Pedigree options in ASReml

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Abstract

ASReml has several options when forming the pedigree. This paper discusses the new developments for Release 2. Briefly, these are constraints on the Genetic groups, changes to the way the Maternal Grandsire model is fitted and provision for a degree of selfing and inbreeding.

Key words: BLUP, linear mixed models, REML, variance components, genetic groups, average information, ASReml, Maternal Grandsire Model, Selfing

1 Introduction

An important development in the use of mixed models was the incorporation of the Numerator Relationship Matrix to account for genetic correlations among animals. The wonder of this approach is that the inverse relationship matrix is in general sparser than the relationship matrix itself and not difficult to form in a recursive manner when parents are listed before their offspring.

However, a few special situations arise in practise which we consider here. First, in some breeding situations, sires and sire groups are tracked but individual dam pedigrees are not tracked. This leads to the Maternal Grandsire model. ASReml Release 1 accomodated this model by simply inserting a dummy dam into the pedigree. We now form the inverse omitting this dummy dam. A further modification is for sex-linked traits when it is just inheritance through the X chromosome that is considered.

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In open pollinated forest trees, a proportion of the open-pollinated flowers are self pollinated. We derive the relationship matrix for a given proportion of selfing when the second parent is unspecified.

In other plant species, for example cereals, the plants are mainly self pollinated and lines are selfed for several generations to produce varieties for release. Alternatively, the pedigree can have varying levels of selfing. The pedigree relationship needs to take this into account.

ASReml now has 3 Ainverse routines. These extensions are implemented as for the method of Meuwissen and Lou (1992) which should be slightly faster than the other methods for large pedigrees.

2 Standard relationship matrix

The standard procedures can be summarised as follows. Let $\mathbf{A} = \{a_{ij}\}$ be the relationship matrix. Let $\mathbf{a}_{i,-j}$ be the *i*th row of \mathbf{A} except for the *j*th element.

- (1) Assume the relationship matrix for the base animals is known for example, are unrelated and not inbred so that their relationship matrix is an Identity matrix.
- (2) The row of the relationship matrix for the progeny (i) of two parents (s and d) is generated as the average of the relationship matrix rows for the parents.

$$\boldsymbol{a}_{i,-i} = \frac{1}{2}(\boldsymbol{a}_{s,-i} + \boldsymbol{a}_{d,-i})$$

(3) The diagonal element of this new animal is $a_{i,i} = 1 + \frac{1}{2}a_{s,d} = 1 + f_i$ where f_i is the inbreeding coefficient.

Applying this rule for two fullsibs and a half-sib generates the following matrix.

0. $0.5 \ 0.5 \ 0.5$ Sire 1. 0. Dam1 0. 1. 0. $0.5 \quad 0.5$ 0. Dam2 0. 1. 0. 0. 0. 0.5SibS1 0.5 0.5 0. 1. $0.5 \ 0.25$ SibS1 0.5 0.5 0. 0.5 1.0 0.25 SibS2 0.5 0. 0.5 0.25 0.25 1.0

Progressively inverting this matrix gives the sequence:

$$\begin{bmatrix} \operatorname{Sire} & 1 & 0 & 0 \\ \operatorname{Dam1} & 0 & 1 & 0 \\ \operatorname{Dam2} & 0 & 0 & 1 \end{bmatrix} \Rightarrow \begin{bmatrix} \operatorname{Sire} & 1.5 & 0.5 & 0 & -1 \\ \operatorname{Dam1} & 0.5 & 1.5 & 0 & -1 \\ \operatorname{Dam2} & 0 & 0 & 1 & 0 \\ \operatorname{SibS1} & -1 & -1 & 0 & 2 \end{bmatrix} \Rightarrow \begin{bmatrix} \operatorname{Sire} & 2 & 1 & 0 & -1 & -1 \\ \operatorname{Dam1} & 1 & 2 & 0 & -1 & -1 \\ \operatorname{Dam2} & 0 & 0 & 1 & 0 & 0 \\ \operatorname{SibS1} & -1 & -1 & 0 & 2 & 0 \\ \operatorname{SibS1} & -1 & -1 & 0 & 0 & 2 \end{bmatrix}$$
$$\Rightarrow \begin{bmatrix} \operatorname{Sire} & 2.5 & 1 & 0.5 & -1 & -1 & -1 \\ \operatorname{Dam1} & 1 & 2 & 0 & -1 & -1 & 0 \\ \operatorname{Dam2} & 0.5 & 0 & 1.5 & 0 & 0 & -1 \\ \operatorname{SibS1} & -1 & -1 & 0 & 2 & 0 & 0 \\ \operatorname{SibS1} & -1 & -1 & 0 & 0 & 2 & 0 \\ \operatorname{SibS1} & -1 & -1 & 0 & 0 & 2 & 0 \\ \operatorname{SibS1} & -1 & -1 & 0 & 0 & 2 & 0 \\ \operatorname{SibS1} & -1 & -1 & 0 & 0 & 2 & 0 \\ \operatorname{SibS1} & -1 & -1 & 0 & 0 & 2 & 0 \\ \operatorname{SibS1} & -1 & -1 & 0 & 0 & 2 & 0 \\ \end{array}$$

The rule for progressively generating these inverses is derived as follows.

