Pseudo-BLUP methodology for maternally affected traits

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Summary

The study extends the existing pseudo-BLUP tools to maternally affected traits. We derive deterministic predictions for the accuracy of breeding values for direct and maternal effects according to the selection index theory. The sources of information for the evaluated individual are individual’s own record, full-sib mean, half-sib mean, dam’s and sire’s breeding value estimate and mean of the estimated breeding values of dams mated to the sire. In addition to the additive relationships for the direct effect, also the relationships of the evaluated individual with the dams of recorded animals are included. The method has been checked by simulating pedigrees for ten generations. The pseudo-BLUP is a compact method to compare the influence of family information and varied genetic parameters on the accuracy of breeding value estimation in maternally affected traits and hence the efficiency of selection given the design of data collection. The approach can be extended to accommodate selection, different types of environmental variation and multiple trait evaluation.

Keywords: maternal traits, selection index, pseudo-BLUP

Introduction

Majority of livestock species are mammals. Therefore, dam’s maternal effects, including care and milk, are important for offspring. Understanding the nature and amount of genetic variation due to maternal effects and, in particular, the sign and magnitude of the genetic correlation between direct and maternal effects in economically important traits is critical (Willham 1963). All this would affect designing the data collection and setting the selection weights in breeding programmes.

The confounding of direct and maternal effects is solved in two ways, either by trying to capture the traits related to maternal effects (e.g. Falconer 1965; Shaat & Mäki-Tanila 2009) or by considering in statistical models the (unobserved) direct and maternal effects embedded in the phenotypic values of offspring (Willham 1963; Muuttoranta et al. 2014). The former is called trait-based approach and the latter variance component based approach (e.g. Bijma 2006; 2011).

Since the study by Thompson (1976), it has been customary to use complicated models in mixed model context (Henderson 1975) that combine information from all possible covariances between relatives and use specific and possibly correlated environmental effects.

The objective of the study is to extend the selection index theory to derive deterministic predictions for the accuracy of breeding values for direct and maternal effects from information on relatives across generations. The outcome is a pseudo-BLUP approach of Wray and Hill (1989) that is used to assess the influence of BLUP estimated breeding values in maternally affected traits. The pseudo-BLUP method is used to quickly understand how different designs of data collection and breeding programmes affect the accuracy of selection. The same method developed for maternal traits would allow similar considerations for such traits.
Development of methodology

Following Willham’s model, individual’s observed phenotypic value can be expressed as the sum of individual’s own direct phenotypic effect and its dam’s maternal phenotypic effect. These underlying effects can be partitioned to direct ($) and maternal addition genetic effects. The total genetic variation available for selection is then (with respective subscripts) and the phenotypic variance is where is the joint environmental variation in the effects (see Eaglen & Bijma 2009).

Discrete generations, nested mating structure ($d$ dams per sire and $n$ offspring from each dam) and no selection of parents are assumed. The efficiency of planned selection depends on the EBV’s accuracy, which can be predicted using the selection index methodology.

The accuracy is computed deterministically by approximating a pseudo-BLUP selection index (Wray & Hill 1989; Villanueva et al. 1993). The index (or estimated breeding value) is made of the following weighted ($) records on sources of (phenotypic and pedigree) information, individual’s own record ($+$ full-sib mean + half-sib mean + dam’s breeding value estimate + sire’s breeding value estimate + mean of the estimated breeding values of dams mated to the sire). The selection index weights are and contains the information records. Each animal with performance information has a single observation. The observations are on one trait while the goal has two components: direct (breeding value) and maternal ($) effect making the goal. For simplicity, we use equal economic traits for the two effects, i.e. The genetic $(co)$variance matrix gives the variance of the breeding goal. The selection index is and with the phenotypic $(co)$variance matrix of information sources and the covariance matrix between information sources and true breeding values we have and the variance of the index is and the accuracy of breeding value estimate for the individual is.

