Sources of information for estimating heritability from selection experiments

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Summary

Maximum likelihood estimation methods with an individual animal model were used to analyse a bi-directional selection experiment, with control, for cannon bone length in Scottish Blackface sheep. A method is described for partitioning the likelihood to allow within- and between-line estimates of genetic variance. It is concluded that both sources of information made substantial contributions to the precision of the base population heritability estimate. The implications for different experimental designs and varying heritability are discussed.

1. Introduction

The heritability of quantitative traits has been estimated in both laboratory and farm animals from comparisons between relatives in unselected populations and from between-line divergence in selected populations. The resultant estimates, referred to as base population heritability and realized heritability respectively, have often been compared to evaluate the efficacy of quantitative genetic theory. Sheridan (1988) reviewed experiments in all animal species in which base population and realized heritability estimates were available and concluded that there was a lack of strong agreement between the base population and realized genetic parameters, although James (1990) suggested that a major cause of the discrepancy appeared to be sampling error.

Simple comparisons of base population and realized heritability estimates are naive even when sampling variances have been estimated appropriately, since the two estimates are not necessarily equivalent in expectation. Firstly, the realized heritability is population-specific in that it will be an estimate of genetic variance that is reduced from the base population value by the combined effects of linkage disequilibrium, structure of the finite breeding population and inbreeding. Secondly, a base population heritability is strictly only relevant to the population before selection whereas the realized heritability is usually obtained after a number of generations of selection. Thirdly, estimation of the base population heritability can use

a variety of genetic relationships whilst realized heritability is based on mid-parent offspring regression. Only if the correct genetic model is fitted can one expect agreement between the estimates of heritability.

Hill (1972) has extensively discussed the appropriate analysis of selection experiments and used divergence between the selected lines and control in terms of selection differential and response to estimate realized heritability. Atkins & Thompson (1986) followed a similar approach and also estimated base population heritability from within the control line. An alternative approach proposed by Sorensen & Kennedy (1984) and Blair & Pollak (1984) would have been to use across-generation relationships in the selected line(s) and a mixed model analysis to separate genetic and environmental trends without recourse to the control line or assumptions of symmetric response by using measures of divergence between the lines. Although the genetic trend is dependent on an assumed base population heritability (Blair & Pollak, 1984), these authors argue that such a value would be available from the control line and/or literature values.

These methods are not alternatives but complementary in the sense that they rely on different sources of information. The realized heritability method of analysis uses information *between* selected lines to describe responses while the mixed model approach relies on information *within* the selected lines. Both approaches use the within control line information as a source of 'unbiased' base population parameters, The more relevant question then is not which is the better method but how both methods of analysis can be combined to use the available

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information most efficiently. Given the relative value of the various information sources, questions of efficiency of design for parameter estimation may then be answered.

Maximum likelihood estimation with an individual animal model has now become feasible for large data sets with derivative-free procedures (Graser, Smith & Tier, 1987) and efficient computing strategies (Meyer, 1989). This method is attractive in that for a selection experiment under an infinitesimal model it will be estimating the same heritability as that estimated from within unselected control lines (Sorensen & Kennedy, 1984). However, these methods do not lend themselves to partitioning sources of information. This paper has several aims. A method is described for partitioning the likelihood to allow within and between line estimates of genetic variation. It is shown how the information available within unselected lines can be quantified by using spectral decompositions. These methods are applied to a selection experiment described by Atkins & Thompson (1986). In particular, the separation of the total amount of variation into its component sources is attempted.

2. Materials and methods

(i) *Selection lines*

The experimental design was described in detail by Atkins & Thompson (1986). Briefly, a flock of 1600 ewes produced lambs in 1954 and 1955 to provide an initial population. Thereafter, the derived lines were a control line, in which selection was at random, and two lines selected for either high or low values of an index of cannon-bone length, adjusted for body weight, measured at 8 weeks of age. During the period 1956 to 1974 inclusive, the three flocks were maintained at approximately 270 ewes per year mated to 10 rams. Ewes were retained in the flocks for five annual matings (2 to 6 years of age) while rams were used for one mating only (1 year of age) and replaced. Selected proportions of young animals were approximately 10% for males and 70% for females.

