

ASYMPTOTIC RATES OF RESPONSE FROM INDEX SELECTION

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ABSTRACT

The reduction in additive genetic variance due to selection is investigated when index selection using family records is practised. A population of infinite size with no accumulation of inbreeding, an infinitesimal model and discrete generations are assumed. After several generations of selection, the additive genetic variance and the rate of response to selection reach an asymptote. A prediction of the asymptotic rate of response is considered to be more appropriate for comparing response from alternative breeding programmes and for comparing predicted and realized response than the response following the first generation of selection that is classically used. Algorithms to calculate asymptotic response rate are presented for selection based on indices which include some or all of the records of an individual, its full- and half-sibs and its parental estimated breeding values. An index using all this information is used to predict response when selection is based on breeding values estimated by using a Best Linear Unbiased Prediction (BLUP) animal model, and predictions agree well with simulation results. The predictions are extended to multiple trait selection.

Asymptotic responses are compared with one-generation responses for a variety of alternative breeding schemes differing in population structure, selection intensity and heritability of the trait. Asymptotic responses can be up to one-quarter less than one-generation responses, the difference increasing with selection intensity and accuracy of the index. Between family variance is reduced considerably by selection, perhaps to less than half its original value, so selection indices which do not account for this tend to place too much emphasis on family information. Asymptotic rates of response to selection, using indices including family information for traits not measurable on the individuals available for selection, such as sex limited or post-slaughter traits, are found to be as much as two-fifths less than their expected one-generation responses. Despite this, the ranking of the breeding schemes is not greatly altered when compared by one-generation rather than asymptotic responses, so the one-generation prediction is usually likely to be adequate for determining optimum breeding structure.

INTRODUCTION

THE reduction of additive genetic variance between families in a population subsequent to selection is well recognized. In the first generation of selection, gametic phase disequilibrium is induced which causes a reduction in additive genetic variance in the selected population (Bulmer, 1971). In subsequent generations, some of the existing disequilibrium is broken down by recombination whilst new disequilibrium is induced by the new selection. In terms of between- and within-family variance, selection reduces the variance between families but in each generation this is partially recovered by

recombination expressed by the within-family variance. The genetic variance is reduced most after the first generation of selection but continues to decline for several generations until an equilibrium is achieved. Similarly, the rate of response to selection is greatest initially and reaches an asymptotic rate after several generations in an infinite population.

Prediction of the asymptotic response is straightforward when phenotypic selection is practised (Bulmer, 1971; Falconer, 1981). However, in the animal breeding context, selection of an individual is often based on an index combining records collected on the individual and its relatives. Under index

selection the additive genetic variance and response per generation will also reach an asymptote but the way in which this is achieved has not been closely examined. Under selection using estimated breeding values from Best Linear Unbiased Prediction (BLUP), predictions of response to selection have only been possible by simulation. This paper presents a method to predict rates of response from selection under an animal model using a selection index which includes records from the individual, its full- and half-sibs and the estimated breeding values of its sire, dam and all dams mated to its sire.

Predicted rate of response to selection is a criterion used to compare alternative breeding schemes differing in population structure, selection intensities and types of relatives' records included in an index. Such comparisons are usually based on the response expected after one round of selection (e.g. Land and Hill, 1975; Nicholas and Smith, 1983; Avalos and Smith, 1987). This paper presents algorithms for finding asymptotic rates of response when index selection is used and the implications are discussed of using only the response rates computed for the first generation in the comparison of breeding schemes.

METHODS

Assumptions

The trait under selection is assumed to be controlled by genes at many unlinked loci, each of small additive effect — the infinitesimal model. Important assumptions, which are discussed later, are that the distribution of the selection criterion is normal even after several generations of selection, that the population is of infinite size and that inbreeding does not accumulate (inbreeding is discussed later). A nested mating structure and random mating of selected animals are assumed and generations are discrete.

Theory

Let $\sigma_{A_t}^2$ be the total additive genetic variance of a trait in a given population at time t . $\sigma_{A_t}^2$ can be partitioned into between ($\sigma_{AB_t}^2$) and within ($\sigma_{AW_t}^2$) family components.

