ADVANCES IN SELECTION THEORY.

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SUMMARY
Recent advances in predictions of rates of response to selection and rates of inbreeding in populations under selection are reviewed. Under the assumptions of the infinitesimal model, discrete generations, truncation selection, equal family sizes and truncation selection these predictions are shown to agree well with results obtained in simulation studies for populations. Particular problems associated with very small populations and relaxation of some of the assumptions are discussed.

1. INTRODUCTION

Rates of response (R) to truncation selection were classically calculated as $R = i \, r \, \sigma_a$, where i is the selection intensity, r is the accuracy of selection and σ_a is the additive genetic standard deviation, all parameters of the base population. Whilst this is an appropriate prediction of the response to the first round of selection, it has been shown to be a considerable overestimate in subsequent generations of selection as a consequence of the reduction in genetic variance attributable to selection and inbreeding. This reduction in additive genetic variance and hence the response to selection is greatest initially due to gametic phase disequilibrium (Bulmer, 1971) and is then gradual as a consequence of the accumulation of inbreeding. Accounting for these factors may alter the optimum breeding scheme, which, in turn, will depend on the time horizon considered.

Rates of inbreeding per generation (ΔF) were classically calculated as $\Delta F = 1/(8M) + 1/(8F)$ (Wright, 1931), where M and F are the number of males and females entering the population each generation. Whilst this is appropriate for randomly selected populations (with Poisson distributed family size), the prediction is recognised as being a considerable underestimate of the rate of inbreeding in selected populations of the same size and structure. The combined overestimation of rates of response and underestimation of rates of inbreeding may have, in the past, severely misrepresented the cost effectiveness of adopting new breeding schemes.

In this paper, relatively new methods of accurately predicting rates of response to selection and rates of inbreeding in selected populations are reviewed by considering in turn infinite populations, finite populations and very small populations (the definition of the size of the latter is somewhat arbitary). The infinitesimal model of gene effects, truncation selection, discrete generations, constant family size and often hierarchical mating are assumed.

2. POPULATIONS OF INFINITE SIZE
In infinite populations no inbreeding accumulates, therefore the consequence of selection on additive genetic variance and rate of response to selection can be considered alone.

Predictions of rates of response to selection
Bulmer (1971), demonstrated that even under the infinitesimal model, additive genetic varinace is reduced by selection. This apparent paradox was resolved not as a result of changes in allele frequency as a consequence of selection but rather via the induction of a negative covarinace between allelic effects at different loci in the selected individuals, that is by gametic phase disequilibrium. In the first generation of selection, gametic phase disequilibrium is induced which causes a reduction of the additive genetic variance in the selected population. In subsequent generations, some of the existing disequilibrium is broken down by

generations and Hill (1979) for overlapping generations, developed an expression for rate of inbreeding ($\Delta F_{1,LH}$) using variances and covariances of family size.This method was not derived for selected populations but for the situation of variance in family size being the result of non-heritable causes. In the selection case, the drift variance must be interpreted as the variance of change in gene frequency at loci neutral with respect to the selected trait. Variances in family size can be predicted with knowledge of i, the selection intensity and ρ, the correlation of EBVs of sibs (equilibrium values, ρ_e).

For populations of full-sibs ($M=F$), the rate of inbreeding is predicted as $\Delta F_B = 0.5P$ (Burrows, 1984a), where P is the probability that a pair of genes chosen at random from distinct selected individuals are contributed by the same individual of the previous generation. P is calculated from the bivariate normal distribution depending on the proportion selected and ρ. The method is extended to populations with a hierarchical mating structure (Burrows, 1984b) but the differential selection intensities for the sexes is not properly accounted for. Burrows method can be generalised using transition matrices ($\Delta F_{1,T}$) (Woolliams, 1989; Wray et al. 1990) which incorporates the correct selection intensities of the sexes. In addition, the ρ changes as a consequence of selection (Bulmer effect); Wray et al (1990) argue that the equilibrium value, ρ_e, should be used. This subject was not discussed by Burrows and his prediction has generally been used the initial correlation (ρ_0).