(ii) *Estimation of heritability for line combinations*

Separate data and pedigree sets were formed for each of the three lines. The base population animals required for each line and the necessary genetic connections between the lines within the base population were maintained in a separate data set. Analyses were then performed for the lines separately and in combination to estimate base population heritability. The line combinations were:

LONG	(H)
SHORT	(L)
CONTROL	(C)
LONG + SHORT	(H + L)
LONG + CONTROL	(H + C)
CONTROL + SHORT	(C + L)
LONG + CONTROL + SHORT	(H + C + L)

Each of the line combinations was analysed for varying numbers of years, 6, 11, 16 and 21 years (representing 4, 9, 14 and 19 years of selection respectively).

Comprehensive analyses (Atkins & Thompson, 1986) had suggested that an appropriate model for the selected trait, cannon-bone length adjusted for body weight, was:

$$y_{ijk} = year_i + dam\ age_j + animal_k + e_{ijk},$$

with the animal effects having variance $\underline{A}\sigma_a^2$ where $\underline{A}$ is the numerator relationship matrix (Henderson, 1976).

Likelihoods were calculated using the algorithm described by Graser *et al.* (1987) for different values of heritability. Within each line, animals were grouped as sires and the remaining animals into families using only female relationships. This allowed the likelihood to be calculated recursively by correcting, in turn, for each of the families, and then sires within each line, and then for base animals, year sand dam age.

For each year-line combination, likelihood values for seven values of heritability around the maximum likelihood estimate were used to approximate the likelihood by a quadratic function in heritability using least squares. The quadratic coefficient was a measure of information of the heritability estimate, and the inverse of this coefficient was the estimated sampling variance of the estimate.

(iii) *Comparisons between lines*

The analysis of high (H) and low (L) lines forms a combined estimate of heritability from between and within lines, and it is of interest to develop a method for comparing the separate estimates. In most comparative studies one can develop extended models to allow estimation of all relevant parameters, but, in this case, it is difficult to reparameterize the individual animal model in terms of heritability within and between lines. However, a sequence of analyses can be constructed that does allow the question to be answered. From analysis of H, L and H + L lines, then the difference in likelihoods (L_{DHL}) between the combined lines and within lines can be constructed. By minimizing L_{DHL} as a function of heritability, one can get, in effect, a between line estimate of heritability. The L_{DHL} in a sense measures the fixed effect X line interaction and the heritability estimate from L_{DHL} will make the estimates of effects between lines as consistent as possible, taking account of the variance structure.

Informally, there are phenotypic means of y_H and $\underline{y}_L$ in H and L lines. We expect that estimates of

environmental means in each year, a, to be approximately linear in h^2 and to be related to phenotypic means by equations of the form

$$y_H = a + s_H(h^2) h^2 \quad \text{with var}(y_H) = V_H, \tag{1}$$

$$y_L = a + s_L(h^2) h^2 \quad \text{with var}(y_L) = V_L. \tag{2}$$

The terms $s_i(h^2) h^2$ can be thought of as responses to selection and $s_i(h^2)$ as a selection differential. These rates of change in a are approximate. These rates of change or approximate selection differentials, $s_i(h^2)$ where i = H, L, can be approximated by:

$$s_i(h^2) = [(a_i(h^2 + \Delta h^2) - a_i(h^2))]/\Delta h^2,$$

where $a_i(h^2)$ is the estimate of effects in line i using heritability h^2.

