AN EVALUATION OF MAXIMUM LIKELIHOOD ESTIMATORS OF NON-ADDITIVE GENETIC VARIANCES

H. L. Chang, R. L. Fernando and D. Gianola
Department of Animal Sciences
University of Illinois at Urbana-Champaign
U.S.A.

SUMMARY

In animal breeding, genetic evaluation and estimation of genetic parameters have centered primarily on normally distributed traits and linear additive genetic models. The present study examined the feasibility of estimating additive, dominance and additive x additive type epistatic genetic variances in linkage equilibrium when these types of effects exist. Computer simulation was used for this purpose. Pseudo-normal records were the sum of a stochastic genetic component and a pseudo-normal environmental deviation. Non-additive genetic components of variance are difficult to estimate due to "confounding" between additive and non-additive genetic effects. However, given an appropriate pedigree, likelihood procedure can extract the information available on these components although it is reasonable to expect that non-additive components are more difficult to estimate well than additive ones. Univariate mixed linear models were used to describe and analyze the data. With normally distributed records, likelihood procedure was used for estimation of the variance components. An average of 7 iterations were required to converge at the fifth decimal point with the Newton-Raphson algorithm for maximum likelihood (ML) in design 4 (the "most efficient" one) for all combinations of genetic parameters considered in the study. Asymptotic theory indicated that in a genetic model with additive, dominance and additive x additive effects, the most difficult parameter to estimate was the variance "due to" epistasis, and that several thousand families were required to obtain reliable estimates of this parameter. In the presence of additive x additive effects, biases, mean squared errors and empirical variances of additive and dominance variance estimators were larger; further, sampling properties mentioned above of the additive and additive x additive variance estimators were affected by linkage.

INTRODUCTION

Animal breeding programs are aimed to improve genetic potential for economic merit through selection and mating plans. When designing an optimum breeding program it is important to know the amount and distribution of genetic variance. A considerable amount of improvement has been achieved through utilization of additive genetic effects. For example, genetic trends have been estimated to be 1.0% of mean milk yield per year in the U.S.A. (Van Vleck, 1977; Skjervold, 1982), and 0.7% for milk fat in New Zealand (Wickham et al., 1978). This is largely a consequence of selection for additive genetic value via artificial insemination and progeny testing of sires. The annual rate of genetic change achieved in breeding programs for other species are: 1.8% in growth and carcass traits (Mitchell et al., 1982) and 1.5% in litter size (Bichard and Seidel, 1982) for pigs in the United Kingdom; 2.9% in litter

size for sheep in New Zealand (Hight et al., 1975), and 0.3% in yearling weight for beef cattle in the United States (Willham, 1982). Whereas, reproduction traits in many species of livestock are lowly heritable, show inbreeding depression and tend to respond favorably to outbreeding (Stewart, 1945; Sellier, 1976; Johnson, 1980; Van Vleck, 1981; Lamberson et al., 1982; Lamberson and Thomas, 1984). This suggests the presence of non-additive genetic variation (Clarke, 1982). However, genetic evaluation and estimation of parameters in animal breeding with large data sets have been largely restricted to continuous traits using a linear additive genetic model. There are two possible reasons for this. First, until recently, "good" methods to estimate non-additive components of variance from animal breeding data have not been available (Willham and Pollak, 1985). Also, it is generally argued that non-additive genetic effects are "non-transmissible" and do not accumulate over generations (Lush, 1945).

MATERIAL AND METHODS

In the simulation, a trait determined by 2 loci in each of 30 pairs of chromosomes, with 2 alleles per locus was considered. Thus, inheritance is multifactorial. Gene frequencies of "favorable" allelic effects are assumed to be the same at all loci, and recombination rate between the two loci in each pair of chromosomes is also assumed to the same across all pairs. The different genetic models considered include: (1) additive (100%) effects, (2) additive (50%) plus dominance (50%) effects, (3) additive (50%) plus additive x additive (50%) effects, and (4) additive (50%), dominance (25%) and additive x additive (25%) effects. The combinations of genetic parameters considered were: (1) recombination rate between loci = 0.1 or 0.5 which represent tight linkage and independent assortment, respectively, (2) gene frequencies in the population = 0.05 or 0.5, and (3) heritability in the broad sense was 0.2 or 0.5. There was only one single fixed factor with two levels of effects generated in the simulation. A phenotypic value for each individual was generated using the above assumptions, i.e., the trait considered was not sex limited. Furthermore, phenotypic variance in the normal scale was set to 1,000.

Four "family designs" for estimating genetic parameters were used to compare the efficiency based on information matrices of maximum likelihood estimates of parameters or, equivalently, the necessary asymptotic variance-covariance matrices. Designs considered in the study include all relationships required to identify the four components of variance assuming absence of maternal effects, genetic and non-genetic. Thus, matings are carried out such that individuals are related through two lines of descent in designs 3 and 4. In order to assess the relative difficulty of estimating the four parameters of interest, the asymptotic coefficients of variation, i.e., the ratio (times 100) between the asymptotic standard error and the true value of the parameter were computed for each of the design. Twenty replicates of design 4 were simulated for each set of genetic assumptions. Empirical bias, mean squared error and sampling variance of estimates of variance components were evaluated using the data from the 20 replications for each set of assumptions.

RESULTS

Maximum likelihood (ML) estimates of variance components were highly inter-correlated for designs considered here. The most highly co-linear estimates were additive and additive x additive variances, with the asymptotic correlation ranging between -0.96 and -0.94, across designs. Estimates of additive variance were positively correlated with those of dominance variance and residual variance. The correlations between estimates of non-additive genetic components were all negative. It was also the case for correlations between estimates of non-additive variance components and of residual components. The asymptotic correlations between ML estimates for the four genetic models were not affected much by the magnitude of heritability. Also, the four designs considered were rather similar in this respect. For all designs, additive x additive variance is the "most difficult" parameter to estimate, followed by dominance, additive and then residual variances.

In the presence of additive x additive effects, biases, mean squared errors and empirical variances of additive and dominance variance estimators were larger; further, sampling properties mentioned above of the additive and additive x additive variance estimators were affected by linkage. The bias, relative to true value, of estimates of additive x additive variance was larger than 10% in most case. This biases were more severe with low heritability. The root mean squared errors of estimates of epistatic variance were larger than 30% of the true parameter value. In general, it appears that linkage not only causes bias in the estimates (if recombination rates are ignored), but it seems to affect dramatically the small sample distribution of these biased estimators. Thus, the assumption of normality may be strained when loci are tightly linked.

CONCLUSIONS

The results of this study confirmed that given the appropriate family structure and the necessary estimability conditions, it is possible to estimate non-additive genetic variances. However, the estimates can be severely biased in "small" samples, indicating that care needs to be exercised when invoking the asymptotic properties of likelihood methods. Further, realistic models for animal breeding use must include maternal genetic and permanent environmental effects, which would further complicate point and interval estimation procedures. An alternative would be to use field records, in which case selection of suitable computing techniques and models would be critical, the reason being that the "balance" of the data would no longer exist. Another possibility would be to search for more efficient designs, perhaps including matings between related individuals so as to reduce segregation variance by some amount. Also, a difficulty in obtaining reasonably unbiased estimates of additive type epistatic variances resides in the fact that many covariances between relatives are affected by linkage among loci. Ignoring these produces bias. At present, most linkage relationships between traits affecting quantitative trait loci are unknown, so this requirement cannot be met at present.

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