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Estimation of additive genetic variance in commercial layer poultry and simulated populations under selection

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Abstract Changes in genetic parameters over generations for a selected commercial population and simulated populations of poultry with different sizes were studied. The traits analyzed from the commercial population were rate of lay, age at first egg, egg weight, deformation, and body weight. In the simulated population, a trait measured on both sexes and a sex-limited trait, measured only on one sex, each with a heritability of 0.1 and 0.5, were analyzed. In the commercial and simulated populations, males and females were selected on the basis of family selection indexes and data was available only after many generations of selection. Parameters for each generation were estimated by fitting an animal model using derivative free maximum likelihood (DFREML) with different data structures. In structure 1, data included the given (base) generation for which the parameters were to be estimated, and all subsequent generations. In structure 2, only data on birds in the given generation and their progeny were included. In both structures, parents of base-generation birds were assumed unrelated and pedigrees traced back to these parents. With commercial data using structure 1, estimates of σ_a^2 and h^2 decreased by 14 to 37% across five generations. With structure 2, no trends were observed, though estimates were lower than for structure 1. For simulated data, with a heritability of 0.1, both structures yielded apparently unbiased estimates of the observed additive genetic variances in the (selected) base generation, no matter how many generations of data were utilized, for both sex-limited and normal traits. However, with a heritability of 0.5 the estimated additive genetic variance for both types of trait decreased with a decrease in the number of generations used in the estimation. Estimates based on the first two generations underestimated, while estimates based on five generations of data overestimated, the observed genetic variances in the defined base. The combinations of conditions that lead to varying degrees of bias remain undefined.

Key words Parameter estimation · Poultry · Relationship matrix

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Introduction

Genetic parameters are often estimated from data on selected animals. Theory indicates that the effect of selection can be accommodated by an appropriate model that includes all data upon which selection decisions were based, tracing back to the unselected base generation (Henderson 1975; Gianola and Fernando 1986). In practice, however, genetic relationships and data rarely trace back to the true base population. In such cases, the parents of animals from the earliest generation of available data are generally assumed to be unrelated, non-inbred and randomly mated, even though these assumptions are unlikely to be true.

In a simulation study, Sorensen and Kennedy (1984) confirmed by analysis of simulated lines that unbiased estimates of genetic variance of the true base population, prior to any selection, were obtained when data came only from later generations, but all relationships to the original base were included. They also concluded, for a simple example, that the estimate of the additive genetic variance of a given generation in a selected population was nearly unbiased when the model included all relationships, data that developed in subsequent generations, and data on all animals in the given generation prior to selection.

Results in a similar study (van der Werf and De Boer 1990) showed that increasing the amount of subsequent data did not affect the mean estimate of genetic variance for a given generation, although that estimate was biased upward in some cases. There were also small biases in estimates of genetic variance of the base unselected genera-

tion in some cases, even with all relationships tracing back to this generation. The present study initially set out to estimate genetic parameters for key traits in a selected layer poultry population. Finding that estimates were affected markedly by the amount of data included in the analysis, the effects on estimates of genetic variance of trait type (sex-limited vs normal), number of generations of data, initial heritability, and intensity of selection were examined in simulated selection lines resembling the commercial population.

Materials and methods

Commercial poultry population

Egg production data from six generations of selection of a commercial egg-layer poultry line, previously selected for more than 30 generations, was used in this study. Many traits were recorded and used in selecting males and females in the commercial selection program. Five economically important traits were analysed to obtain estimates of the genetic and phenotypic variances and covariances in each generation from 1980 to 1985. The traits were age at first egg, rate of lay (onset of lay to 283 days of age), body weight (at the age of 265 days), egg weight (from an average of four eggs per hen at the age of 265 days), and deformation (from an average of four eggs per hen). Means and standard deviations for all five traits are given in Table 2.

Most of the sires and all the dams in each generation were selected from the previous generation, but a small number of males were used in more than one generation based on their progeny test. The number of dams and sires used in each generation is given in Table 1. The sires in each generation were selected on information from their half-sib and full-sib part records and the dams were selected on their own half-sib and full-sib part-records, but the exact selection criterion is not known. Within each year, there were either one or two hatches of birds.