In the base population, before selection has taken place at generation $t = 0$, $\sigma_{AB_0}^2 = \sigma_{AW_0}^2 = \frac{1}{2}\sigma_{A_0}^2$. When selection is practised, the between-family variance is reduced each round of selection by a factor $k\rho_{t-1}^2$ (Pearson, 1903, where ρ_{t-1} is the accuracy of selection in generation $t - 1$, and $k = i(i - x)$ where i is the selection intensity and x is the standardized deviation of the truncation point from the mean:

$$\sigma_{AB_t}^2 = \frac{1}{2}(1 - k\rho_{t-1}^2)\sigma_{AB_{t-1}}^2.$$

The within-family variance is not affected by selection and remains at $\sigma_{AW_t}^2 = \frac{1}{2}\sigma_{A_0}^2$ (Bulmer, 1971). Response to selection in generation t , R_t , is calculated as: $R_t = i\rho_t\sigma_{A_t}$. For mass selection ρ_t is simply h_t where h_t^2 is the heritability of the trait in generation t .

For index selection using half-sib records it is necessary to consider a further partitioning of the between family variance into between sire family ($\sigma_{AS_t}^2$) and between dam family ($\sigma_{AD_t}^2$) variances, such that $\sigma_{AS_0}^2 = \sigma_{AD_0}^2 = \frac{1}{4}\sigma_{A_0}^2$,

$$\begin{aligned}\sigma_{AS_t}^2 &= \frac{1}{4}(1 - k_s\rho_{st-1}^2)\sigma_{AS_{t-1}}^2 \\ \text{and } \sigma_{AD_t}^2 &= \frac{1}{4}(1 - k_d\rho_{dt-1}^2)\sigma_{AD_{t-1}}^2,\end{aligned}$$

where k_s and k_d allow for different selection of selection intensities and ρ_s and ρ_d allow for different accuracies of selection of sires and dams. The variance of estimated breeding values for individuals in generation t is $\rho_{st}^2\sigma_{AS_t}^2$ for sires and $\rho_{dt}^2\sigma_{AD_t}^2$ for dams. Truncation selection is imposed directly on the estimated breeding values and these variances are reduced to $(1 - k_s)\rho_{st}^2\sigma_{AS_t}^2$ and $(1 - k_d)\rho_{dt}^2\sigma_{AD_t}^2$ for the selected sires and dams respectively.

The variance attributed to the common environment to full-sibs is σ_C^2 and the individual environmental variance is σ_E^2 . The total phenotypic variance in generation t is, $\sigma_{P_t}^2 = \sigma_{A_t}^2 + \sigma_C^2 + \sigma_E^2$.

The selection indices are set up to estimate the breeding value of an individual (A_i) for a single trait. In the nested mating structure m dams are mated to each sire and each dam has n offspring. Three indices are considered using different amounts of information on relatives.

1. Index IFS using records from the

TABLE 1
Variance-covariance matrix, \mathbf{P}_t and vector \mathbf{G}_t

$$\mathbf{P}_t = \begin{bmatrix} \sigma_{P_t}^2 & \sigma_{A_{St}}^2 + \sigma_{A_{Dt}}^2 + \sigma_C^2 + (\sigma_{A_{Wt}}^2 + \sigma_E^2)/n & \sigma_{A_{St}}^2 + (\sigma_{A_{Dt}}^2 + \sigma_C^2)/m + (\sigma_{A_{Wt}}^2 + \sigma_E^2)/mn & V(\hat{A}_d)/2 & V(\hat{A}_d)/2m & V(\hat{A}_s)/2 \\ \sigma_{A_{St}}^2 + \sigma_{A_{Dt}}^2 + \sigma_C^2 + (\sigma_{A_{Wt}}^2 + \sigma_E^2)/n & \sigma_{A_{St}}^2 + (\sigma_{A_{Dt}}^2 + \sigma_C^2)/m + (\sigma_{A_{Wt}}^2 + \sigma_E^2)/mn & V(\hat{A}_d)/2 & V(\hat{A}_d)/2m & V(\hat{A}_s)/2 \\ \sigma_{A_{St}}^2 + (\sigma_{A_{Dt}}^2 + \sigma_C^2)/m + (\sigma_{A_{Wt}}^2 + \sigma_E^2)/mn & V(\hat{A}_d)/2m & V(\hat{A}_d)/2m & V(\hat{A}_s)/2 \\ & V(\hat{A}_d) & V(\hat{A}_d)m & 0 \\ & & V(\hat{A}_d)m & 0 \\ & & & V(\hat{A}_s) \end{bmatrix}$$

symmetric

$$\mathbf{G}_t' = [\sigma_{A_t}^2 \quad \sigma_{A_{St}}^2 + \sigma_{A_{Dt}}^2 + \sigma_{A_{Wt}}^2/n \quad \sigma_{A_{St}}^2 + \sigma_{A_{Dt}}^2/m + \sigma_{A_{Wt}}^2/mn \quad V(\hat{A}_d)/2 \quad V(\hat{A}_d)/2m \quad V(\hat{A}_s)/2]$$

individual and the mean of n (including its own) full-sib records (X_i, \bar{X}_{fs}).