An estimate of heritability from (1) and (2) is:

$$h^2 = RS^{-1},$$

with

$$S = [V_H^{-1} s_H(h^2) - V_L^{-1} s_L(h^2)]' (V_H^{-1} + V_L^{-1})^{-1}$$
$$\times [V_H^{-1} s_H(h^2) - V_L^{-1} s_L(h^2)]$$

and

$$R = [V_H^{-1} s_H(h^2) - V_L^{-1} s_L(h^2)]' (V_H^{-1} + V_L^{-1})^{-1}$$
$$\times [V_H^{-1} y_H - V_L^{-1} y_L].$$

If $V_H^{-1} = V_L^{-1}$, then

$$S = [s_H(h^2) - s_L(h^2)]' 2 s_H^{-1}[s_H(h^2) - s_L(h^2)]$$

and

$$R = [s_H(h^2) - s_L(h^2)]' 2 V_H^{-1}[y_H - y_L].$$

This is the form of a weighted regression estimate of generation differences $(y_H - y_L)$ on differences in selection differentials similar to that used in the estimation of realized heritability.

(iv) *Information on heritability within unselected lines*

In order to give some benchmark to the amount of information on heritability to be obtained from data, calculations were carried out to quantify the information available in different pedigree structures. Using the results of Patterson & Thompson (1971), the asymptotic information matrix of estimates of σ_a^2 and σ_e^2 for a pedigree with relationship matrix A can be shown to be:

$$\begin{bmatrix} b & c \\ c & d \end{bmatrix}^{-1} = \begin{bmatrix} B & C \\ C & D \end{bmatrix} \tag{3}$$

with $b = \Sigma \lambda_i^2/(\sigma_e^2 + \lambda_i \sigma_a^2)^2,$

$c = \Sigma \lambda_i/(\sigma_e^2 + \lambda_i \sigma_a^2)^2,$

$d = \Sigma 1/(\sigma_e^2 + \lambda_i \sigma_a^2)^2,$

$A = P \lambda P'.$

The matrix P is an orthogonal matrix and the rows of P are eigenvectors of A and λ is a diagonal matrix with ith diagonal element λ_i so that λ_i are eigenvalues of A. P is a transformation that produces n independent sums of squares and the maximum likelihood technique can be thought of as weighted least squares using independent quadratic forms as observations, and expected values functions of λ_i, σ_a^2 and σ_e^2, and weights inversely proportional to $2/(\sigma_e^2 + \lambda_i \sigma_a^2)^2$.

A first approximation to information on the heritability estimate, $h^2 = \sigma_a^2/(\sigma_a^2 + \sigma_e^2)$, is:

$$[(1 - h^2)^2 B - 2h^2(1 - h^2) C + h^4 D]/\sigma_p^2 \tag{4}$$

with σ_p^2 the phenotypic variance $(= \sigma_a^2 + \sigma_e^2)$.

Several simple designs were considered with parents randomly selected to produce animals in the next generation. In these designs, each individual has n half-sib offspring and one of these offspring is chosen to have n offspring, the process being repeated for g generations to give (gn + 1) animals. The data can be summarized as:

y_{i1}, y_{i2} (i = 1 ... g) with y_{g1} the observation of the parent in generation g and y_{g2} the mean of the other animals in generation g and s is the sum of squares within generations of non-parents, with expected mean square $(\sigma_e^2 + 0 \cdot 5 \sigma_a^2)$ and g(n − 2) degrees of freedom.

Variance of y_1 and y_{g1}	$= \sigma_a^2 + \sigma_e^2$
Variance of y_{g2}	$= \sigma_a^2 + \sigma_e^2/n$
Covariance between y_1 and y_{g1}	$= (\frac{1}{2})^{g-1} \sigma_a^2$
Covariance between y_{g1} and y_{g2}	$= (\frac{1}{4}) \sigma_a^2$
Covariance between y_{g1} and y_{hi}	$= (\frac{1}{2})^{(h-g)} \sigma_a^2$
	$h > g (i = 1, 2)$
Covariance between y_{g2} and y_{hi}	$= (\frac{1}{2})^{(h+g+2)} \sigma_a^2$
	$h > g (i = 1, 2).$

Therefore A and P for y can be calculated and hence (4) evaluated. Patterson & Thompson (1971) show that similar formulae to (3) hold when fixed effects are fitted. The information on heritability was estimated for this balanced design for variable numbers of offspring and generations, and across a range of heritabilities.

The approach was then extended to the unbalanced design of the control line. Variances of heritability, for a range of heritability values, were calculated for the control line using pedigree information (a) on female parent to offspring, (b) male parent to offspring and (c) all relationships in the data.