Only those birds with records for all five traits were used in the estimation of variances and covariances to obtain an equal design matrix for all traits. This is unlikely to cause any bias since only a handful of records were eliminated. The number of records used in each year and the means and standard deviations for the five traits used in the multiple trait evaluation are given in Table 2.

Simulated poultry population

Selected poultry populations were simulated for ten generations with 20 replicates of each population type. Populations had either 960 or 2880 individuals per generation. Two standardized selection differentials for both females and males were obtained by changing the average full-sib family size from eight (four females and four males) to 12 (six females and six males). With an average full-sib family size of 12, base populations were obtained as offspring of non-related, randomly chosen eight males and 80 females, for a population of 960, and 24 males and 240 females for a population of 2880. For an average full-sib family size of eight, the base populations were obtained as non-related, randomly chosen 12 males and 120 females for a population size of 960, and 36 males and 360 females for a population size of 2880. For a sex-limited trait, only the females had records, but for a normal trait both males and females had records.

An observed loss rate of 10% from 1-day old to maturity for both males and females in commercial data was accounted for in simulated data by adjusting the mean and variance of the full-sib family size. The loss rate after selection was assumed to be zero. In each year the progeny of each full-sib family were divided between two hatches and the hatch effects were randomly chosen with a mean of zero and a variance equal to 3.165% of the phenotypic variance, as estimated from commercial data.

Table 1 Distribution of number of hatches, number of sires, number of dams and the number of records across the 6 years of commercial data

Number of hatch	Number of sires[a]	Number of dams	Number of records
2	48	339	2945
2	48 (48, 0, 0, 0)	342	2890
1	47 (37, 10, 0, 0)	382	2760
2	45 (38, 7, 0, 0)	353	2872
1	54 (42, 10, 2, 0)	378	2932
1	51 (44, 0, 6, 1)	378	3025
		Total	17424

[a] Number of males coming from 1, 2, 3 and 4 generations, previous given in parentheses

The additive genetic value of each progeny was simulated assuming an infinitesimal additive genetic model, as $A_p=0.5\times A_s+0.5\times A_d+A_m$, where A_p, A_s and A_d are the additive genetic values of the progeny, sire and the dam and A_m represents the Mendelian sampling of gametes from the sire and dam with a mean of zero and a variance of $0.5\times[1-0.5(F_s+F_d)]\sigma_a^2$, where F_s and F_d are the inbreeding coefficients for the sire and dam, calculated for each generation using Tier's (1990) algorithm.

The phenotypic value of each progeny was simulated as $P_p=A_p+H+E_p$, where H is the hatch effect and E_p is a random error term, with mean zero and variance σ_e^2. The error variance was assumed constant across generations. The initial parameter values were $\sigma_p^2=100$ with heritability $h^2=0.1$ or 0.5. The observed additive genetic variance in each generation was calculated as the variance of additive genetic values of simulated individuals prior to selection.

Selection of breeding birds

For a sex-limited trait, the indexes for males were calculated from full-sib and half-sib averages after adjustment for the fixed effect. Adjustments for the fixed effects were estimated as the mean of all observations within the fixed-effect level. The index for females, and for males with a non-sex-limited trait, was calculated from its own half-sib and full-sib records after being adjusted for fixed effects.

Rates of inbreeding were restricted by selecting a maximum of two males per full-sib and a maximum of six males per half-sib family and a maximum of five females per full-sib and 30 females per half-sib family. Full and half-sib matings were avoided.

Methods and models

Estimation of genetic parameters

The variances and covariances for the five traits in each generation from the commercial poultry population were estimated using DFREML (Meyer 1986) animal models with two different data structures [see van der Werf and De Boer (1990) for a fuller description of this type of analysis applied to a very similar data structure]. In all cases, the models included year×hatch fixed effects and additive genetic relationships tracing back to parents of the base generation as defined below. A regression on inbreeding coefficient was considered unnecessary since changes in inbreeding levels were small (see Results).

Single-trait analyses were used to obtain estimates of genetic variances and heritabilities, and these estimates were then used in a multiple-trait analysis of all five traits to obtain genetic covariances and correlations among traits.

