e. $\tau^*(1)$) are directly related to the proportion of genes in these individuals from the selected group of individuals and the phenotypic selection differential $s(0)$, we have

$$\tau^*(1)=B^*(1)\,P s(0).$$

Thus the effect of selection that will be observed in the young ones (that is one year old males and females) at time $t=2$ is

$$(P-Q)\,\tau^*(1)=(P-Q)\,B^*(1)\,P s(0).$$

The response vector at time $t=2$ is then

$$r(2)=(P-Q)\,B^*(1)\,P s(0)+Q r(1).$$

As the proportion of genes in individuals at time $t-1$ coming from the individuals at time $t=0$ is given by the elements of P^{t-1}, the increments in transmittable genetic values will be given by

$$\tau^*(t-1)=B^*(t-1)\,P^{t-1}s(0).$$

Hence the response vector at time t will be given by

$$r(t)=(P-Q)\,B^*(t-1)\,P^{t-1}s(0)+Q r(t-1), \qquad t>1. \tag{2b}$$

This then is the fundamental recurrence relation for response to selection in populations where the matings are nonrandom and generations overlap. The corresponding expression for random mating situation is obtained from Eqs. (2) by taking $B^*(t)$ equal to $h^2 I_0$, where h^2 is the heritability coefficient and I_0 is a diagonal matrix of order $u+v$ having elements as unities in positions corresponding to the non-zero elements of $B^*(t)$. Thus under random mating situation

$$\begin{aligned} r(1)&=(P-Q)\,h^2 I_0\, s(0)\\ &=(P-Q)\,g;\\ r(2)&=(P-Q)\,h^2 I_0\, P s(0)+Q r(1)\\ &=(P^2-QP)\,g+(QP-Q^2)\,g\\ &=(P^2-Q^2)\,g; \end{aligned}$$

and so on; where $g=h^2 s(0)$ is the vector of genetic selection differentials corresponding to the one cycle of selection at $t=0$.

Under repeated selection the response at time t will be obtained by summing the responses due to selection in each time period prior to t. Thus the cumulative response at time t will be given by

$$r_c(t)=\sum_{j=1}^{t} r_j(t) \tag{3}$$

in which $r_j(t)$ is the response at time t, due to selection at time $t-j$.

3. Illustration: Response to Selection Under Full-sibbing

Consider a breeding population of pigs in which boars and sows are used for two mating seasons, having progeny born when they are at 12 and 18 months old. The matings are only between full-sibs of the same age. The unit of time is taken as 6 months so that $u=v=3$. We assume that among the new-borns at time t, a fraction P_2 have parents aged 2 time units, and $P_3=1-P_2$ have parents aged 3 time units at time t. The P and Q matrices for this breeding population are then

$$P=\begin{bmatrix} 0 & \frac{1}{2}P_2 & \frac{1}{2}P_3 & 0 & \frac{1}{2}P_2 & \frac{1}{2}P_3 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ & & & & & \\ 0 & \frac{1}{2}P_2 & \frac{1}{2}P_3 & 0 & \frac{1}{2}P_2 & \frac{1}{2}P_3 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \end{bmatrix}, \quad Q=\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ & & & & & \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \end{bmatrix}.$$

For translating the foregoing system of matings in terms of coefficient of deviation from random mating, we extend the notions of average coefficients of consanguinity and kinship to include age structure.

The average coefficient of consanguinity $f(i, t)$, of individuals in class i at time t is the probability that alleles of a randomly chosen individual of that class are identical by descent. These coefficients will be represented by a vector $f(t)$. The following relations are valid for the present example:

$$f(j, t)=f(3+j, t), \qquad j=1, 2 \text{ and } 3; \tag{4a}$$

and

$$f(j, t)=f(j-1, t-1), \qquad j\neq 1, 4. \tag{4b}$$

For relating $f(1, t)$ to the previous time period, we will make use of the fact that the coefficient of consanguinity of an individual is equal to the coefficient of kinship of its parents. Among one unit old males at time t, a fraction P_2 of them were having their male parents in class 2 at time $t-1$; their female parents were in class 5. Because of overlapping generations the degree of kinship relation between these parents may not be unique. Therefore, with respect to 2-time unit old male parents, conceptually, the 2 unit old female parents can be split in groups, each (group) having a specific degree of relationship. The weighted average of the corresponding kinship coefficients (weights being the frequency of each group) is then the average coefficient of parentage $\varphi(2, t-1)$ associated with the sex-age class 2 at time $t-1$. Thus the probability that the paternal gene of a randomly selected individual of one time unit old at time t (who belong to the fraction P_2 of the whole group) is identical with the maternal gene is $\varphi(2, t-1)$. Similar coefficients $\varphi(i, t-1)$, may be defined for the sex-age classes $i=3$, 5 and 6 at time $t-1$.

From the foregoing, the probability that the homologous genes of a randomly chosen individual of age class 1 at time t are identical by descent is given by

$$f(1, t)=\frac{P_2}{2}\varphi(2, t-1)+\frac{P_3}{2}\varphi(3, t-1)+\frac{P_2}{2}\varphi(5, t-1)+\frac{P_3}{2}\varphi(6, t-1). \quad (4c)$$

Likewise, the expression for $f(4, t)$ may be obtained which is equal to $f(1, t)$ in our example.