Verrier et al (1990) extended the method of Burrows (1984) to predict level of inbreeding each generation in a breeding programme. The method accounts for differential selection intensities of the sexes and utilises correlations of EBVs of sibs appropriate for that generation, accounting for the reduction in genetic variance due to selection. The method is a one generation method in the sense that it only examines probabilities of co-selection of sibs but it utilises the whole range of ρ values from ρ_0 to ρ_e. The asymptotic rate of inbreeding from this method is equivalent to Burrows with ρ_e

Two generation methods
A superior parent is expected to contribute more offspring to the next generation than an average or inferior parent because the offspring will inherit his superior genes. A superior grandparent is expected to contribute more grandoffspring for two reasons. Firstly, he would have been superior as a parent and would already have contributed more offspring and therefore has more grandoffspring *available* for selection. Secondly the grandoffspring will inherit superior genes from him. The variance of family size method has been extended to two generations using variances of family size from grandparents to grandoffspring as well as from parents to offspring ($\Delta F_{2,LH}$, Wray et al. 1990). In addition, the transition matrix method has been extended to two generations ($\Delta F_{2,T}$. Wray et al. 1990).

Long-term methods.
The argument of the inheritance of selective advantage discussed for two generation methods can be extended over all generations as the selective advantage conferred on descendants by the superiority of their ancestors.

Robertson (1961) was the first to discuss the prediction of rates of inbreeding for populations undergoing selection. For populations of full-sibs (or half-sibs, but not both) Robertson's rate of inbreeding ΔF_R can be expressed as, $\Delta F_R = \Delta F_0 (1 + Q^2 i \rho^2)$, where ΔF_0 is the rate of

Predictions of rates of response to selection have been compared to simulation results (Wray and Hill, 1989) and show good agreement; asymptotic rate of response were found to be as much as 25 per cent less than rates of response predicted for the first generation and by 40 per cent for sex-limited traits. Between family variance was found to stabilise at less than 50 per cent of its original value in some cases, thereby changing the assumed ratio of between:within family variance from 1:1 to 1:2. Family selection indices therefore tend to give too much emphasis to family information and too little to the individual's own record. When establishing a breeding programme, there is growing evidence to suggest that after initial rounds of selection eliminating the very worse families, that selection should continue on a within-family basis depending on the time horizon considered (Dempfle, 1975).

3. LARGE FINITE POPULATIONS

In finite populations, accumulation of inbreeding must be considered, and it is important for two reasons. Firstly, inbreeding at loci controlling the selected trait causes a reduction in the genetic variance available for selection, and hence cumulative response. Secondly, increased homozygosity at loci for which heterosis is important, particularly loci associated with fitness, can result in reduced performance, *i.e.*inbreeding depression.

Rates of inbreeding calculated in simulation studies have been found to be considerably greater for selected populations compared to randomly selected populations of the same size and structure (Table 1) and this increase becomes realtively greater as more relatives records are included into the selection criterion. This increase is attributable to the increased probabilities of co-selection of sibs due to the increased correlation of their EBVs. In addition, increase in rates of inbreeding have been observed to be several fold greater than the increases in rates of response when increasing the amount of information included from relatives. The increase in rates of inbreeding in selected populations has been recognised for some time, but prediction of these rates has received relatively little attention. Rate of inbreeding is defined as $\Delta F = (F_t - F_{t-1})/(1 - F_t)$, where F_t is the level of inbreeding in time t.

Table 1. Rates of inbreeding in populations selected using different amounts of records on family members, presented relative to the rate of inbreeding in a randomly selected population (0.0129/generation). Populations are hierarchically mated with 10 sires, 100 dams, 3 offspring of each sex per dam and discrete generations (100 replicates).