Table 2 Mean and standard deviation (in parentheses) for the five traits in the commercial data in each year

Year	Number of records	Rate of lay (%)	Body weight (g)	Egg weight (g)	Deformation (μm)	Age at first egg (days)
1980	2944	90.19 (6.78)	1569.6 (189.29)	57.54 (3.85)	25.26 (3.02)	160.25 (10.02)
1981	2890	89.32 (6.61)	1560.5 (180.00)	57.06 (3.71)	23.52 (3.88)	156.90 (8.01)
1982	2760	89.73 (6.53)	1541.2 (176.99)	58.16 (3.98)	22.04 (2.90)	149.83 (4.96)
1983	2872	90.52 (5.79)	1557.6 (171.40)	59.01 (3.80)	20.76 (2.84)	160.37 (7.22)
1984	2932	90.56 (5.75)	1485.0 (166.78)	60.49 (4.12)	21.72 (3.05)	152.51 (4.80)
1985	3025	87.05 (6.56)	1614.3 (186.51)	58.90 (3.70)	23.35 (3.34)	135.96 (7.43)

Table 3 Number of generations of data used and estimated additive genetic variances of the five traits in the commercial data in each generation, using data structure 1

Year	Number of generations	Rate of lay ($\%^2$)	Body weight (g^2)	Egg weight (g^2)	Deformation (μm^2)	Age at first egg ($days^2$)
1980	6	7.99	25211	13.33	4.14	26.06
1981	5	7.46	24219	12.87	4.24	19.19
1982	4	6.89	22667	13.71	3.44	16.15
1983	3	5.86	21004	11.32	3.14	21.23
1984	2	5.86	19515	10.59	3.20	16.47

Structure 1

In structure 1, the estimates for a particular generation were obtained using the performance data from that generation and all later generations. For example, estimates for the year 1980 were obtained using data from year 1980 and all later generations; for year 1981 the data from year 1981 and all later generations were used and so on. Thereby, the number of generations of data and pedigree information for each year varied (see Table 3). For each estimate, parents of birds from that generation were assumed to form a randomly mated, non-inbred and unrelated base population, and pedigrees traced back to these parents.

Structure 2

In structure 2, the estimates for a particular generation were obtained by using performance data from that generation and from its progeny. For example, the estimates for the year of 1980 were obtained by using data from the years of 1980 and 1981, and for the year of 1981 from 1981 and 1982 and so on. Thereby, the number of generations of data and pedigree information used to obtained the estimates for each generation was constant (see Table 4). Again, the parents of the generation for which parameters were being estimated were assumed to be randomly mated, unrelated and non-inbred, and pedigrees traced back to these parents.

Similar methods and models were used to estimate parameters in the simulated populations, with the following modifications. Generation 6 was considered the first possible generation to have data available, so that the population was in stable-state gametic-phase disequilibrium. Structure 1 was modified slightly such that generation 6 was always the first generation with data, but increasing numbers of subsequent generations were included in the estimation. This was done since the principal question raised by the analysis of commercial data was whether the results were a function of the number of generations of data used. Here the base remains constant and only the number of subsequent data is altered. Structure 2 was identical to that described for the commercial population.

Results and discussion

Commercial poultry population

Estimated additive genetic variance in each generation with structure 1

Estimated additive genetic variances for all five traits decreased across generations with structure 1 data (Table 3). The total reductions across the 5 years were 26.78%, 22.59%, 20.55%, 22.71% and 36.8% for rate of lay, body weight, egg weight, deformation, and age at first egg, respectively. The reduction in additive genetic variance of age at first egg was more erratic than for other traits. This may be due to differences in the average age at the start of recording egg production across years, which caused variation across years in the percentage of birds already laying when recording started.

Inbreeding

Realized average inbreeding coefficients, for selected and unselected birds born in each year, when assuming the parents of 1981 birds formed a non-related randomly mated base population, are shown in Fig. 1. The estimated inbreeding for the first 2 years was zero, as expected when half-sib and full-sib matings are avoided. The estimated inbreeding in subsequent years is expected to increase asymptotically toward the true inbreeding rate of the population as the estimated relationship structure of the population approaches that of the true relationship structure. It would appear that the estimated rate of inbreeding