Assume we have A_1 and A_1^{-1} for a set of animals including the parents of a new animal. Let p be a vector which performs the operation of averaging the parental rows of A_1 . It will be all zero except that the positions corresponding to the parents will be 0.5.

Then
$$\mathbf{A}_2 = \begin{pmatrix} \mathbf{A}_1 & \mathbf{A}_1 \mathbf{p} \\ \mathbf{p}' \mathbf{A}_1 & 1 + \frac{1}{2} a_{s,d} \end{pmatrix}$$
 is the expanded relationship matrix.

The standard expression for the inverse of a partitioned matrix is

$$\left(egin{array}{c} m{A} \ \ m{B} \\ m{B'} \ m{C} \end{array}
ight)^{-1} = \left(egin{array}{c} m{A^{-1}} + m{A^{-1}} m{B} m{Q} m{B'} m{A^{-1}} \ \ m{A^{-1}} m{B} m{Q} \\ m{Q} m{B'} m{A^{-1}} \ \ m{Q} \end{array}
ight) ext{ where }$$

$$\boldsymbol{Q} = (\boldsymbol{C} - \boldsymbol{B}'\boldsymbol{A}^{-1}\boldsymbol{B})^{-1}.$$
 In this case, $\boldsymbol{B} = \boldsymbol{A}_1\boldsymbol{p}$ so that $\boldsymbol{A}^{-1}\boldsymbol{B} = \boldsymbol{p}.$
Thus $\boldsymbol{A}_2^{-1} = \begin{pmatrix} \boldsymbol{A}_1^{-1} + q\boldsymbol{p}\boldsymbol{p}' & -q\boldsymbol{p} \\ -q\boldsymbol{p}' & q \end{pmatrix}$ where $q = (1 + \frac{1}{2}a_{s,d} - \boldsymbol{p}'\boldsymbol{A}_1\boldsymbol{p})^{-1}.$

Since \boldsymbol{p} has such a simple structure, $q = 1/(1 - \frac{1}{4}(a_{s,s} + a_{d,d})) = 4/(2 - (f_s + f_d))$ which simply requires the inbreeding coefficients for each parent.

To test **ASReml** we obtain A^{-1} , invert it, and check the result. We will use the following pedigree which includes inbreeding and selfing.

 $\begin{array}{ccccccc} 1 & 0 & 0 \\ 2 & 0 & 0 \\ 3 & 0 & 0 \\ 4 & 1 & 1 \\ 5 & 1 & 1 \\ 6 & 2 & 2 \\ 7 & 4 & 6 \\ 8 & 5 & 6 \\ 9 & 7 & 8 \\ 10 & 9 & 9 \end{array}$

The following was produced with **ASReml** qualifiers !METHOD 0 !GIV !DIAG. First is the relationship matrix obtained by inverting the Inverse relationship matrix. Rounding errors occur because of the moderate precision of the Ainverse .giv file. Next is the Ainverse as returned in the .giv file and finally the inbreeding coefficients as returned in the ainverse.dia file.

1 1.0 2 0.0 1.0 3 0.0 0.0 1.0 4 1.0 0.0 0.0 1.500 5 1.0 0.0 0.0 1.000 1.500 6 0.0 1.0 0.0 0.000 0.000 1.500 7 0.5 0.5 0.0 0.750 0.500 0.750 1.0000 8 0.5 0.5 0.0 0.500 0.750 0.750 0.6250 1.0000 9 0.5 0.5 0.0 0.625 0.625 0.750 0.8125 0.8125 1.3125 10 0.5 0.5 0.0 0.625 0.625 0.750 0.8125 0.8125 1.3125 1.65625 1 5.0 2 .0 3.0 3 .0 .0 1.0 4 -2.0 .0 .0 3.0 5 -2.0 .0 .0 .0 3.0 6 .0 -2.0 .0 1.0 1.0 4.0 7 .0 -2.0 .0 -2.0 .0 .0 4.5 8 .0 .0 .0 .0 -2.0 -2.0 0.5 4.5 .0 -1.0 -1.0 9 .0 .0 .0 .0 .0 4.90909 10 .0 .0 .0 .0 .0 .0 .0 .0 -2.90909 2.90909 Identity Inbreeding DiagofAinverse 0.0000 1 5.0000 2 0.0000 3.0000 3 0.0000 1.0000 4 0.50000 3.0000 5 0.50000 3.0000 6 0.50000 4.0000 7 0.0000 4.5000