2. Index IHS using the records in IFS plus the mean of mn (including the n full-sibs) half-sib records ($X_i, \bar{X}_{fs}, \bar{X}_{hs}$).

3. Index ISD using the records in IHS plus the estimated breeding values of the dam, the mean of the estimated breeding value of all dams mated to the sire and the sire ($X_i, \bar{X}_{fs}, \bar{X}_{hs}, \hat{A}_d, \bar{A}_d, \hat{A}_s$). \hat{A}_d, \bar{A}_d and \hat{A}_s are assumed to be estimated from ancestral and collateral records of the dams and sire but not from their progeny (i.e. the sibs of the individual).

In generation t selection indices are set up such that $\mathbf{I}_t = \mathbf{b}_t'$, where \mathbf{b}_t is a vector of weighting factors of linear functions of records contained in vector \mathbf{x}_t . The usual selection index equations are used as $\mathbf{P}_t \mathbf{b}_t = \mathbf{G}_t$, where \mathbf{P}_t is the variance-covariance matrix of \mathbf{x}_t and \mathbf{G}_t is the vector of covariances of \mathbf{x}_t with A_i . With the order of variables as in 3 above \mathbf{P}_t and \mathbf{G}_t are given in Table 1. The \mathbf{P}_t and \mathbf{G}_t matrices must be constructed each generation with $V(\hat{A}_s) = \rho_{S_{t-1}}^2(1-k_s)\sigma_{A_{t-1}}^2$ and $V(\hat{A}_d) = \rho_{D_{t-1}}^2(1-k_d)\sigma_{A_{t-1}}^2$. They are then used to update \mathbf{b}_t and to calculate the variance of the index $\sigma_{I_t}^2$, the accuracy of selection (ρ_t) and the response to selection (R_t).

To facilitate computation, the index could be set up using independent linear functions of the records so that \mathbf{P}_t is diagonal. For example, \mathbf{P}_t for index ISD would have diagonal elements:

$$[V(X_i - \bar{X}_{fs}), V(\bar{X}_{fs} - \bar{X}_{hs} - \hat{A}_d/2 + \hat{A}_d/2), V(\bar{X}_{hs} - \hat{A}_s/2 - \hat{A}_d/2), V(\hat{A}_d/2)]$$

and $\mathbf{G}_t' =$

$$[V(A_i - \bar{A}_{fs}), V(\bar{A}_{fs} - \bar{A}_{hs} - \hat{A}_d/2 + \hat{A}_d/2), V(\bar{A}_{hs} - \hat{A}_s/2 - \hat{A}_d/2), V(\hat{A}_d/2)].$$

Selection index weights in practice are not updated and optimized each generation to account for the change in the genetic parameters. This can easily be incorporated into the algorithm affecting $\sigma_{I_t}^2$ and ρ_{t-1} , but has little effect on the final asymptotic response illustrating the robustness of selection index to incorrect parameters (Sales and Hill, 1976). Index ISD will approximate response from selection using a BLUP animal model (Henderson and Quaas, 1976). In an animal model, information from ancestral and collateral relatives can be included by using the full inverse numerator relationship matrix; however ISD ignores records on cousins and more distant collateral and non-collateral relatives, but these contribute little to accuracy, particularly in populations under selection. Breeding value predictions from BLUP are independent of changes in variance due to selection (Henderson, 1975) and are therefore independent of selection intensity and k . Predictions from index ISD are also independent of k because all previous selection is totally accounted for by inclusion of the predicted parental breeding values (a check is given in the APPENDIX). Thus, index weights are independent of selection intensity in any generation; but in the examples given later, and in practice, selection intensity and family size are confounded, so there appears to be a dependency on selection intensity.

The predictions can be extended to selection using multiple trait information; details are presented in the APPENDIX.

SIMULATION

The predictions of response obtained from the indices presented above were compared with results obtained from simulation.