	Initial heritability		
Information used	0.1	0.2	0.4
Individual selection	1.24	1.37	1.45
Index of individual and full-sib records	1.91	2.00	1.92
Index of individual, full- and half-sib records	3.11	2.85	2.36
Animal model BLUP	3.96	3.18	2.46

3.1 METHODS OF PREDICTING RATES OF INBREEDING IN SELECTED POPULATIONS.

Methods of predicting rates of inbreeding can be classified on the basis of the number of generations of probabilities of co-selection they include. One generation methods consider only probabilities of co-selection of sibs which depend on relationships that can be traced back one generation (to the parents). Two generation methods consider probabilities of co-selection of cousins tracing relationships to the grandparent generation and long-term methods account for probabilities of co-selection of all relatives. As more generations are included we expect to get better predictions.

One generation methods.

By considering variances of change in gene frequency (drift), Latter (1959) for discrete

recombination of genes, 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 the recombination expressed by the within family variance. The genetic variance is reduced most after the first generation of selection but continues to decline until an equilibrium is achieved. Similarly, the rate of response to selection is greatest initially and reaches and asymptotic rate after several generations in an infinite population. Bulmer (1971) considered the reduction in genetic variance under mass selection but the method is easily extended to other types of selection (Meuwissen, 1989; Wray and Hill, 1989). The derivation assumes that normality of genetic effects is maintained even after many generations of selection; under the infinitesimal model and truncation selection, departures from normality are negligible (Bulmer, 1980).

The additive genetic variance of the unselected population born in time t (σ_{At}^2), can be divided into between family (σ_{ABt}^2) and within family variance (σ_{AWt}^2), $\sigma_{At}^2 = \sigma_{ABt}^2 + \sigma_{AWt}^2$. When $t = 0$, $\sigma_{AB0}^2 = \sigma_{AW0}^2 = \frac{1}{2}\sigma_{A0}^2$. Within family variance is not affected by selection (Fisher, 1918) and in an infinite population remains as $\sigma_{AWt}^2 = \frac{1}{2}\sigma_{A0}^2$. However, when selection is practised the between family variance is reduced by a proportion $k\,r_{t-1}^2$ (Pearson, 1903), where r_{t-1}^2 is the accuracy of selection at time $t-1$ and k represents the proportionate reduction in the variance of the selection criterion of the selected group. The between family variance can be further partitioned into between sire family variance (σ_{ASt}^2) and between dam family variance (σ_{ADt}^2); $\sigma_{AS0}^2 = \sigma_{AD0}^2 = \frac{1}{4}\sigma_{A0}^2$, and

$$\sigma_{ASt}^2 = (1 - k_s\,r_{s\,t-1}^2)\,\sigma_{A\,t-1}^2, \qquad\qquad \sigma_{ADt}^2 = (1 - k_d\,r_{d\,t-1}^2)\sigma_{A\,t-1}^2$$

thus allowing for different selection intensities (via k_s and k_d) and different accuracies of selection for the sexes.

Under single trait index selection using family records, $I_t = \mathbf{b}_t\,\mathbf{x}_t$, where I_t is an index value predicting the true breeding value of an individual, A, $\mathbf{b}_t$ is a vector of weightings for a linear combination of the relatives' records contained in the vector $\mathbf{x}_t$. The standard index equations $\mathbf{P}_t\,\mathbf{b}_t = \mathbf{G}_t$ can be formed where $\mathbf{P}_t = \text{var}(\mathbf{x}_t)$ and $\mathbf{G}_t = \text{cov}(\mathbf{x}_t, A)$; the elements of these matrices change each generation and depend on σ_{ASt}^2, σ_{ADt}^2 and σ_{AWt}^2 as defined above. Accuracy and variance of the index can then be calculated using standard index theory, and rate of response in generation t is $R_t = i\,r\,\sigma_{At}$.