The average coefficients of parentage associated with the classes 1 and 4 at time $t-1$ can be defined based on the possible matings at that time. These coefficients are represented by the vector $\varphi(t-1)$, with $\varphi(i, t-1)$, $i=1, \ldots, 6$, as its components. Now Eqs. (4) can be combined into a single expression as follows:

$$f(t)=(P-Q)\,\varphi(t-1)+Q\,f(t-1). \quad (5)$$

The computation of average coefficient of parentage as a weighted mean would be a stupendous task. This difficulty can be overcome by a simple but realistic assumption that the mating frequencies are in proportion to the frequencies of the prevailing degrees of kinship relations. This assumption, for the pig example, implies that

$$\varphi(2, t)=\varphi(1, t-1);\ \varphi(3, t)=\varphi(2, t-1)=\varphi(1, t-2), \text{ etc.} \quad (6a)$$

The average coefficient of parentage of class 1 at time t is obtained as follows. As $\varphi(1, t)$ is the probability that two homologous genes sampled, one from an individual of class 1 and another from one of its possible mates belong to class 4, are identical by descent,

$$\begin{aligned}\varphi(1, t)=&\frac{1}{4}\left\{\frac{1}{2}P_2[1+f(2, t-1)]+\frac{1}{2}P_3[1+f(3, t-1)]\right\}\\ &+\frac{1}{4}\left\{\frac{1}{2}P_2[1+f(5, t-1)]+\frac{1}{2}P_3[1+f(6, t-1)]\right\}\\ &+\frac{1}{2}\left\{\frac{1}{2}P_2[\varphi(2, t-1)+\varphi(5, t-1)]+\frac{1}{2}P_3[\varphi(3, t-1)+\varphi(6, t-1)]\right\} \quad (6b)\end{aligned}$$

in which the quantities within the flowery brackets are the conditional probabilities of identity of the sampled homologous genes given that, in order, both are of paternal origin; both are of maternal origin and one is of paternal and the other of maternal origin.

The Eqs. (6) may be represented more succinctly in matrix form as

$$\varphi(t)=\frac{1}{4}\,J_{1,4}+\frac{1}{4}\,(P-Q)\,f(t-1)+\frac{1}{2}\,(P+Q)\,\varphi(t-1) \tag{7}$$

in which

$$J_{1,4}=(1,0,0,1,0,0)'.$$

In our example, since the foundation stock consists of sets of full-sibs of different ages that are derived from a random mating population, $\varphi(0)=\frac{1}{4}1$ and $f(0)=0$ where 1 and 0 are respectively unit and null vectors of order 6. The values of $f(t)$ and $\varphi(t)$, $t\geqq 1$, can then be obtained by making use of relations (5) and (7).

Now, incurring $\delta_j(t)$, $(j\neq 1, 4)$, on $\varphi(j,t)$, from MURALIDHARAN and JAIN (1992b), the transmittability coefficients can be approximated as

$$\beta_j(t)=[1+\varphi(j,t)]\,[1+f(j,t)]\,b, \qquad j\neq 1,4;\ t\geqq 1$$

and hence

$$\beta_j^*(t)=2\,[1+f(j,t)]\,b, \qquad j\neq 1,4;\ t\geqq 1 \tag{8}$$

where b is initial estimate of the transmittability coefficient.

4. Numerical Results

As a numerical example we consider the situation where $P_2=P_3=\frac{1}{2}$. Let us assume that a single selection is practised for live-weight gain among one time unit old males and females at time $t=0$ with phenotypic selection differential in males as 125 gm/day and in females as 87.5 gm/day. Then the vector $s(0)$ becomes

$$s(0)=(125,0,0,87.5,0,0)'.$$

We will take the initial value of transmittability coefficient, b as 0.2.

Now we detail the computation of $r(t)$ at a specific time $t=6$. The one unit old individuals at $t=6$ were born at $t=5$; the coefficients of deviation from random mating corresponding to their parental classes 2, 3, 5 and 6 are respectively .5, .438, .5 and .438. The vector of average coefficients of consanguinity at time $t=5$ is obtained as

$$f(5)=(.406,.375,.3125,.406,.375,.3125)'.$$

The matrix of transmittability coefficients from Eq. (8) is then

$$B^*(5) = \mathrm{diag}(0, .55, .525, 0, .55, .525).$$

By using Eqs. (2), the response vector at time $t = 6$ is obtained as

$$r(6) = (21.25, 27.23, 13.28, 21.25, 27.23, 13.28)'.$$

In this manner the responses can be worked out for successive time periods. The results are summarized in Table 1. For comparison, the corresponding results under random mating situation are also given in the table. For figuring out the results in the latter situation, heritability coefficient is taken as 0.4; with this value of heritability, the vector of genetic selection differentials becomes

$$g = (50, 0, 0, 35, 0, 0)'.$$

Table 1

Response (live-weight gain, gm/day in individuals of 1 unit old) to one-time selection

Time	Sib-mating	Random mating
1	0.00	0.00
2	21.25	21.25
3	21.25	21.25
4	13.28	10.63
5	27.23	21.25
6	21.25	15.94
7	22.25	15.94
.	.	.
.	.	.
.	.	.
19	30.28	17.01
20	30.51	17.01

It may be observed from Table 1 that in both the situations response to selection exhibits considerable variation from one time period to the next, especially in the early periods. This is because of uneven flow of "selected genes" between the sex-age classes. The response under full-sibbing is more than that under random mating. This is mainly due to the gradual increase in the value of regression coefficient of offspring on parent from generation to generation, resulting from inbreeding. This result, however, should not be considered to mean that "sibbing is preferable over random mating", as no allowance has been made for "inbreeding depression".

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