The simulated population consisted of 10 males each mated randomly to 10 females ($m = 10$), each female having six offspring (three male, three female) ($n = 6$, $i = 1.66$, $k_s = 0.866$, $k_d = 0.714$, $k = 0.790$). Generations were discrete. The record of an individual was simulated as the sum of its breeding value, an environmental effect common to all full-sibs and an individual environmental effect. The breeding value was sampled from a normal distribution with mean $\frac{1}{2}(A_s + A_d)$, the mean parental breeding value, and variance $\frac{1}{2}\sigma_{A_0}^2(1 - \bar{F})$ where \bar{F} is the mean inbreeding coefficient of the parents. The common and individual environmental effects were sampled from normal distributions with means 0 and variances σ_C^2 and σ_E^2 respectively. The total phenotypic variance in the base population was $\sigma_{P_0}^2 = \sigma_{A_0}^2 + \sigma_C^2 + \sigma_E^2 = 100$ with $\sigma_C^2 = 10$ units and a range of initial heritabilities ($\sigma_{A_0}^2/\sigma_{P_0}^2$) was considered: 0.1, 0.2, 0.4, 0.6, 0.8. Each simulation was replicated 100 times.

Four methods of selection were used, phenotypic selection, an index of individual and full-sibs records, an index of individual, full- and half-sib records and BLUP using a reduced animal model (Quaas and Pollak, 1980). The last three methods correspond to the predictions using indices IFS, IHS, ISD. Since no fixed effects were included, the BLUP here is strictly the most accurate selection index utilizing all the available information to optimize continuously the selection index weights.

Results are presented for response after at least six generations of selection, by which time the reduction in between-family variance as a consequence of selection is close to the asymptote. However, the simulation is of a finite population in which inbreeding accumulates, F_t being the mean inbreeding coefficient of individuals born in generation t . The inbreeding will also reduce the additive genetic variance, such that the within-family variance in generation t is $\sigma_{Aw_t}^2 = (1 -$

TABLE 2
Simulated† and predicted asymptotic rates of response per generation to selection for a population of 10 sires and 100 dams ($m = 10$) with six offspring per dam ($n = 6$)

	Adjusted heritability				
	0.075	0.160	0.350	0.550	0.765
Phenotypic selection					
Generation‡	20.3	15.3	11.3	10.3	10.5
Simulated response (units)	1.12	2.31	4.61	6.77	8.96
Predicted response	1.16	2.34	4.66	6.79	8.89
Predicted initial response	1.23	2.59	5.58	8.60	11.72
Individual and full-sib index, IFS					
Generation‡	13.0	10.5	8.7	9.0	10.5
Simulated response (units)	1.28	2.51	4.68	6.76	8.91
Predicted response	1.34	2.55	4.76	6.80	8.92
Predicted initial response	1.48	2.99	5.97	8.79	11.72
Individual, full- and half-sib index, IHS					
Generation‡	8.0	7.3	6.7	8.0	9.7
Simulated response (units)	1.49	2.79	4.82	6.79	8.98
Predicted response	1.62	2.84	4.97	6.90	8.97
Predicted initial response	1.90	3.48	6.34	9.00	11.82
BLUP, ISD					
Generation‡	6.5	6.3	6.5	8.0	9.7
Simulated response (units)	1.63	2.98	4.86	6.87	8.98
Predicted response	1.67	2.89	5.02	6.96	9.02
Predicted initial response	2.01	3.65	6.59	9.27	12.06

† Standard errors of the simulated responses ranged from 0.02 to 0.12 and increased with heritability.

‡ The generation number (t) for which the mean inbreeding coefficient F_t gave the adjusted heritability.

$F_{t-1})\sigma_{Aw_0}^2$, whereas in the infinite population case $\sigma_{Aw_t}^2 = \sigma_{Aw_0}^2$. The heritability of a trait in the base population can be written as $2\sigma_{Aw_0}^2/[2\sigma_{Aw_0}^2 + \sigma_C^2 + \sigma_E^2]$. In a finite population the response to selection depends on the amount of inbreeding that has accumulated, so to verify the results of the prediction by simulation, the effect of the inbreeding must be eliminated. Therefore, the predictions are not based on the initial heritability but one adjusted for inbreeding: $h^2 = [2\sigma_{Aw_0}^2(1 - F_{t-1})]/[2\sigma_{Aw_0}^2(1 - F_{t-1}) + \sigma_C^2 + \sigma_E^2]$. All indices were adjusted to the same heritabilities so that responses are presented after a variable number of generations (t). Linear interpolation of response rate was used when t was not integral.

For the predicted responses selection intensities appropriate for infinite population size were used, as the population was sufficiently large that corrections for finite size and correlations between family members (Hill, 1976 and 1977) had little impact. The same selection criteria were used to select males and females, so $\rho_s = \rho_d = \rho$.