Wray and Hill (1989) used this method to predict rates of response to selection from animal model BLUP using an index of an individual's own records, the mean of the records of its full- and half-sibs and the estimated breeding values (EBVs) of its sire, its dam and all the mates of its sire, where the parental breeding values are based on records of their ancestral and collateral relatives, not their descendants. Unlike an actual animal model, the prediction ignores information from cousins and more distant relatives, but these contribute little to the accuracy. Breeding values predicted from BLUP are independent of changes in variance due to selection (Henderson, 1975) and are therefore independent of selection intensity and k. Therefore, the use of the prediction index seems inconsistent with this observation at first sight, since the $\mathbf{b}$ weights contain components dependent on k. However, the k-values of the components of $\mathbf{b}$ cancel, leaving the weights and hence the EBVs independent of k (Appendix, Wray and Hill, 1989). This apparent paradox is explained throught the total accounting of all previous selection via the inclusion of the parental EBVs.

inbreeding in a population of similar structure undergoing random selection. The term $i\,\rho^2$ represents the increment in rate of inbreeding attributable to the probability of co-selection of sibs, or the selective advantage that parents superior for the selected trait give to their offspring. Q expresses the way in which selective advantage accumulates over many generations expressed relative to that accounting for only one generation. Therefore, accounting for only a single generation of selective advantage $Q=1$ by definition and the prediction is similar to that of all one generation methods presented above (except for higher order terms). Accounting for two generations of selective advantage Robertson argued that $Q=3/2$ and the prediction is then attempting to predict the same quantity as two generation methods above. The final prediction, however, accounts for all generations of selective advantage from ancestors to descendants. Robertson argued that Q increases as the sum of a geometric series asymptoting to a limiting value of 2. The prediction is pioneering in its attempt to account for al generations of selective advantage, but has been found to overpredict rates of inbreeding in populations when i or ρ are high. Using simulation Wray and Thompson (1990) examined values of Q and found it to stabilise at values considerably less then 2 under these conditions. For example, a population selected on individual performance of 20 full-sib families, with 3 offspring of each sex per family, Q was found to stabilise at 1.87 when $h^2=0.1$ and 1.46 when $h^2 = 0.6$. This observation is attributed to the increasing 'competitiveness' of contemporaries, *i.e.* all contemporaries of the descendants of a superior ancestor are also descendants of selected ancestors and therefore the selective advantage conferred by the superior ancestor is not worth as much as if the contemporaries were descendants of the whole group of ancestors, superior, average and inferior. It was found that as h^2 approached zero, Q approached 2, therefore making it a limiting case.

Wray and Thompson (1990) presented a recursive method for predicting rates of inbreeding which can be viewed as an extension of Robertson's method in which the value of Q is correctly accounted for and which is appropriate for heirarchically mated populations ($M \leq F$). The additive genetic relationship matrix was decomposed into 'contribution matrices' which describe the contribution of the Mendelian sampling of genes of ancestors in a given generation to the relationship between descendants in later generations. The elements of these contribution matrices were found to stabilise with time and the value to which they stabilised was found to be related to the asymptotic rate of inbreeding. The rate of inbreeding (ΔF_{WT}) expressed in terms of the mean (μ_r) and variance (σ_r^2) of these long–term contributions or relationships

is,
$$\Delta F = \frac{\mu_r + \sigma_r^2}{4N},$$

where N is the number of parents each generation ($N = M+F$). Prediction of μ_r and σ_r^2 involves the prediction of the linear regression (b_t) of number of descendants born in generation t on breeding value of ancestors. For example, b_2 is the regression of number of offspring (born at $t =2$) on the breeding value of their parents. The ratio b_∞/b_2 when $M= F$ is a measure of the relative selective advantage, the Q of Robertson's equation.

Comparison of methods to predict rates of inbreeding in selected populations.

Prediction methods described above have been compared over a range of mating ratios, family sizes and heritabilities for populations undergoing mass selection (Wray et al. 1990). In Table 2 results for two populations are considered, $M = 20$ and $F=20$ or 100 and number of offspring of each sex per dam (n) is 3 and predictions are compared to rates of inbreeding calculated from simulation (ΔF_{sim}), mean of 100 replicates.