Assuming that the individual is included in the full-sib family and also together with its full-sib family within the half-sib family, the components due to direct and maternal effects are given in Table 1. In the case of a single genetic component for a trait, the optimum weights for the elements depend on the additive relationship of the evaluated individual with those being recorded and on the genetic variances and covariances (Wray and Hill 1989). With maternal traits, we also need the additive relationships of the evaluated individual with the dams of recorded animals and the genetic covariances among the direct and maternal component (cf. Van Vleck 1970). The two rows of relationships are given by (Table 2). In the selection index formula we then have The accuracy is for direct effect / and for maternal effect / where and refer to the columns of related to direct and maternal genetic effect (c.f. Villanueva et al. 1993).

The improved accuracy due to BLUP breeding value prediction is approximated by repeating few (5-10) times the updating of the matrix and elements with the respective $(co)$variances of the parents’ breeding value estimates for direct and maternal effects deduced from the index variance and thereby arriving at a pseudo-BLUP method (Wray and Hill 1989).

The details of the pseudo-BLUP method was checked first for an offspring generation from a base generation parents with the core selection index part made of information on individual, and . A more important part was to compare the pseudo-BLUP accuracy with a full BLUP method. For an easy comparison this was done by resorting to the selection index way to compute the accuracies. For the full BLUP context we generated by simulation a pedigree (without individuals’ genotypic and environmental effects) with the R program (R Core Team 2017) over ten generations. The accuracy was computed with mixed model equations having the incidence matrix for direct effects as and as for maternal effects. The additive relationship matrix is obtained with R package MCMCGlmm (Hadfield 2010). To allow straightforward comparison, we use the selection index matrix parameters and have and to compute the index coefficients. For a focussed individual the relationship coefficients (corresponding to ) and selection index weights.
were picked from and the latter are multiplied by economic values to have and further the respective variance of the index. Then the accuracy of direct and maternal EBV are obtained like above with simulation for the extension with added parents’ EBV’s represented by an example of Figure 1.

The pseudo-BLUP method can be applied to different family structures. As an example, Figure 1 shows the results how the EBV accuracy in maternal effects is improved by records on large full-sib families and by their genetic correlation with direct effects.

**Discussion and conclusions**

All selection schemes are now based on evaluating animals with a BLUP animal model which is accommodating any type of relatives and depth of pedigree and simultaneously considering any fixed environmental effects. Therefore, the methods giving estimates about the accuracy of selection by BLUP are useful. The comparison of accuracy values given by simulation shows that the presented algorithm is reliable.

Maternal traits belong to indirect genetic effects on which the research initiated by Griffing (1967) has been extended and generalised in animal breeding by Muir and Bijma (see Muir et al. 2010). The main emphasis has been on competition like social interaction where the number of required parameters complicate the construction of pseudo-BLUP machinery (Khaw et al. 2014). Maternal traits are a simple category among social interaction effects and allow a straightforward treatment of the required set of direct and interaction effects.

The compact pseudo-BLUP methodology has been used in comparing the influence of type and volume of family information (Wray & Hill 1989; Villanueva et al. 1993), in predicting the benefits from genomic selection (Dekkers 2007), assessing the consequences in rate of inbreeding from artificial long-term selection (e.g. Sørensen et al. 2005). The methodology is flexible and can accommodate influence of selection (Bulmer effect), common environmental variation (Wray and Hill 1989) and extensions to multiple trait BLUP (Villanueva et al. 1993) also for maternally affected traits.

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Table 1. The components in the variance-covariance matrix $P$.

Table 2. The matrix for the covariance of the individual with the sources of information in the first row and with the respective dam(s) in the second row corresponding to the direct and maternal effects.
Figure 1. The accuracy of BLUP estimates of breeding values for direct (a) and maternal (m) effects with the accrued information over generations (x axis). At each generation, the number of sires is 10 with 10 dams per sire and 6 offspring per dam. There is random mating without selection and uncorrelated (or correlated) effects with
Figure 2. The asymptotic accuracy given by pseudo-BLUP for uncorrelated or correlated direct (a) and maternal (m) effects with different values for . There are d dams per sire and n offspring per dam (varying on x-axis) keeping d n = 60 with no selection.