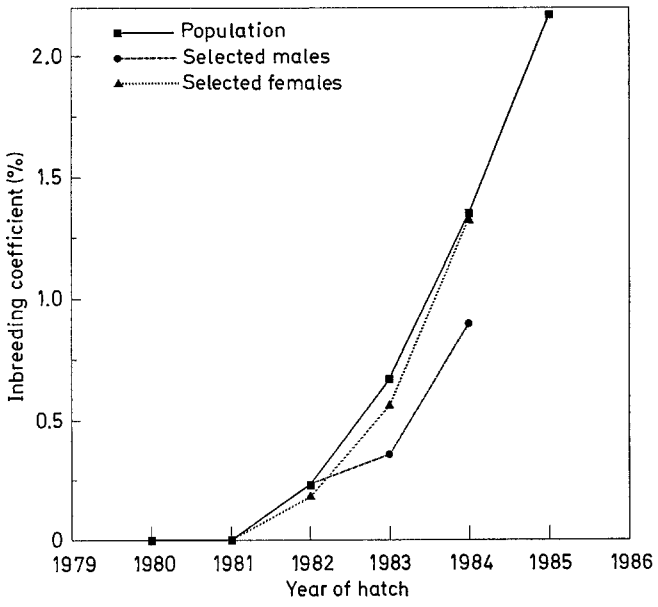

Fig. 1 Estimated average inbreeding coefficient in the female population prior to selection and the inbreeding coefficient among the selected males and females when assuming the parents of birds in year 1980 were unrelated

between 1984 and 1985 is close to, but probably not yet at, the equilibrium rate. Thus the asymptotic rate of inbreeding in this population is probably a little less than 1% per annum.

There was little difference in inbreeding between the unselected and selected females, but selected males born in 1983 and 1984 had considerably lower inbreeding coefficients. Selected birds might be expected to have lower inbreeding coefficient than unselected if the inbreeding level were negatively correlated with performance, due to inbreeding depression. This effect might be much more noticeable for males than females, since males are selected primarily on their full-sister average performance. Any inbreeding depression of the full-sister group (all of the same inbreeding coefficient) would be relatively well estimated. With females, their own performance would carry the greatest weight and much of the selection would effectively remain within families. Selection would partially act on those individuals within families not exhibiting inbreeding depression and selection would thus have less, perhaps very little, effect on average inbreeding level.

Reduction in additive genetic variance

As shown by Bulmer (1971, 1980), the reduction in variability due to gametic-phase disequilibrium in a population which has been selected for a long period should be balanced by recombination of alleles in each generation such that genetic variance remains constant over time. In such cases any reduction in genetic variance across generations might be due to an increase in inbreeding among the birds. Assuming steady state gametic-phase disequilibrium, the genetic variance in generation t is expected to be approximately,

$$V_t = V_o(1 - F_{t-1})$$

where V_o is the additive genetic variance at zero inbreeding and F_{t-1} is the average inbreeding coefficient of parents of the t^{th} generation. Assuming that the increase in inbreeding in each generation was 1%, as estimated from the data, and starting with the estimated genetic variance in 1980 from structure 1, the observed reduction in estimated additive genetic variance across years (Table 3) was considerably larger than the expected 5% reduction due to the increase in inbreeding.

Changes in selection intensity could cause changes in genetic variance due to altered levels of gametic-phase disequilibrium, but the relationship between intensity and genetic variance is markedly non-linear (Bulmer 1971, 1980) such that large changes in intensity above any weak selection cause little change in genetic variance. This population was under continuous selection and any changes in selection intensity across generations would be small and could not account for the amount of change in variance observed here.

Estimated additive genetic variance in each generation with structure 2

The estimated additive genetic variances of the five traits in each generation when structure 2 was used are given in Table 4. Other than age at first egg in 1980 the estimated additive genetic variances for all the traits in each generation were lower than the values estimated with structure 1. Estimated additive variances for rate of lay with both structure 1 and structure 2 decreased over years. The relative difference between the estimates from the two structures decreased across generations for body weight, egg weight, and deformation. In large part, this reflects the decrease in the difference in the number of generations of data used to estimate the genetic parameters with the two structures. With 1984 as the base population, the data used in the two structures were identical. Overall it would appear that the estimated additive genetic variances in the selected base population for each trait decreased as the number of generations used in the analysis decreased, and that changes observed across generations with structure 1 were method-dependant rather than a reflection of real changes in genetic variances.