3. Results

(i) *Comparisons between lines*

Estimates of heritability and standard errors for combinations of lines for varying numbers of years are presented in Table 1. The derivation of the

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Table 1. *Summary of heritability estimates and standard errors for various combinations of lines and year**

Flock	Year 6	Year 11	Year 16	Year 21
H	0·640 ± 0·060	0·618 ± 0·042	0·627 ± 0·034	0·640 ± 0·030
L	0·578 ± 0·068	0·585 ± 0·048	0·599 ± 0·039	0·647 ± 0·032
C	0·731 ± 0·064	0·667 ± 0·042	0·683 ± 0·033	0·695 ± 0·028
H + L	0·598 ± 0·037	0·596 ± 0·024	0·593 ± 0·019	0·610 ± 0·016
H + C	0·649 ± 0·041	0·621 ± 0·027	0·634 ± 0·022	0·648 ± 0·019
C + L	0·658 ± 0·044	0·631 ± 0·030	0·636 ± 0·023	0·660 ± 0·020
H + C + L	0·630 ± 0·033	0·615 ± 0·021	0·641 ± 0·017	0·631 ± 0·014
DHL	0·366 ± 0·126	0·504 ± 0·069	0·501 ± 0·058	0·543 ± 0·046
DCL	0·640 ± 0·129	0·622 ± 0·085	0·574 ± 0·058	0·572 ± 0·053
DHL	0·565 ± 0·067	0·586 ± 0·036	0·568 ± 0·028	0·569 ± 0·024

* *DXY* indicates an estimate from the difference between the likelihood from combined flocks *X* and *Y* with the likelihood within flocks *X* and *Y*.

Table 2. *Total information [and information per individual] for various combinations of lines and years. Information is expressed as the inverse of the sampling variance**

Flock	Year 6	Year 11	Year 16	Year 21
H	278 [0·30]	569 [0·30]	852 [0·30]	1144 [0·27]
L	213 [0·22]	425 [0·23]	671 [0·23]	990 [0·25]
C	248 [0·25]	578 [0·30]	925 [0·32]	1249 [0·32]
H + L	717 [0·38]	1787 [0·47]	2824 [0·50]	3853 [0·49]
H + C	589 [0·31]	1360 [0·35]	2074 [0·36]	2865 [0·36]
C + L	521 [0·27]	1142 [0·30]	1898 [0·34]	2591 [0·31]
H + C + L	942 [0·33]	2293 [0·40]	3657 [0·43]	4994 [0·43]
DHL	63	214	297	472
DCL	60	139	302	352
DHL	226	794	1301	1719

* *DXY* indicates an estimate from the difference between the likelihood from combined flocks *X* and *Y* with the likelihood within flocks *X* and *Y*.

standard errors (and total information as the inverse of the sampling variance, Table 2) is shown in Fig. 1 for several line combinations at the end of the experiment (year 21).

The heritability estimates were remarkably consistent both other years and across lines (Table 1). The Control line yielded estimates that were slightly but consistently higher than the estimates from all other line combinations. The derived estimates for the between-line heritabilities tended to be lower than the within-line estimates, with the difference approaching significance by the end of the experiment.

The information on heritability increased approximately linearly with time, since the information per individual hardly varied across years for any line combination except for a consistently lower value up to Year 6 (Table 2). The lower value in the initial years reflected the proportionally greater contribution of base population animals. The between-flock contrasts in Table 2 show that by the end of the experiment, High versus Low contributed 1719 of the 4994 total information, or that within-line information was approximately two-thirds as valuable as the total

response. The comparison of High and Low was almost four times as valuable as the comparison between either selected line with the Control, as might be expected since the selection differentials in the first case were twice those in the second case (Table 2).