Simulated and predicted responses to selection are presented in Table 2. The simulated responses are substantially less than those expected from the first generation prediction, but they are predicted fairly well by the algorithms which account for the reduction in genetic variance due to selection. The index ISD predicts well the response from BLUP animal model selection, even at low heritabilities. After selection the between-family variance is no longer distributed normally, but the within-family and environmental components maintain normality throughout. The overall departures from normality are small so that the prediction algorithms, which assume normality, approximate well the simulation results. The different number of generations of selection needed to achieve the adjusted heritabilities reflects the differences in rates of inbreeding induced by the selection methods.

COMPARISON OF BREEDING SCHEMES

In the literature there are numerous examples of comparisons among breeding

schemes using rates of response from the first round of selection. For example, Land and Hill (1975) investigated the response expected from introducing a superovulation scheme into a beef cattle performance testing programme. This is an interesting example to discuss as it considers a range of mating ratios (m) and offspring per donor (n) and therefore also a range of k_s , k_d , k and i ; all the alternatives of Land and Hill (1975) were considered but only a sample will be presented here. The trait under selection was live weight at 13 months with a heritability assumed to be 0.5 and phenotypic standard deviation of 40 kg. Land and Hill (1975) presented annual selection intensities (i/L , $L = 2$) as this is proportional to response after one round of selection. However, asymptotic responses to selection are no longer proportional to i/L so absolute responses in kg are given. Table 3 presents responses expected from one round of selection and the proportion of that response predicted by the asymptotic rate. For this trait asymptotic rates of response are as much as proportionately 0.26 less than the one-generation response rates. The reductions are greatest when family sizes are large because of the higher accuracy of selection and, for indices other than ISD, because of the higher selection intensity. Table 4 shows the ratio of $\sigma_{ABt}^2/\sigma_{AB0}^2$ and demonstrates how the asymptotic additive genetic variance depends on selection intensity and accuracy of selection. Land and Hill (1975) considered a mating ratio of eight with six offspring per donor to be a plausible superovulation scheme to be used in practice. For this scheme, they predicted a rate of response of 16 kg/year, however, the asymptotic response is only proportionately 0.80 of this at 12.8 kg/year, a substantial difference. In addition, they stated that selection using a full-sib index would be 0.09 more efficient than phenotypic selection; this increased efficiency reduces to only 0.04 when comparing asymptotic responses. From first generation responses IHS is expected to be 0.10 and ISD 0.12 more efficient than phenotypic selection for this example and these reduce to 0.04 and 0.05 respectively when considering asymptotic responses. Therefore the advantage of family information

TABLE 3

Response per generation to one round of selection (R_1 in kg) for a trait with $h^2 = 0.5$ and phenotypic standard deviation 40 kg and the proportion of this response expected from the prediction of the asymptotic response rate (R_∞/R_1)

No. offspring per donor (<i>n</i>)		Mating ratio (<i>m</i>)				
		1	2	4	8	16
Phenotypic selection						
2	$\{R_1$	0.00	3.99	6.35	8.23	9.84
	$\{R_\infty/R_1$	1.000	0.901	0.885	0.878	0.874
6	$\{R_1$	10.91	12.95	14.65	16.14	17.48
	$\{R_\infty/R_1$	0.812	0.805	0.801	0.799	0.797
10	$\{R_1$	14.00	15.77	17.31	18.68	19.94
	$\{R_\infty/R_1$	0.801	0.797	0.794	0.792	0.791
Full-sib index, IFS						
2	$\{R_1$	0.00	4.12	6.56	8.50	10.16
	$\{R_\infty/R_1$	1.000	0.890	0.874	0.866	0.862
6	$\{R_1$	11.87	14.10	15.95	17.57	19.03
	$\{R_\infty/R_1$	0.775	0.767	0.763	0.760	0.758
10	$\{R_1$	15.53	17.50	19.20	20.73	22.12
	$\{R_\infty/R_1$	0.756	0.751	0.748	0.746	0.745
Full and half-sib index, IHS						
2	$\{R_1$	0.00	4.15	6.67	8.73	10.51
	$\{R_\infty/R_1$	1.000	0.887	0.866	0.854	0.847
6	$\{R_1$	11.87	14.15	16.07	17.76	19.28
	$\{R_\infty/R_1$	0.775	0.766	0.761	0.758	0.756
10	$\{R_1$	15.53	17.53	19.28	20.85	22.27
	$\{R_\infty/R_1$	0.756	0.751	0.748	0.746	0.745
Full and half-sib and parent index, ISD						
2	$\{R_1$	0.00	4.32	6.92	9.02	10.84
	$\{R_\infty/R_1$	1.000	0.880	0.860	0.850	0.845
6	$\{R_1$	12.06	14.36	16.30	18.01	19.56
	$\{R_\infty/R_1$	0.767	0.759	0.754	0.751	0.749
10	$\{R_1$	15.65	17.67	19.44	21.02	22.46
	$\{R_\infty/R_1$	0.756	0.747	0.744	0.742	0.740

Therefore, the same optimum breeding programme is likely to be chosen whether asymptotic or one generation predictions are used.