Heritabilities and additive genetic correlations

Estimated heritabilities and additive genetic correlations among the five traits using data from all 6 years are given in Table 5. Estimates of heritabilities showed the same pattern as additive genetic variance when data structure and the amount of data were altered (Tables 3 and 4). Estimates of genetic correlations showed smaller changes than heritabilities and variances as the number of generations of data

Table 4 The number of generations of data used and the estimated additive genetic variances of the five traits in the commercial data in each generation, using data structure 2

Year	Number of generations	Rate of lay ($\%^2$)	Body weight (g^2)	Egg weight (g^2)	Deformation (μm^2)	Age at first egg ($days^2$)
1980	2	7.97	18339	7.63	3.43	33.43
1981	2	7.21	18174	8.17	3.40	14.50
1982	2	5.69	19779	10.88	2.32	11.92
1983	2	5.31	16873	9.37	2.25	17.90
1984	2	5.86	19515	10.59	3.20	16.47

Table 5 Estimated heritabilities (diagonal), additive genetic correlations (above diagonal) and phenotypic correlations (below diagonal) among the five traits when data from all six generations of commercial data were used. Standard errors in parentheses

Trait	Rate of lay	Body weight	Egg weight	Deformation	Age at first egg
Rate of lay	0.19 (0.07)	0.07 (0.11)	–0.29 (0.11)	0.44 (0.14)	–0.16 (0.13)
Body weight	0.02	0.68 (0.05)	0.58 (0.03)	0.09 (0.07)	0.32 (0.05)
Egg weight	–0.16	0.48	0.73 (0.05)	0.38 (0.06)	0.07 (0.06)
Deformation	0.04	0.05	0.04	0.38 (0.06)	–0.01 (0.09)
Age at first egg	–0.03	0.17	0.09	–0.01	0.48 (0.05)

Table 6 Estimated heritabilities (diagonal) and additive genetic correlations (above diagonal) among the five traits when data from years 1984 and 1985 in the commercial data were used. Standard errors in parentheses

Trait	Rate of lay	Body weight	Egg weight	Deformation	Age at first egg
Rate of lay	0.15 (0.04)	0.01 (0.12)	–0.32 (0.12)	0.40 (0.20)	–0.18 (0.13)
Body weight		0.57 (0.07)	0.50 (0.07)	0.04 (0.12)	0.28 (0.08)
Egg weight			0.63 (0.09)	0.09 (0.13)	0.08 (0.10)
Deformation				0.30 (0.07)	0.01 (0.13)
Age at first egg					0.41 (0.06)

decreased. However, as illustrated in Table 6, all genetic correlations were lower when only two generations of data were used (1984–85) than when all six generations were used (Table 5). Thus, positive genetic correlations decreased somewhat and negative genetic correlations become more negative.

Since using data from all six generations provides the most accurate estimates, further discussion focuses on the results in Table 5. Estimated heritability for rate of lay was lowest among the five traits and was slightly higher than the average estimate of 0.17, reported from the literature by Fairfull and Gowe (1990), based on sire and dam components. The estimate was however at the top end of the range of 0.15 to 0.19 reported by these authors. Moderate heritabilities were obtained for deformation and age at first egg. The estimated heritability for deformation was well within the range of 0.28 to 0.60 and close to the mean of 0.4 reported by van Tijen and Kuit (1970) from sire components and sire and dam components of variance. Similarly, the heritability value obtained for age at first egg was well within the range of 0.07 to 0.90 and close to the mean of 0.42 reported by Kinney (1969) from the literature. The estimated heritabilities for body weight and egg weight were well above the means of 0.48 and 0.45 but within the range of 0.17 to 0.89 and 0.3 to 0.86 reported in the literature (Kinney 1969).

Only the genetic correlations between rate of lay and egg weight (–0.29), rate of lay and deformation (0.44), body weight and egg weight (0.58), and body weight and age at first egg (0.32), were statistically significant ($P<0.05$). The correlation between egg weight and deformation (0.13) approached statistical significance ($P<0.1$). All estimates were well within published ranges (Kinney 1969; van Tijen and Kuit 1970; Fairfull and Gowe 1990). Phenotypic correlations were generally similar to, but somewhat smaller in absolute terms than, genetic correlations. The exception was the correlation between rate of lay and deformation, with a phenotypic correlation of 0.04 and a genetic correlation of 0.44. This would imply that the environmental correlation between these two traits would be negative.