All predictions were found to agree well with each other and with the simulation value when selection is random ($h^2=0$). ΔF_{WT} is found to agree well to simulation values of the whole

Table 2. Rates of inbreeding (% per generation) from simulation and prediction.

h^2	ΔE_{sim}	ΔE_B ρ_e§	$\Delta E_{1,LH}$ ρ_e	$\Delta E_{2,LH}$ ρ_e	$\Delta E_{1,T}$ ρ_0†	$\Delta E_{1,T}$ ρ_e	$\Delta E_{2,T}$ ρ_e	ΔE_{WT}	ΔE_R $Q=2$	(Q)@
$M=20, F=20, n=3$										
0.0	1.07	1.05	1.03	1.03	1.04	1.04	1.05	1.04	-	-
0.1	1.23	1.11	1.08	1.11	1.10	1.10	1.13	1.19	1.23	1.20(1.87)
0.2	1.33	1.15	1.12	1.16	1.17	1.14	1.17	1.30	1.38	1.31(1.77)
0.4	1.42	1.22	1.18	1.24	1.30	1.21	1.25	1.42	1.61	1.43(1.60)
0.6	1.50	1.26	1.23	1.31	1.43	1.25	1.32	1.47	1.72	1.46(1.46)
$M=20, F=100, n=3$										
0.0	0.71	0.69	0.70	0.70	0.71	0.71	0.70	0.71		
0.1	0.82	0.72	0.74	0.75	0.76	0.75	0.76	0.89		
0.2	0.94	0.78	0.82	0.87	0.93	0.84	0.87	0.99		
0.4	1.05	0.78	0.82	0.87	0.93	9.84	0.87	1.07		
0.6	1.02	0.80	0.85	0.90	1.05	0.87	0.91	1.05		

† ρ_0 using initial genetic variances, covariances and correlations prior to selection.

§ ρ_e using genetic variances, covariances and correlations at equilibrium.

@ using predicted Q values presented in parenthesis.

range of population structure and heritabilities. ΔF_R overpredicted ΔF_{sim} when $Q=2$ was used, but was a good predictor with the correct Q value. When ρ_e was used, the one and two generation methods are always underpredictors of ΔF_{sim} to a variable and unpredictable degree. $\Delta F_{1,LH}$ and $\Delta F_{2,LH}$ generated very similar predictions to $\Delta F_{1,T}$ and $\Delta F_{2,T}$ for these examples. The methods incorporating two generations of selective advantage were always superior to the one generation methods, but not greatly so. ΔF_B agreed well with $\Delta F_{1,T}$ when $M=F$, but it was considerably worse for hierarchical populations demonstrating the error incurred by not correctly accounting for differential selection intensities of the sexes. Predictions for $\Delta F_{1,T}$ were calculated using both ρ_0 and ρ_e, at first sight the predictions using ρ_0 appear superior. This apparent superiority is coincidental; the overestimation of family correlations by ρ_0 compensates for the incomplete account of the inheritance of selective. advantage. Indeed in some cases using ρ_0 may generate overpredictions of ΔF_{sim} .

Prediction of rates of inbreeding under index selection.
The methods of predicting rates of inbreeding are easily extended to the situation when selection is based on an index of family records, expressed via the ρ the correlation between the selection criteria of sibs. Some results for index selection using full-sib and full- and half-sib information are expressed in Table 3, for ΔF_{sim}, $\Delta F_{1,LH}$ and ΔF_{WT} (Wray and Thompson, 1991). The predictions of ΔF_{WT} are less good than under mass selection but are usually superior to $\Delta F_{1,LH}$; this 'one-generation' predictor is relatively better under index selection than under mass selection. The likely explanation is that under index selection information from relatives is used so that the breeding values of individuals are known with greater accuracy. Therefore, the initial selective advantage of an ancestor to its offspring is greater than for mass selection and the increase in relative selective advantage over generations is reduced. This hypothesis can be investigated by examining the regression coefficients of number of descendants on ancestors' breeding value. For an example of $M=F=20$, $n=3$ and $h^2=0.1$, $b_2=.14$ under mass selection and $b_2=0.28$ under individual and full-sib index selection, but the ratio b_∞/b_2 is 1.87 for mass selection and 1.61 for index selection.