As an illustration of the way the between line information is used, Table 3 shows the year estimates for the first 11 years of the three lines for three values of heritability near to the estimates for these data. In the High line, as heritability increases, the predicted genetic merit increases and so the year effects, which are corrected for the genetic merit, decline. The decline becomes larger with time due to the continuing selection. In the Low line, the reverse happens with the year effects increasing with time. There is relatively little change in the Control line as parents are selected at random. Differences between the columns divided by the heritability are a measure of the selection differential and are given in Table 4. The selection differential terms change linearly with time and, to a first approximation, are independent of heritability. The terms are approximately equal in magnitude for the selected lines, showing symmetry between the
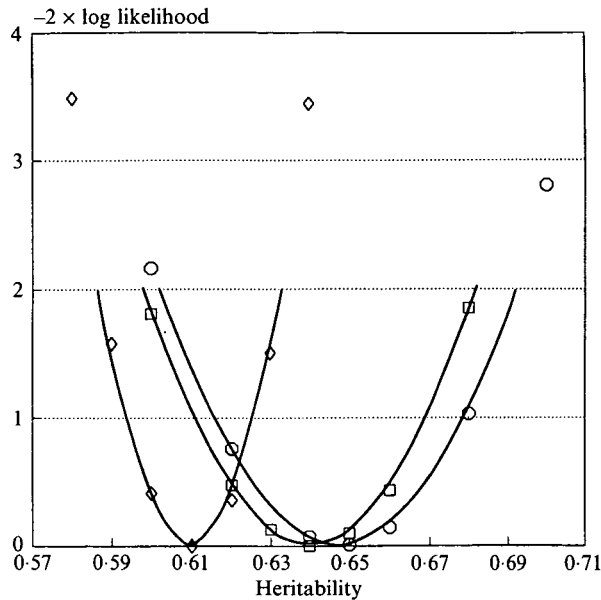
Fig. 1. Relationship between ($-2 \times \log$ likelihood) and heritability around the point of maximum likelihood for the High line ($\square$), Low line ($\bigcirc$), and the High + Low lines ($\lozenge$), using all information up to year 21.

lines, and larger than in the Control line. For comparative purposes, Table 4 also shows the cumulative selection differentials reported by Atkins & Thompson (1986) for the High and Low lines. The cumulative selection differentials, which are based solely on phenotypic differences between selected and unselected animals, were consistently greater in magnitude than the weighted selection differentials calculated here.

The difference of likelihoods L_{DHL} between lines H and L takes a value of heritability to minimize differences between fixed effects in the two lines taking account of the variance-covariance structure of the estimates. An example of the structure of the variance matrix of the year estimates (a_t) is given in Table 5. The variance increases with time and the covariance ($a_t, a_s; t > s$) converges to a constant value as t increases. The structure of this directly observed

Table 4. *Selection differentials for each selected line as a deviation from the control line*

	HIGH		LOW	
Years	WSD*	CSD†	WSD*	CSD†
1	−0·3	0·0	0·5	0·0
2	−0·2	0·0	0·2	0·0
3	1·8	1·8	−2·0	−4·4
4	2·8	3·6	−2·2	−4·4
5	4·0	5·2	−3·3	−4·7
6	4·2	5·3	−3·6	−5·6
7	5·5	6·7	−4·6	−7·0
8	6·4	8·4	−6·5	−9·2
9	7·1	8·9	−7·4	−10·2
10	8·7	10·3	−8·5	−11·5
11	9·8	11·5	−8·2	−12·0

* WSD, Weighted selection differential estimated at $h^2 = 0·6$ using $\Delta h^2 = 0·02$ (see text).
† CSD, Cumulative selection differential as calculated by Atkins & Thompson (1986).

Table 5. *Variance–covariance matrix of year estimates in the Control flock (heritability = 0·60)*

Years	1	2	3	4	5	6	7	8	9	10	11
1	32	—	—	—	—	—	—	—	—	—	—
2	8	38	—	—	—	—	—	—	—	—	—
3	12	10	27	—	—	—	—	—	—	—	—
4	10	10	15	29	—	—	—	—	—	—	—
5	10	10	13	17	31	—	—	—	—	—	—
6	10	10	13	15	19	31	—	—	—	—	—
7	10	10	13	15	17	20	35	—	—	—	—
8	10	11	13	16	17	18	22	38	—	—	—
9	10	11	14	17	18	19	20	25	43	—	—
10	10	10	13	16	19	19	20	30	28	45	—
11	9	10	13	15	19	19	21	27	25	30	46

matrix is similar to those developed by Hill (1972), invoking assumed values for drift variance and measurement error, for the variance of generation means in selection experiments.