Simulated populations

Observed genetic variances and inbreeding

The observed additive genetic variance and the average inbreeding coefficient at generation 5 for several combinations of simulation parameters are given in Table 7.

Due both to build up of gametic-phase disequilibrium and inbreeding, genetic variances at generation 5 were 20 to 40% lower than initial genetic variances. When other parameters were held constant, the proportional reductions in genetic variance by generation 5 were largest for sex-limited traits, the higher heritability, the smaller population size and the larger family size, though the contrast between sex-limited and normal traits was only seen for the high heritability of 0.5.

Average inbreeding coefficients at generation 5 lay between 0.03 and 0.15, being at the top end for the smaller population size and larger family size. There was also ev-

Table 7 Estimated genetic variance for various combinations of population size, type of trait, heritability and number of generations of simulated data[a]

Population size	Full-sib family size[b]	Trait	h^2	Observed[c] σ_a^2	Inbreeding[c] coefficient	Data from	Estimated σ_a^2
960	12	Sex limited	0.1	7.18 (0.18)	0.15 (0.003)	Gen 6–7	10.23 (1.38)
						Gen 6–8	8.40 (0.89)
						Gen 6–9	9.03 (0.73)
						Gen 6–10	8.47 (0.93)
2800	12	Sex limited	0.1	8.25 (0.13)	0.05 (0.001)	Gen 6–7	8.29 (0.56)
						Gen 6–8	8.07 (0.58)
						Gen 6–9	8.37 (0.58)
						Gen 6–10	8.79 (0.58)
2800	8	Sex limited	0.1	8.32 (0.13)	0.04 (0.001)	Gen 6–7	8.28 (0.65)
						Gen 6–8	8.79 (0.60)
						Gen 6–9	8.49 (0.51)
						Gen 6–10	8.80 (0.47)
2800	8	Normal	0.1	8.30 (0.14)	0.04 (0.001)	Gen 6–7	8.22 (0.46)
						Gen 6–8	8.07 (0.58)
						Gen 6–9	8.56 (0.37)
						Gen 6–10	8.66 (0.35)
960	12	Sex limited	0.5	32.19 (0.18)	0.15 (0.003)	Gen 6–7	27.10 (2.12)
						Gen 6–8	31.11 (2.23)
						Gen 6–9	34.71 (2.19)
						Gen 6–10	35.94 (2.38)
960	8	Sex limited	0.5	35.05 (0.69)	0.10 (0.002)	Gen 6–7	36.92 (2.16)
						Gen 6–8	36.24 (2.19)
						Gen 6–9	39.28 (1.97)
						Gen 6–10	39.73 (1.83)
2800	12	Sex limited	0.5	36.59 (0.73)	0.05 (0.001)	Gen 6–7	32.91 (1.63)
						Gen 6–8	36.55 (1.44)
						Gen 6–9	37.99 (1.49)
						Gen 6–10	39.53 (1.45)
2800	8	Sex limited	0.5	39.01 (0.56))	0.04 (0.001)	Gen 6–7	34.37 (1.63)
						Gen 6–8	37.86 (1.44)
						Gen 6–9	38.88 (1.49)
						Gen 6–10	40.25 (1.45)
2800	8	Normal	0.5	35.55 (0.36)	0.03 (0.002)	Gen 6–7	29.81 (1.50)
						Gen 6–8	33.94 (1.50)
						Gen 6–9	36.26 (1.06)
						Gen 6–10	38.34 (0.92)

[a] Standard errors from 20 replicates in parentheses
[b] Proportion selected, P=0.0185 for males and 0.185 for females when FS size=12, and P=0.0278 for males and 0.2778 for females when FS size=8
[c] Variance of observed additive genetic values of birds prior to selection in generation 5

idence of a small decrease for a normal versus a sex-limited trait when the heritability was high. These observations on inbreeding and variance are consistent with the effect of accuracy of selection on gametic-phase disequilibrium (Bulmer 1980) and on various factors involving the probability of co-selection of relatives and hence inbreeding (Wray and Thompson 1990; Brisbane and Gibson 1995).