Extension of this example to consider a range of heritabilities for the trait under selection demonstrates a similar pattern in reduction in predicted response when the asymptotic rather than the classical response is predicted. Table 5 lists the reductions in response for the two extreme examples of phenotypic selection, $m = 2$, $n = 2$ and $m = 8$, $n = 10$ for phenotypic and ISD selection. This reduction in response increases with heritability and is relatively greater at high selection intensities. The correlations between asymptotic and one-generation

TABLE 4

Ratio of asymptotic and base generation between family variance ($\sigma_{AB\infty}^2/\sigma_{AB0}^2$) for a trait with initial heritability of 0.5

No. offspring per donor (n)		Mating ratio (m)				
		1	2	4	8	16
2	Phenotypic	1.000	0.742	0.703	0.685	0.675
	IFS	1.000	0.731	0.691	0.673	0.663
	IHS	1.000	0.729	0.687	0.665	0.651
	ISD	1.000	0.711	0.668	0.646	0.631
6	Phenotypic	0.525	0.508	0.499	0.493	0.489
	IFS	0.488	0.471	0.462	0.457	0.453
	IHS	0.488	0.469	0.456	0.448	0.441
	ISD	0.482	0.464	0.452	0.443	0.436
10	Phenotypic	0.499	0.488	0.482	0.478	0.475
	IFS	0.451	0.441	0.435	0.430	0.427
	IHS	0.451	0.438	0.430	0.424	0.419
	ISD	0.448	0.436	0.427	0.421	0.417

in a selection index is generally over emphasized.

Accurate prediction of response in absolute units is necessary for comparison with realized response once a breeding programme is underway. However, prior to adopting a breeding programme possible alternatives are compared and it is the ranking of these alternatives that is the most important criterion. The correlation over all alternatives between asymptotic response and one generation response was 0.996 with a rank correlation of all the alternatives of 0.995.

TABLE 5

Ratio of predicted asymptotic response to one generation response (R_∞/R_1) over a range of heritabilities for two extreme examples of population structure

Heritability	$m = 2, n = 2$		$m = 8, n = 10$	
	Phenotypic	ISD	Phenotypic	ISD
0.1	0.978	0.964	0.931	0.784
0.2	0.948	0.923	0.881	0.760
0.4	0.913	0.888	0.814	0.743
0.6	0.890	0.875	0.773	0.739
0.8	0.876	0.871	0.747	0.738

response over all alternatives were greater than 0.99 for all heritabilities.

In the discussion above, it was concluded that too much weight is placed on family information in selection indices which do not take account of changes in variance due to selection; the between-family variance is reduced considerably whilst the within-family variance is maintained, thus the individual's own record becomes relatively more important. There are numerous examples in which selection is for a trait not measurable on candidates available for selection for example post-slaughter or sex-limited traits for which individuals are selected on the basis of the performance of their sibs. First-generation responses and the proportion of this achieved by the asymptotic response rate are presented in Table 6 for a trait with heritability of 0.2 and phenotypic standard deviation 10, measurable only in females with no common environment effect of full-sibs. Males are selected on an index of some or all of records from its full- and half-sibs and predicted breeding values of its parents, while indices for females also include their individual records. Mating ratios of one sire to eight or 16 dams and 20, 40, 60 or 80 female offspring per dam are considered. One male is available from each full-sib family for selection. This example could represent

selection for egg-production based on part-records in poultry. The asymptotic responses are only 0.6 of the first-generation responses, a considerable reduction.