Table 3. *Year estimates for each line for different heritability values*

	HIGH (h^2)			LOW (h^2)			CONTROL (h^2)		
Years	0·58	0·60	0·62	0·58	0·60	0·62	0·58	0·60	0·62
1	0·93	0·94	0·94	1·50	1·50	1·49	0·85	0·83	0·83
2	2·06	2·07	2·07	2·55	2·55	2·54	2·10	2·10	2·09
3	1·30	1·26	1·23	2·06	2·10	2·14	1·96	1·93	1·92
4	3·20	3·15	3·09	3·61	3·65	3·70	3·67	3·65	3·64
5	1·13	1·06	0·98	1·64	1·70	1·77	1·51	1·51	1·52
6	1·87	1·79	1·70	3·03	3·10	3·17	2·65	2·65	2·64
7	2·98	2·87	2·76	3·26	3·35	3·45	3·38	3·38	3·37
8	2·84	2·71	2·58	3·22	3·35	3·48	3·06	3·07	3·07
9	2·28	2·14	2·00	2·78	2·92	3·07	2·51	2·52	2·53
10	1·75	1·58	1·40	2·60	2·77	2·94	2·66	2·66	2·66
11	2·31	2·12	1·93	2·35	2·51	2·68	2·41	2·41	2·42

Table 6. *Information per individual (expressed as the inverse of the sampling variance) for maximum · likelihood estimates of heritability (h^2) for various h^2, family sizes (n) and generations (g)*

g	n	$h^2 = 0.05$	$h^2 = 0.1$	$h^2 = 0.4$	$h^2 = 0.6$
1	2	0·182	0·177	0·170	0·184
1	3	0·221	0·213	0·181	0·193
1	5	0·278	0·251	0·182	0·190
1	9	0·362	0·301	0·166	0·168
1	17	0·476	0·347	0·134	0·131
2	2	0·239	0·224	0·190	0·203
2	3	0·275	0·251	0·192	0·204
2	5	0·331	0·285	0·184	0·193
2	9	0·412	0·323	0·161	0·167
2	17	0·515	0·350	0·127	0·129
4	2	0·280	0·256	0·202	0·216
4	3	0·318	0·276	0·198	0·211
4	5	0·365	0·302	0·184	0·195
4	9	0·439	0·330	0·158	0·167
4	17	0·532	0·346	0·124	0·128
Control line					
Year 6					
Female		0·251	0·238	0·210	0·232
Male		0·503	0·319	0·118	0·124
Year 21					
Female		0·335	0·287	0·198	0·214
Male		0·542	0·332	0·114	0·119

Table 7. *Distribution of eigenvalues (familiogram) for the Control line data at Years 6, 11, 16 and 21*

	Proportion			
Eigenvalue	Year 6	Year 11	Year 16	Year 21
< 0·15	0·036	0·044	0·047	0·050
0·15 − 0·35	0·178	0·215	0·232	0·241
0·35 − 0·55	0·359	0·374	0·357	0·353
0·55 − 0·75	0·091	0·092	0·101	0·101
0·75 − 1·0	0·102	0·091	0·087	0·085
1·0 − 1·5	0·095	0·062	0·064	0·062
1·5 − 2·0	0·061	0·033	0·030	0·031
2·0 − 3·0	0·043	0·040	0·033	0·030
3·0 − 4·0	0·011	0·019	0·016	0·014
4·0 − 6·0	0·006	0·011	0·012	0·013
6·0 − 8·0	0·007	0·005	0·005	0·006
8·0 − 10·0	0·003	0·004	0·004	0·004
10·0 − 14·0	0·005	0·005	0·004	0·004
14·0 − 18·0	0·004	0·002	0·003	0·002
18·0 − 22·0	—	0·003	0·002	0·002
22·0 − 26·0	—	0·001	0·001	0·002
> 26·0	—	—	0·001	0·001