Estimation of additive genetic variance for a sex-limited trait

Estimates of genetic variance for generation 5 using data from different numbers of generations are given in Table 7. In general, estimates of genetic variance did not show any clear trend as the number of generations of data increased when the heritability was 0.1. For the large population size, the estimated genetic variances were not significantly different from the observed additive genetic variances of generation 5. For the smaller population size estimated genetic variances were significantly higher (P<0.05) than the observed genetic variance when two or four generations of data were utilised.

With a heritability of 0.5, the estimated variances increased with an increase in the number of generations of data used in the estimation (Table 7). Increases were significant (P<0.05), except for the population size of 960 and full-sib family size of eight. When data from generations 6 and 7 were used, most estimates of genetic variance were statistically significantly lower than the total additive genetic variance of generation 5 (Table 7). The exception was

Table 8 Estimated genetic variance for a simulated sex-limited trait with a constant number of generations of data at two heritabilities[a]

Population size	Full-sib family size[b]	h^2	Observed $\sigma^{2\,c}_a$	Gen.	Average inbreeding coefficient	Data from	Estimated variance
2800	8	0.1	8.32 (0.13)	5	0.04 (0.001)	Gen 6–7	8.28 (0.65)
			8.47 (0.13)	6	0.05 (0.001)	Gen 7–8	7.77 (0.80)
			8.41 (0.11)	7	0.06 (0.001)	Gen 8–9	8.22 (0.71)
			8.45 (0.14)	8	0.07 (0.001)	Gen 9–10	8.66 (0.70)
2800	8	0.5	39.01 (0.56)	5	0.04 (0.001)	Gen 6–7	34.37 (1.63)
			37.55 (0.47)	6	0.05 (0.001)	Gen 7–8	32.52 (1.45)
			37.10 (0.54)	7	0.06 (0.001)	Gen 8–9	33.72 (1.66)
			37.14 (0.55)	8	0.07 (0.001)	Gen 9–10	31.74 (1.47)

[a] Standard errors for 20 replicates in parentheses
[b] Proportion selected=0.0278 for males and 0.2778 for females
[c] Variance of observed additive genetic values of birds prior to selection in the stated generation

with a population of 960 and family size of 12, where the estimated genetic variance using data from generations 6 and 7 was slightly, but not significantly, higher than the observed additive genetic variance of generation 5. In all cases where estimated genetic variances were lower than the observed genetic variance at that generation, estimates were higher than the additive genetic variance among the selected sires and dams (data not shown). In all cases the estimated genetic variances when using data from all later generations were considerably higher than the observed total additive genetic variance of generation 5, but the difference was statistically significant only in the population size of 960 with average full-sib family size of eight for a sex-limited trait with a heritability of 0.5. In no case did the estimate approach the additive variance in the original unselected base generation (σ^2_{ao}), or the expected variance at generation 5 if only inbreeding had affected variance [i.e., $\sigma^2_{ao}(1–0.03)$].

With a sex-limited trait, when the base generation was altered and data was always from two subsequent generations (Table 8), the estimated additive genetic variances were not significantly different from each other. The estimates were significantly lower than the observed additive genetic variances of each generation when the initial heritability was 0.5, but very close to observed values when heritability was 0.1.

Estimation of additive genetic variance for a trait measured in both sexes

The estimated additive genetic variance for a trait measured in both sexes, with heritabilities of 0.1 and 0.5 with a population size of 2880, are given in Table 7. As observed with a sex-limited trait, the estimated genetic variance did not show any clear trend as the number of generations of data was increased, when the heritability was 0.1. Also, the estimates of genetic variance using data from different numbers of generations were not significantly different from the observed additive genetic variance of generation 5.

For an initial heritability of 0.5, the estimates of genetic variance increased as the number of generations of data increased (Table 7). As observed with a sex-limited trait, the estimated genetic variance using data from generations 6 and 7 was significantly lower than the observed total additive genetic variance of generation 5. Similarly, the estimated genetic variance when using data from all later generations was significantly higher than the observed additive genetic variance of generation 5.