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Table 3 Rates of inbreeding (%/generation) from simulation and predicted for populations undergoing index selection.

h^2	Individual and full-sib index			Individual full- and half-sib index		
	ΔF_{sim}	$\Delta F_{1,LH}$	ΔF_{WT}	ΔF_{sim}	$\Delta F_{1,LH}$	ΔF_{WT}
$M=20, F=20, n=3$						
0.1	2.62	2.40	2.55			
0.2	2.52	2.28	2.46			
0.4	2.31	2.04	2.19	same as individual and full-sib		
0.6	1.03	1.81	1.95			
$M=20, F=100, n=3$						
0.1	1.71	1.41	1.90	2.43	2.22	2.42
0.2	1.78		1.83	2.23	1.98	2.34
0.4	1.57	1.33	1.55	1.83	1.60	1.81
0.6	1.41	1.21	1.32	1.45	1.31	1.45

Standard errorrs of ΔF_{sim} ranged from 0.02-0.08

3.2 PREDICTION OF RATES OF RESPONSE IN FINITE POPULATIONS.

In finite populations, additive genetic variance and rates of response to selection are reduced by both gametic phase disequilibrium and inbreeding. The methodology discussed in section 2 can be extended to account for the effects of inbreeding.

In a randomly selected population the genetic variance in generation t about a mean of zero is $\sigma_{At}^2 = (1 - F_t)\,\sigma_{A0}^2$ (Falconer, 1981), and the within family variance is $\sigma_{AWt}^2 = \frac{1}{2}(1 - F_{t-1})\sigma_{A0}^2$, therefore by difference $\sigma_{ABt}^2 = \frac{1}{2}(1 + F_t - 2F_{t-1})\,\sigma_{A0}^2$. The between family variance can be expressed as a function of the total genetic variance in generation $t-1$,

$$\sigma_{ABt}^2 = \tfrac{1}{2}\sigma_{At-1}^2 (1 + F_t - 2F_{t-1})/(1 - F_{t-1}).$$

Thus, when selection is imposed,

$$\sigma_{ABt}^2 = \tfrac{1}{2}\sigma_{At-1}^2 (1 - k\,r_{t-1}^2)(1 + F_t - 2F_{t-1})/(1 - F_{t-1});$$

similar expressions can be made for σ_{ASt}^2 and σ_{ADt}^2. The level of inbreeding can be calculated from predicted rates of inbreeding as, $F_t = 1 - (1 - \Delta F)^{t-1}$.

In Table 4 some predicted rates of response to the 10th round of selection are presented for mass selection and selection on indices using records of individual and full-sibs and half-sibs. Predicted rates of response are in good agreement with those observed from simulation and the predictions are robust to errors in the predicted rates of inbreeding.

Alternatively, Verrier et al (1990) presented an algorithm to calculate level of inbreeding (using the method described in section 3.1), genetic mean and genetic variance in generation t which depend on these factors in generation $t-1$. Their expression of genetic variance is,

$$\sigma_{At}^2 = \tfrac{1}{4}\left(1 - \tfrac{1}{M}\right)(1 - k_s\,r_{st-1}^2)\sigma_{At-1}^2 + \tfrac{1}{4}\left(1 - \tfrac{1}{F}\right)(1 - k_d\,r_{dt-1}^2)\sigma_{At-1}^2 + \tfrac{1}{2}(1 - F_{t-1})\sigma_{A0}^2$$

This defintion is a within generation variance about the parental mean. Both approaches are good predicitve methods when compared to simulation results.