(ii) *Information within unselected lines*

As a benchmark to show how information varies with different designs, the information per observation on heritability for the simple, balanced pedigree structure described earlier is given for different heritabilities, family sizes and generations in Table 6. In practice there are other branches in the pedigree, and many links providing information are ignored. Pedigrees using links between dams and offspring in species such as sheep or pigs are modelled by small values of n, larger family sizes are more appropriate for pedigrees linked by sire and offspring. These results show the gain from increasing generations in increasing the information per observation of heritability, especially at small n. In one sense, there are families of size (gn − 1) with unequal covariances between members. For example, there are gn(n + 1)/2 half sibs and gn offspring pairs. Qualitatively, these results mimic Robertson (1977) who considered estimation from two generations.

The information on heritability shows that approximately twice as much information is given by dam-linked families than by sire-linked families within the Control line (Table 6). This is consistent with the model calculations in Table 6 in that smaller families are relatively more informative than larger family sizes. The estimated information separately from male and female families is not simply additive since the dam linked families ignore links between males that impose correlations between the families. For example, at year 21 and heritability of 0·7, the total information in the pedigree was 1249 (Table 2) while the contributions from male and female families was 592 and 957 respectively. However, the information from female families would still make a greater contribution to the overall information than the information from male families.

Distributions of eigenvalues are shown in Table 7 for the Control line in Years 6, 11, 16 and 21. These distributions show the sizes of independent families that would give the same information as the pedigree and are called familiograms. There are a large proportion of eigenvalues of 0·5 and 0·75 representing comparisons between parents and offspring and comparisons within half-sib families respectively.

3. Discussion

There have been few attempts to disentangle how information from an individual animal model influences heritability estimates. Within an unselected population, we have shown that the relative contribution of information from male and female families will depend on the size of the families, the number of generations in the pedigree and the value of heritability. For the specific situation of cannon-bone length in sheep (heritability of 0·6–0·7), information from female families was relatively more important than that from male families. One other attempt to disentangle information sources was the study of Visscher & Thompson (1992) who did so by fitting a model with male and female heritabilities. They showed that in a British dairy cattle population, approximately two-thirds of the total information on heritability came from female relationships, most of that being dam–daughter information.

In a similar manner, information on heritability arises from both between and within selected lines in a selection experiment. The between-line information for the divergence between the high and low selection lines for cannon-bone length yielded a heritability estimate of 0·569 with an estimated standard error of ±0·024 (Tables 1 and 2). Atkins & Thompson (1986) reported a realized heritability estimate from the regression of divergent response on divergent selection differential of 0·52. This value was adjusted, by allowing for the expected reduction in genetic variance arising from linkage disequilibrium, to the equivalent of a base population estimate of heritability of 0·57 ± 0·026. The agreement in estimate and standard error between the two different estimators was very close, indicating the value of the methods proposed by Hill (1972) to appropriately account for genetic drift and the correlations that drift induces between annual estimates of response.

The relative value of alternative designs for contributing information to the estimate of heritability can be determined from the information per individual (Table 2). Over the whole experiment with two divergent selection lines and a control line (H + C + L, year 21), the information per individual was 0·43. If the experiment had been conducted as a single flock with no selection, the information per individual would have been 0·32 (C, year 21). Alternatively, restricting the design to the selected lines only (H + L, year 21) would have resulted in information per individual of 0·49. The proportional cost in information from including the control line in the design must be balanced against the need to test for symmetry of estimates in both directions which, of course, necessitates a control line.

In conclusion, both between-line and within-line information in multi-generation selection experiments designs can make substantial contributions to the precision of an estimate of heritability. In the experiment reported by Atkins & Thompson (1986), between-line analysis of realized responses and within-line analysis of the control line utilized about 60 % of the available information. Alternatively, within-line analysis of all lines separately would have utilized about 65 % of the available information. This contribution of within- and between-line information was specific to this experiment. In selection experiments with lower heritabilities and more effective selection among females, the relative contribution of within-line information would be less important.

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