General discussion

An animal model tracing all relationships from the unselected base population is expected to give an unbiased estimate of additive genetic variance of the base population (Henderson 1975; Sorensen and Kennedy 1984; Gianola and Fernando 1986). When data from the earliest generations are not available, the estimates for a selected base population may be influenced by the selection of ancestors (van der Werf and De Boer 1990). In the present analysis of commercial data, estimates of heritabilities decreased across years, coincident with a reduction in the number of generations of information used (data structure 1), but not when the number generations of information remained constant (data structure 2). Changes in estimates across years were too large to be explained by changes in inbreeding or in gametic-phase disequilibrium, due to changes in selection intensity. In the simulated study, estimates of observed genetic variances were substantially biased for a sex-limited and a normal trait of high heritability, with the direction of bias depending on the number of generations of data used. Biases were only observed for traits of low heritability for two combinations of data and population parameters, and were then overestimates of observed variances. In all cases, estimates of genetic variance were substantially lower than genetic variance in the true base unselected populations.

The structure of our simulations is similar to that of van der Werf and De Boer (1990), except that these authors had smaller populations (five breeding males and 20 breeding

females), with phenotypic selection in males and no selection of females for a trait with a heritability of 0.5. In three of the four situations, which matched those explored here, van der Werf and De Boer (1990) found that genetic variance in the defined generation was overestimated by 8–9%, while in the fourth case no bias was observed. Sorensen and Kennedy (1984) simulated population structures very similar to van der Werf and De Boer (1990) but, in the one case examined, observed no bias in estimation of genetic variance in the defined generation. Combined with our own results, these studies argue that biases in the estimation of genetic variance for a given generation could be anywhere from –20% to +15%, and biases in estimates of true base-generation variance (prior to any selection) range from about –45% to –10%. These biases are relevant to most practical situations since it is rare for pedigrees to be available back to a previously unselected base generation.

The results do not, however, point clearly to the conditions under which biases occur and the likely sizes of such biases in a given situation. To help determine the causes of bias, further studies could compare the effects different selection criteria (e.g., phenotypic, progeny test, family index, BLUP), and their interaction with heritability and selection intensity, at various populations sizes to control for inbreeding rate. Given the number of replicates required for accurate estimates of bias and the number of combinations of possible contributing factors, this would, however, be a daunting task. It woud also be useful to extend the number of generations of data analysed, although the trends observed in Table 7 do not indicate that biases would be much reduced from those observed here.

A failing of the current study is that no comparison was made with more traditional methods of estimating genetic variances and heritabilities, such as parent-offspring regression and half-sib covariances, which would also be subject to bias in most selection populations (Robertson 1977; Ponzoni and James 1978). Robertson (1977) showed that parent-offspring regressions gave unbiased estimates of heritability in the presence of phenotypic selection, but it can easily be shown that this would not be true for most other forms of selection. It would be instructive to examine the difference in degree of bias between parent-offspring regression and animal model approaches in a variety of selected populations.

The estimates of additive genetic correlations between the five traits in the commercial poultry population were not significantly different across the 6 years analysed, though all showed a small decrease coincident with reducing the number of generations of data used in the estimation. Since the data structure affects estimates of genetic variance, it may be expected that estimates of covariance will also be affected, though whether genetic correlations would be affected is unclear. In general, simultaneous positive or negative selection of two traits will decrease, or make more negative, the correlation between those traits due to gametic-phase disequilibrium (Villanueva and Kennedy 1990). Conversely, positive selection on one trait with negative selection on another will tend to increase the correlation. The simulation studies here did not address biases in estimates of genetic covariances or correlations, but it seems likely that since both are affected by gametic-phase disequilibrium, both would also be subject to biases in estimation.

Conclusions

The simulations confirmed the empirical observations with a commercial poultry population, that estimates of genetic variance were affected by the amount of data used in the analysis when actual genetic variances were constant, at least for traits of high heritability. The results suggest that with traits of high heritability the estimates based on two generations of data may be biased downward by somewhere between 0 to 20% compared to the actual genetic variance in that generation. Conversely the estimates based on five generations of data are likely to be biased upward by 0 to 15%. But, since biases depend on the true heritability and most likely also the exact nature of selection and other parameters, and since the biases are currently estimated with high standard errors, there is considerable uncertainty as to the bias likely to apply to a given trait in practice. The data structures examined here, where relationships back to a truly unselected base generation are not available, are those likely to be encountered in most practical situations, implying that estimates of genetic variance using this method will be subject to unpredictable biases.

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