Table 4. Rates of repsonse to selection in generation 10 (in original phenotypic standard deviations) from simulation (R_{sim}), predicted from a one generation argument (R_1) and completely predicted (R_{pred}).

h^2	Mass selection			Individual and full-sib index			Individual full- and half-sib index		
	R_{sim}	R_1	R_{pred}	R_{sim}	R_1	R_{pred}	R_{sim}	R_1	R_{pred}
M=20, F=20, n=3									
0.1	.94	1.09	.93	1.04	1.48	1.06			
0.2	1.71	2.18	1.77	1.88	2.75	1.91	same as individual and full-sib		
0.4	3.31	4.36	3.32	3.33	4.94	3.39			
0.6	4.73	6.54	4.78	4.70	6.91	4.78			
M=20, F=100, n=3									
0.1	1.30	1.52	1.32	1.56	2.06	1.53	1.53	2.31	1.62
0.2	2.47	3.03	2.50	2.73	3.82	2.73	2.67	4.05	2.77
0.4	4.67	6.06	4.66	4.67	6.86	4.82	4.84	6.98	4.82
0.6	6.72	9.09	6.70	6.77	9.60	6.75	6.60	9.64	6.74

Standard errorrs of R_{sim} were of the order 0.20

4. SMALL POPULATIONS

In small populations several complicating factors arise and the approximations of the predictions methods may not be valid. The approximations might be affected by the correlation fo EBVs of sibs, the number of families and the number of offspring per family within the population. Therefore, the use of the word 'small' is somewhat arbitary , for example, 'small' may be $M < 10$ for populations undergoing mass selection with $n \leq 3$, but may be $M < 20$ if the population was changed to have $n=6$ or selection to be on an index of family records.

Selection intensity and k-values.

In large populations selection intensities are calculated from normal distribution theory; in smaller populations these must be calculated using order statistics, or more readily by approximations (Burrows, 1972). In addition, Hill (1976) and Rawlings (1976) demonstrated that selection intensity is further reduced when candidates available for selection are related and a correlation exists between their selection criteria; this is particularly important when EBVs are calculated using family records. They presented simple approximations for calculating reduced selection intensities which have been further improved by Meuwissen (1990) to account properly for populations of a mixed family structure of full- and half-sibs. For example in a population of 32 offspring of 4 families, the reduced i when 25 per cent is selected is 1.235 when $\rho=0$ and 1.154 when $\rho=0.5$, compared to the normal distribution i of 1.271; these will clearly affect the prediction $R_t = i r_t \sigma_{At}$. Furthermore, Hill (1977) demonstrated that genetic selection intensities (those appropriate for selection on EBVs) are reduced to an even greater extent than the phenotypic selection intensities discussed above. However, no simple approximation exists for these and so they have rarely been applied.

Both the predictions of rates of response over many generations and the predictions of rates of inbreeding are functions of k, from normal distribution theory $k = i (i - x)$. Clearly, when i is reduced by population size and correlation of EBVs, k will also be affected. This subject has received very little attention because of the enormous computing problem of calculating true k values from variances and covariances of order statistics. For example in a population of 32 offspring of 4 families, the k-value when 25 per cent is selected is .750 when $\rho=0$ and .808 when $\rho=0.5$ (calculated from simulation), compared to the normal distribution k of .758; thus predictions may be affected particularly when ρ is non-zero.

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Prediction of rate of response.

Despite the problems outlined above in terms of the k-values and genetic variance, Ruane (1989) compared the prediction of section 3.2 (using ΔF from simulation, reduced i but normal theory k) to rates of response observed from simulation for a population of $M=4,8$, $F=16,32,64$, $n=8$ in a dairy MOET scheme and found good agreement. Therefore, it is likely that for small populations of practical importance that the predictions are robust. Verrier et al (1990) tested their algorithm on a small population and also found good agreement between simulation and predictions.

Prediction of rate of inbreeding.

