

ESTIMATION OF DIRECT AND CORRELATED RESPONSE TO SELECTION
BY SINGLE TRAIT AND MULTIPLE TRAIT ANIMAL MODELS

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SUMMARY

Estimates of genetic trend in two egg layer populations by single trait and multiple trait animal models suggest that single trait estimates can be biased if the population has been selected. A computer simulation study was performed to demonstrate the possible nature of the bias.

INTRODUCTION

In a well designed experiment, genetic parameters such as selection response can be effectively estimated separating genetic and environmental sources of variation. Typically this is done using control lines, or using divergent selection. In a breeding program, control lines are seldomly available, and one attempts to estimate selection response using other approaches. One that is advocated is the use of animal models. The availability of more powerful computers and the development of efficient algorithms are making possible to compute genetic variances and breeding values in a unified approach using REML (restricted maximum likelihood) procedures (Smith and Graser, 1986; Meyer, 1989). An estimate of genetic trend is then obtained by taking averages of the relevant estimated breeding values.

When the REML estimates of genetic parameters are used as priors, the animal model has the advantage that it can account for several forms of selection and non-random mating, and it can separate phenotypic trends into its genetic and environmental components. These properties hold though, under the assumption that the model used to analyse the data is the correct one, a condition which is difficult to test. An example of the use of an incorrect model is the implementation of a single trait approach to estimate parameters from data that have been subject to multitrait selection. The researcher may be forced into this situation because multitrait REML algorithms under an animal model, while available (K. Meyer, personal communication), are computationally very demanding. It has been shown that use of the wrong (co)variance matrix as priors in the mixed model equations in populations under selection, can lead to biased prediction of breeding values (Henderson, 1975) and of selection response (Thompson, 1986; Meyer and Thompson, 1984).

In an experiment with two egg layer populations, it was discovered that genetic trends estimated with a multiple trait animal model, in some instances deviated systematically from estimates from the same population obtained with a single trait model. In order to confirm whether these deviations were consistent with those that arise when a single trait analysis on a correlated trait fails to account for changes associated with selection on primary traits, a simulation study was undertaken. Selection was practised for 5 generations on trait one, and at the end of the experiment, a single trait analysis using an animal model was carried out on trait two, in order to estimate genetic trend.

MATERIAL AND METHODS

Study on real data

From 1987 to 1989 two egg layer strains (Rhode Island Red and New Hampshire White) were selected on feed consumption and egg mass using a multitrait animal model containing both traits. The aim was to improve egg mass production genetically without increasing feed consumption. The model contained as fixed effects the combination of year and hatching and the effect of deck level. Random effects were animals and residuals. A contemporaneous White Leghorn population was kept as control. The required estimates of genetic parameters to start the experiment were obtained from data on the two lines during 1985 to 1987. All subsequent analyses as well as the predictions of breeding values were therefore made using 1985 as the base population. Totally there were 2513 New Hampshire observations and 3554 Rhode Island Red observations in the data.

A canonical transformation on the data was performed so that two uncorrelated traits were constructed (Arnason, 1982). Breeding values for each trait were calculated by transforming back to the ordinary scale. Variance components were estimated with a single trait model using a derivative free approach (Graser and Smith, 1987) and the resulting (co)variance structure was used in the transformation of the data to canonical scale. Genetic trends were estimated averaging breeding values within generations for each method.

Simulation study

An infinitesimal animal model was simulated using a bivariate form of the model used by Sorensen (1988). Each generation, 40 males and 200 females were selected for trait 1 on the basis of predicted breeding values obtained using a single trait animal model. After 5 cycles of selection using the 4840 records available on trait 2, a single trait animal model was used to compute genetic trend. The simulated traits were genetically uncorrelated, but the environmental correlation was assumed to be 0.5.

RESULTS

Study on real data

The production results in years 1985 to 1989 expressed as egg mass (EM) were 43.0 and 47.9 and as feed consumption (FC) 118.9 and 130.9 grams/day and corresponding standard deviations were for egg mass 8.2 and 7.3 and for feed consumption 11.2 and 7.7 grams/day for New Hampshire and Rhode Island Red, respectively. Estimates of genetic parameters using all the data with a single trait REML animal model are shown in table 1. These do not deviate much from estimates obtained using the first three generations of data. The high heritability estimate of feed consumption is in agreement with other studies, and accounts for the high variability in the estimates of genetic trend. Both genetic and environmental correlations are positive and the environmental correlation is higher than the genetic in both lines. The resulting genetic trends estimated from single trait and multitrait methods are presented in Table 2. For egg mass there has been a steady progress and both methods give similar trends. For feed consumption single trait estimates of genetic trend are more unfavourable than multiple trait estimates.