| 8 | 0.0000 | 4.5000 |
|---------------|---------|--------|
| 9 | 0.31250 | 4.9091 |
| 10 | 0.65625 | 2.9091 |
| Wed 08/09/200 | 04 | |

3 Maternal Grandsire Model

In this situation, dam pedigree is incomplete. The dam of the dam is regarded as a base animal but the sire of the dam is known. Consider the relationship matrix for a Maternal Grandsire, Sire, Dam and Progeny given by

| Sire of Dam | $1 + f_g$ | r | 0 | $(1+f_g)/2$ | $(1+f_g+2r)/4$ |
|-------------|------------------------|------------------------|---------------|---------------------|-------------------|
| Sire | r | $1 + f_s$ | 0 | r/2 | $(2+2f_s+r)/4$ |
| Dam of Dam | 0 | 0 | 1 | 0.5 | 0.25 |
| Dam | $(1+f_g)/2$ | r/2 | 0.5 | 1 | (1 + r/2)/2 |
| Progeny | $\frac{(1+f_g+2r)}{4}$ | $\frac{(2+2f_s+r)}{4}$ | $\frac{1}{4}$ | $\frac{(1+r/2)}{2}$ | $1 + \frac{r}{4}$ |

We see that the Progeny line is half the Sire line plus a quarter of the Maternal Grandsire line except that the diagonal element is 1 plus a quarter of the relationship between the sire and the maternal grandsire.

The algebra is as before except for a different definition of p and q.

For the non-zero elements of \boldsymbol{p}_s being $\frac{1}{2}$ and $\frac{1}{4}$ for sire and maternal grandsire respectively, $\boldsymbol{A}_m = \begin{pmatrix} \boldsymbol{A}_1 & \boldsymbol{A}_1 \boldsymbol{p}_s \\ \boldsymbol{p}'_s \boldsymbol{A}_1 & 1 + \frac{r}{4} \end{pmatrix}$ and $\boldsymbol{A}_m^{-1} = \begin{pmatrix} \boldsymbol{A}_1^{-1} + \boldsymbol{p}_s q_s \boldsymbol{p}'_s & -\boldsymbol{p}_s q_s \\ -\boldsymbol{p}_s q_s & q_s \end{pmatrix}$

where

г

$$q_s = (1 + r/4 - \boldsymbol{p}'_s \boldsymbol{A}_s \boldsymbol{p}_s)^{-1} = (1 - (1 + f_g + 4(1 + f_s))/16)^{-1} = \frac{16}{11 - (f_g + 4f_s)}.$$

The following results are from ASReml using the same pedigree file as before but with qualifiers !METHOD 0 !MGS !GIV !DIAG where the !MGS qualifier causes the third field to be interpreted as the maternal grandsire.

```
1 1.0000

2 0.0000 1.0000

3 0.0000 0.0000 1.

4 0.7500 0.0000 0. 1.2500

5 0.7500 0.0000 0. 0.5625 1.2500

6 0.0000 0.7500 0. 0.0000 0.0000 1.2500

7 0.3750 0.1875 0. 0.6250 0.2812 0.3125 1.0000
```

8 0.3750 0.1875 0. 0.2813 0.6250 0.3125 0.2188 1.0000 9 0.2812 0.1406 0. 0.3828 0.2969 0.2344 0.5547 0.3594 1.0547 10 0.2109 0.1055 0. 0.2871 0.2227 0.1758 0.4160 0.2695 0.7910 1.2637 1 2.63636 1 2 2 1.81818 3 3 1.00000 1 4 -1.09091 4 1.86480 5 1 -1.09091 5 1.86480 -1.09091 6 2 4 0.205128 0.205128 6 1.65967 5 7 4 -0.820513 6 -0.410256 7 2.00466 8 5 -0.820513 6 -0.410256 7 0.181818 8 1.73193 9 7 -0.727273 8 -0.363636 9 2.29358 10 9 -1.1187210 1.49162 Identity Inbreeding DiagofAinverse 0.0000 2.6364 1 2 0.0000 1.8182 3 0.0000 1.0000 4 0.25000 1.8648 5 0.25000 1.8648 6 0.25000 1.6597 7 0.0000 2.0047 8 0.0000 1.7319 9 0.54688E-01 2.2936 10 0.26367 1.4916

4 Honey Bee breeding Model

Bienefeld et al (2007) describes a breeding program for Honey Bees which leads to another variation on the A matrix rules. The male bee is haploid. There is a mother queen mated to produce 'drone bearing' queens that produce the drones for mating. Each mother queen has several daughters and these have several sons. The scheme is quantified by two parameters q, the number of drone bearing queens, and d the average number of drones a queen mates with. So a queen is produced by combining the genetic material in a drone with that of the queen. But the drone is derived from the mother queen.