Evidence from simulation studies lends insight into the extent of problems of prediction of rates of inbreeding in small populations. Firstly, rate of inbreeding is inversely related to population size when population size is moderate or large, but in small populations observed rates of inbreeding tend to be less than one would expect (Wray and Thompson, 1991). This discrepancy can be partly attributed to the effect of k-values and may also arise larger populations when family information is included in the selection criterion. Another example of this limit to inbreeding is the following; under mass selection one would expect the rate of inbreeding to increase with heritability of the selected trait. However, as an example, in a population of $M=3$, $F=25$, $n=3$ Verrier et al (1990) observed equal rates of inbreeding for traits with $h^2 =0.5$ and 0.9. In this population most of the inbreeding will come from the male side and can take on only a very limited range of values compared to a larger population with the same mating ratio and family size; broadly speaking, minimum inbreeding will be achieved by selecting one male from each sire family and maximum inbreeding will be achieved when all three males are selected from a single sire family. Under selection, it is likely that the maximum inbreeding will be achieved when $h^2=0.5$ and then cannot increase further as the heritability increases despite the increase in the correlation of EBVs. Finally, in very small populations asymptotic the rate of inbreeding may not be achieved quickly; under this motivation, Verrier et al (1990) developed their generation by generation algorithm for F_t and genetic variance.

The prediction method of Wray and Thompson (1990) assumes a linear regression of number of descendants on ancestors' breeding values which is unlikely to hold in small populations. As a consequence the method tends to overpredict rates of inbreeding in small populations. One generation methods therefore often seem better predictors for small populations, although this apparent superiority is really a consequence of two compensating factors (limited rates of inbreeding in small populaitons vs. ignoring long-term contributions of ancestors). Further work is required in this area to understand the accumulation of rates of inbreeding in small populations and to predict them accurately.

5. DISCUSSION

This paper has investigated recent advances in selection theory under the assumptions of infinitesimal model of gene effects, truncation selection, discrete generations and equal family size and sometimes heirarchical mating design. These assumptions perhaps reflect only the most simple cases, but are still relevant to a wide range of practical situations. The prediction methods discussed give insight into the manner in which additive genetic variance declines, level of inbreeding accumulates and their interaction and impact on rates of response. The next step is to use this basic framework to examine the consequences of relaxing or changing these assumptions. In addition, only single trait selection but in principle extension of the prediction methods to multiple trait selection is straightforward (Wray and Hill, 1989; Wray and Thompson, 1991).

The assumption of discrete generations of discrete generations is not severe for predictions of rates of response; using approximate average figures the prediction equations hold (unpublished results). For predictions of rates of inbreeding Hill (1979) demonstrated that the

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discrete generation derivation of the Latter-Hill holds for overlapping generations when averaged over generation interval. This is also likely to be true for the method of Wray and Thompson (1990) which attempts to predict asymptotic rates of inbreeding. However, prediction of levels of inbreeding each year would require an integration of the methods described in section 3 and the approach of Johnson (1977) which used transition matrices to predict the levels of inbreeding each year in a randomly selected population with overlapping generations.

Simulation results of variable family size have shown that rates of response are only slightly reduced compared to similar populations of similar structure but constant family size (Ruane, 1989; Wray and Simm, 1990). Ruane (1989) also found only slight differrences in rates of inbreeding in a dairy MOET scheme using family size normally distributed with mean 16 (range 0-32). However, in larger populations Wray and Simm (1990) found a considerable increase in inbreeding in some cases up to 48 per cent when considering variable family size appropriate for beef MOET schemes for which field data suggests the distribution is hyperbolic in shape.

Having achieved adequate predictions of rates of response and rates of inbreding in selected populations, a practical application is to utilise these in the design of optimum breeding programmes aiming to maiximise rates of response whilst limiting rates of inbreeding. Toro et al (1988) and Toro and Perez-Enciso (1990) have investigated such scenarios by simulation and have shown that it is possible to maintain most of the rate of response whilst restricting level of inbreeding. The prediction procedures should help to generalise these results and give insight into the mechanism by which they are achieved.

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