Table 3 shows estimated trends, averaged over breeds, using deviations from the control, and using multitrait and single trait approaches, without the control.

For egg mass, all three methods give a consistent picture. For feed consumption, the deviations from control and the multitrait approach show a small initial decline, followed by an increase in the later stages of the experiment. The single trait estimates though, show a consistent increase throughout.

Table 1. Genetic parameters for each line estimated by a single trait mixed model on data from 1985-89. Genetic correlations above, environmental correlations beneath and heritability on the diagonal. EM = egg mass; FC = feed consumption.

Trait	New Hampshire White		Rhode Island Red	
	EM	FC	EM	FC
EM	0.24	0.36	0.13	0.15
FC	0.53	0.56	0.50	0.47

Table 2. Genetic progress estimated from single trait (S) and multiple trait (M) animal models. Results expressed as deviations from 1985.

Trait	Year	New Hampshire White		Rhode Island Red	
		M	S	M	S
EM	86	0.37	0.36	0.32	0.32
	87	1.38	1.42	1.38	1.38
	88	2.77	2.80	2.40	2.40
	89	4.63	4.66	3.41	3.40
FC	86	0.46	0.69	-0.34	0.08
	87	-0.49	0.37	0.18	1.24
	88	-0.44	1.00	0.72	2.24
	89	2.93	4.71	0.43	2.24

Table 3. Genetic progress estimated as deviations from control (C), and from single trait (S) and multitrait (M) animal models, averaged over breeds. Results expressed as deviations from 85.

Year	C		M		S	
	EM	FC	EM	FC	EM	FC
86	0.94	-0.18	0.33	-0.11	0.33	0.26
87	2.12	-0.53	1.38	-0.12	1.39	0.85
88	0.62	-1.48	2.58	0.17	2.59	1.70
89	3.37	2.21	3.94	1.52	3.95	3.32

Simulation study

The results of the simulation study are summarised in Table 4. There is good agreement between predicted and true response for the selected trait. For trait 2, the genetic means computed using the animal model are biased upwards. In both traits, the true heritabilities were used as priors. Using an approach similar to Henderson (1975), it can be shown that in the case of the model used in this simulation, the positive bias is due to the positive phenotypic selection differential in trait 2 induced by selection on trait 1, due to the positive environmental correlation between both traits. The univariate animal model assigns a genetic component to this phenotypic selection differential, thus creating a bias.

Table 4. Average differences between predicted and true breeding values for trait 1 (PBV1-BV1) and 2 (PBV2-BV2) and empirical standard deviations of the difference (SD) in 5 cycles of selection. Heritability of both traits is 0.5; genetic correlation = 0; environmental correlation = 0.5 (average of 5 replicates; i.e. standard error = $SD/\sqrt{5}$)

Cycle	PBV1 - BV1	PBV2 - BV2	SD
0	-0.01	0.07	0.162
1	-0.04	0.38	0.317
2	0.02	0.44	0.425
3	0.00	0.72	0.439
4	-0.01	0.85	0.619
5	0.02	1.10	0.617

Average BV1 at cycle 5 = 7.40 units. Initial genetic standard deviation of trait 2: 5 units.

DISCUSSION

Animal breeding programs must compete for financial and other resources. Monitoring of genetic progress is crucial in deciding on their success and affect decisions concerning their continuing implementation. In the example presented here, conclusions concerning changes in feed consumption vary according to whether they are based on the single trait or the multitrait estimates. Relative to the multitrait and the control estimates, those obtained from the single trait analysis seem to be biased upwards. This is consistent with the simulation results, which assumed that the traits were genetically uncorrelated. A non-zero genetic correlation would contribute negatively to the bias of the estimate of genetic change of the correlated trait.

In the poultry selected data, genetic parameters were estimated using a single trait animal model. A multitrait model will be used in the near future. The available single trait estimates are likely to be biased due to the multitrait selection that took place, which will in turn affect the multitrait estimates of genetic trend. In the present situation though, the multitrait and the control estimates give a reasonably consistent picture. How to compute response if control lines are not available? In order to minimise bias, it seems necessary to use multitrait methods in the estimation of (co)variance components, perhaps in the initial subset of the data, if computing requirements are limiting. These estimates should then be used as priors in the analysis of the whole data set, again, with multitrait procedures. Alternatively, through design such as use of frozen semen, simpler estimators can be used which rely on a smaller set of assumptions than the animal model.

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