As a simple example of selection on multiple traits, consider the selection in pigs for average daily gain (ADG) measured in g/day, and backfat thickness (BT) measured in mm. Using the parameters of Toro, Silio, Rodrigañez and Dobao (1988), let the heritabilities be 0.3 and 0.4, the phenotypic variances be 2025 and 4 and the economic values be £0.01 and -£0.04 for ADG and BT respectively. Asymptotic responses to selection were predicted by the method presented in the APPENDIX for index ISD for a population with 10 females mated to each male and with each female having three offspring of each sex. The overall response was reduced from £0.287/year in the first generation to an asymptote of £0.218/year. On an individual trait basis, response per year was reduced from 27.9 g/day to 21.2 g/day for ADG and from -0.21 mm to -0.14 mm for BT. The predicted changes in genetic and phenotypic parameters are presented in Table 7. As in a single trait case the genetic and therefore the phenotypic variances for each trait are reduced as a consequence of selection attributed to a negative gametic phase disequilibrium

TABLE 6
Response per generation to one round of selection (R_1) for a trait measurable only on females with $h^2 = 0.2$ and phenotypic standard deviation 10 and the proportion of this response expected from the prediction of the asymptotic response rate (R_∞/R_1)

No. female offspring per dam (n)	Mating ratio (m)							
	8				16			
	10	20	40	80	10	20	40	80
Full-sib index								
R_1	4.46	5.30	6.04	6.66	4.86	5.75	6.51	7.14
R_∞/R_1	0.634	0.596	0.575	0.565	0.630	0.592	0.571	0.561
Full and half-sib index								
R_1	4.71	5.44	6.10	6.67	5.20	5.92	6.58	7.17
R_∞/R_1	0.625	0.598	0.578	0.567	0.620	0.594	0.574	0.563
Full- and half-sib and parent index								
R_1	4.80	5.49	6.12	6.68	5.30	5.98	6.61	7.18
R_∞/R_1	0.609	0.590	0.575	0.566	0.604	0.586	0.571	0.562

component or negative covariance between loci for each trait. In this example, the genetic and phenotypic variances between ADG and BT increase, which is attributed to selection in opposite directions (from the signs of the economic values) for the traits, resulting in a positive gametic phase disequilibrium component or positive covariance between loci of the two traits (Robertson, 1977). The genetic correlation increases, in this example, as a consequence of selection to an asymptote of 0.258.

DISCUSSION

Comparison of predicted response with responses from simulation suggest that the algorithms presented for predicting asymptotic response are fairly reliable. Accurate prediction of response to selection in absolute units may be important for economic considerations prior to adopting a breeding programme and are necessary for comparison with long-term realized responses. Prediction of response to selection expected when selecting on breeding values estimated by using a BLUP animal model is in itself a useful result, as until now simulation of this situation has been the only way to predict response. The prediction of response from the selection indices assumes that the records are pre-corrected without error for fixed effects, in practice this assumption is likely to be violated. Response from the use of BLUP will be higher (because of the simultaneous estimation of fixed effects and prediction of random effects) than from index ISD but both will be less than that predicted here. Also, in practice, ISD will be worse than BLUP since the weights for ISD would not be updated each generation and so the index

would not be continuously optimized to account for the effects of selection. In the APPENDIX the prediction algorithms are extended to the situation of multiple trait selection. The method can easily be adapted to differing availability of records of different traits on relatives and provide a prediction of response to selection expected from using a multi-trait animal model.

Asymptotic responses were found to be considerably less than one-generation responses over a range of examples. The reduction in between-family variance causes more weight to be given to individual performance in the asymptotic indices, so the asymptotic rates of response to selection for traits not measurable in candidates for selection are reduced to a greater extent over the one-generation response. Selection for traits with a high common environment component are affected least by reduction in between-family variance since individual performance is always given a relatively high weighting.

Comparison of asymptotic and one-generation responses over a wide range of possible population structures shows that alternatives identified as relatively superior from one-generation responses maintain their superiority although to a lesser degree in the asymptotic response; therefore the relative merits of different methods of selection (e.g. Falconer, 1981, Figure 13.1) is altered by any previous selection. However, the ranking of alternatives is not greatly changed. Therefore, the classical comparison of breeding schemes using one-generation responses is likely to be sufficient to ensure that the optimal scheme is chosen. That is, one-generation responses are sufficient for obtaining the qualitative comparison of schemes and an approximate

TABLE 7
Changes in predicted genetic and phenotypic parameters for selection on ADG and BT

Generation	σ_{At}^2		$Cov_A(ADG, BT)$	r_A	σ_{Pt}^2		$Cov_P(ADG, BT)$	r_P
	ADG	BT			ADG	BT		
0	608	1.60	6.24	0.200	2025	4.00	36.0	0.400
1	495	1.59	7.07	0.252	1912	3.99	36.8	0.421
2	480	1.59	7.11	0.257	1897	3.99	36.8	0.423
3	478	1.59	7.11	0.258	1895	3.99	36.9	0.424
10	477	1.59	7.11	0.258	1984	3.99	36.9	0.424

ranking; if absolute comparisons are required then asymptotic responses must be used. This result is likely to hold for non-hierarchical mating structures.