This scenario is similar to the Maternal Grandsire Model except the vector \boldsymbol{p} will have coefficients $\frac{1}{2}$ for the mating queen and p for the mother queen (which produced the mating drone).

??
$$\boldsymbol{A}_m = \begin{pmatrix} \boldsymbol{A}_1 & \boldsymbol{A}_1 \boldsymbol{p}_s \\ \boldsymbol{p}'_s \boldsymbol{A}_1 & 1 + \frac{r}{4} \end{pmatrix}$$
 and $\boldsymbol{A}_m^{-1} = \begin{pmatrix} \boldsymbol{A}_1^{-1} + \boldsymbol{p}_s q_s \boldsymbol{p}'_s & -\boldsymbol{p}_s q_s \\ -\boldsymbol{p}_s q_s & q_s \end{pmatrix}$ where

$$q_s = (1 + r/4 - \mathbf{p}'_s \mathbf{A}_s \mathbf{p}_s)^{-1} = (1 - (1 + f_g + 4(1 + f_s))/16)^{-1} = \frac{16}{11 - (f_g + 4f_s)}$$

The following results are from ASReml using the same pedigree file as before but with qualifiers !METHOD 0 !BEE 0.367 !GIV !DIAG where the !BEE 0.367 qualifier causes the third field to be interpreted as the mother queen with path coefficient p = 0.367.

```
1.0000
                          A matrix
0.0000 1.0000
0.0000 0.0000
                1
0.8670 0.0000
                0 1.3670
0.8670 0.0000
                0 0.7517 1.3670
0.0000 0.8670
                0 0.0000 0.0000 1.3670
0.4335 0.3182
                0 0.6835 0.3758 0.5017 0.9488
0.4335 0.3182
                0 0.3758 0.6835 0.5017 0.3720 0.9488
0.3758 0.2759
                0 0.4797 0.4388 0.4350 0.6110 0.5342 1.0854
0.3259 0.2392
                0 0.4159 0.3804 0.3771 0.5297 0.4632 0.9410 1.3472
                0 0.2079 0.1902 0.1886 0.2649 0.2316 0.4705 0.6736 1.3368
0.1629 0.1196
0.1196 0.0878
                0 0.1526 0.1396 0.1384 0.1944 0.1700 0.3454 0.4944 0.2472 1.1814
Inbreeding
0.0 0.0 0.0 0.3670 0.3670 0.3670 -0.0512 -0.0512 0.0854 0.3472 0.3368 0.1814
A-inverse
3.4433
0.0000
        2,2216
0.0000
        0.0000
                  1
-1.4090 0.0000
                 0 2.2163
                 0 0.0000 2.2163
-1.4090 0.0000
0.0000 -1.4090
                 0 0.4338 0.4338 2.2621
0.0000 0.0000
                 0 -1.1821 0.0000 -0.8677
                                           2.7925
0.0000
        0.0000
                 0 0.0000 -1.1821 -0.8677 0.3143 2.5950
0.0000
                 0 0.0000 0.0000 0.0000 -0.8564 -0.6286 3.1276
        0.0000
0.0000
        0.0000
                 0 0.0000 0.0000 0.0000 0.0000 -1.6318 2.2668
0.0000
        0.0000
                 0 0.0000 0.0000 0.0000 0.0000 0.0000 -0.5000
                                                                           1.0
0.0000 0.0000
                 0 0.0000 0.0000 0.0000 0.0000 0.0000 -0.3670
                                                                           0.0 1.000
Identity Inbreeding
                     Diag_of_Ainv Offspring-Parent
                                                     Pedigree
          0.0000
                      3.4433
                                Parent
                                                     1 0 0
  1
                                                      2 0 0
  2
          0.0000
                      2.2216
                                Parent
          0.0000
                      1.0000
  3
                                Offspring
                                                      3 0 0
                                                      4 1 1
         0.50000
                      2.2163
  4
                                Parent
  5
         0.50000
                      2.2163
                                Parent
                                                      5
                                                        1
                                                           1
  6
         0.50000
                      2.2621
                                Parent
                                                      6 2
                                                           2
         0.81836E-01
                                                      74
  7
                      2.7925
                                Parent
                                                           6
  8
         0.81836E-01
                      2.5950
                                Parent
                                                     85
                                                           6
                      3.1276
                                                     97
  9
         0.21838
                                Parent
                                                           8
                                                     10 9 9
 10
         0.48017
                      2.2668
                                Parent
                                                     11 10
 11
          0.0000
                      1.0000
                                 Offspring
                                                           0
                      1.0000
                                                     12 0 10
          0.0000
 12
                                 Offspring
```