In the prediction of asymptotic response, it was assumed that the population was of infinite size and that no inbreeding accumulated. Clearly, animal populations are finite and inbreeding will accumulate which will reduce both between- and within-family additive genetic variation. The reduction in genetic variance due to gametic phase disequilibrium is substantial however, occurring quickly over the initial generations, whilst the impact of inbreeding is gradual and long term. It therefore seems appropriate to disentangle the two causes of reduction in genetic variance and to consider them separately. The way in which inbreeding accumulates when selection takes place, however, merits further investigation. With no selection, inbreeding accumulates in a finite population due to sampling of gametes. But when selection is operating, related individuals are more likely to be chosen to become parents and so inbreeding accumulates more rapidly (Robertson, 1961; Wray and Thompson, 1989). In addition, the more records on relatives included in an index, the greater the accuracy of the index and the higher the rate of inbreeding.

A further assumption in the prediction algorithms was that generations were discrete. With overlapping generations there are several subpopulations determined by age each having undergone different amounts of selection and each with different reductions in genetic variance. However, after several generations of selection the variance of all subpopulations should have reached the same asymptote and the response to selection is the change in the mean genetic value of the subpopulations from one generation to the next. To determine the exact rate of response to this situation, simulation is required but the algorithms are likely to give a reasonable prediction. In addition, the predictions assume a balanced design mating design; responses from non-balanced designs could be approximated from this algorithm using average mating ratios and offspring per dam.

The asymptotic response to selection

presented here is computed and discussed for populations in which the trait of interest has not already been subject to selection and for which within-family variance is not known. If selection has already been practised then between-family variance is likely to have already reached an asymptote which may only change slightly under a new selection scheme. The asymptotic ratios of between-family to within-family variance (Table 4) demonstrate how estimation of σ_A^2 from, for example, between-sire-family variance as $\sigma_A^2 = 4\sigma_{AS}^2$ may severely underestimate the total genetic variance present in populations subject to selection but in which the selection can not be traced back to a base generation. The magnitude of the within-family variance suggests benefits of within-family selection as advocated by Dempfle (1975).

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where

$$G_1(j, k)_t = \text{Cov}_{AS}(j, k)_t + \text{Cov}_{AD}(j, k)_t + \text{Cov}_{AW}(j, k)_t/n,$$

$$P_1(j, k)_t = G_1(j, k)_t + \text{Cov}_C(j, k) + \text{Cov}_E(j, k)/n,$$

$$G_2(j, k)_t = \text{Cov}_{AS}(j, k)_t + \text{Cov}_{AD}(j, k)_t/m + \text{Cov}_{AW}(j, k)_t/mn,$$

$$P_2(j, k)_t = G_2(j, k)_t + \text{Cov}_C(j, k)/m + \text{Cov}_E(j, k)/mn$$

$G_1(j)_t$, $P_1(j)_t$, $G_2(j)_t$ and $P_2(j)_t$ are as above, replacing the covariance terms with variances.

$$C_s(j) = \text{Cov}(A_j, I)_{t-1} (1 - k_s)$$

$$V(\hat{A}_s) = \sigma_{It-1}^2 (1 - k_s)$$

$$\text{Cov}(A_j, I)_t = \sum_{i=1}^t G_i(j, i) b_i(i)$$

$$\text{Cov}_{AS}(j, k)_t =$$

$$\frac{1}{2} [\text{Cov}_A(j, k)_{t-1} - \frac{\text{Cov}(A_j, I)_{t-1} \text{Cov}(A_k, I)_{t-1}}{\sigma_{It-1}^2} k_s]$$

$C_d(j)_{t-1}$, $V(\hat{A}_d)$ and $\text{Cov}_{AD}(j, k)_t$ are obtained similarly, replacing k_s with k_d . The variance of the index, accuracy of the index and the overall response to selection are found in the usual way.

Accuracy of selection with respect to trait j :

$$\rho(j)_t = \frac{\text{Cov}(A_j, I)_t}{\sigma_A(j)_t \sigma_{It}}$$

Response to selection with respect to trait j :

$$R(j)_t = i \text{Cov}(A_j, I)_t / \sigma_{It} L.$$

For a more complete index approximating a multi-trait animal model, predicted breeding values of the sire, dam and mean of all dams mated to the sire for each trait may be included in the index.