The above numbers are not correct because Inbreeding cannot be negative!

5 Genetic groups

The **ASReml** qualifier !GROUPS g indicates that the first g identifiers in the pedigree file relate to genetic groups rather than to individuals in the popula-

tion. When genetic groups are present, the SIRE and DAM fields should both be zero for the group lines. All other lines must specify one of the genetic groups as SIRE or DAM if the actual parent is unknown.

In release 1.62, the option was added to apply 'sum to zero' constraints on group effects. If the pedigree file includes genetic groups without constraint, the 'constant term' will be included in the genetic group effects. The constant term is unlikely to be the population average and may generate singularities in unpredictable locations because of the ordering of the 'sparse' equations. This may be undesirable. The **!LAST** qualifier has been added to force the 'group' equations to be absorbed last so that any singularities in them will appear where expected. However, singularities in the pedigree factor also mess up the REML likelihood evaluation because they mess up the degrees of freedom count.

'Sum to Zero' constraints are applied to sets of genetic group effects by following the set with a dummy genetic group (one with no animals in it). ASReml then modifies the A inverse to apply a constraint in place of this dummy genetic group. That is, when there are two or more groups containing animals followed by a group with no animals, the A inverse line for the empty group is replaced with a line containing 1's for the preceding set of groups, and zero otherwise. This Lagrangian constrains the genetic group effects to sum to zero.

The following results from ASReml !METHOD 0 !GRP 3 !GIV !DIAG. We use the same pedigree file as before but now the first three lines are genetic groups. Notice that there are no individuals assigned to the third group. When AS-Reml has formed the A-inverse, it notes that this 'group' is empty and inserts Lagrangian off diagonal elements for this equation.

For the purpose of checking the inverse, the A matrix was calculated after zeroing the intersection between groups and individuals.

```
%ex/ex11/amg00.txt
\input /data/ex/ex11/amg00.txt
1 0.33333
2-0.33333 0.33333
3 0.33333 0.66667-0.66667
4 0.00000 0.00000 0.00000 1.00
5 0.00000 0.00000 0.000 0.00 1.00
6 0.00000 0.00000 0.0000 0.00 1.00
7 0.00000 0.00000 0.0000 0.50 0.00 1.0
8 0.00000 0.00000 0.00000 0.50 0.05 1.000
8 0.00000 0.00000 0.00000 0.50 0.50 0.55 0.250 1.000
9 0.00000 0.00000 0.00000 0.25 0.25 0.5 0.625 0.625 1.125 1.5625
```

1 1 2.00000

```
2
            2
                1.00000
     3
            1
                1.00000
                             2
                                 1.00000
                                             3
                                                  0.00000
     4
            1
               -1.00000
                             4
                                 1.50000
     5
            1
               -1.00000
                             5
                                 1.50000
     6
            2
              -1.00000
                             4
                                0.500000
                                                 0.500000
                                                                   2.00000
                                             5
                                                              6
     7
            4
               -1.00000
                             6
                                -1.00000
                                             7
                                                  2.50000
     8
            5
               -1.00000
                                -1.00000
                                             7
                                                 0.500000
                                                              8
                                                                   2.50000
                             6
            7
     9
               -1.00000
                             8
                                -1.00000
                                             9
                                                  4.28571
    10
            9
               -2.28571
                            10
                                 2.28571
Identity
                  Inbreeding
                                DiagofAinverse
            1 -1.0000
                             2.0000
            2 -1.0000
                             1.0000
            3 -1.0000
                             0.0000
            4
               0.0000
                             1.5000
            5
               0.0000
                             1.5000
            6
               0.0000
                             2.0000
            7
               0.0000
                             2.5000
               0.0000
                             2.5000
            8
            9 0.12500
                             4.2857
           10 0.56250
                             2.2857
```

Wed 08/09/2004

6 Partial selfing

| Female Parent | $1 + f_f$ | r | $1 + f_f$ | $(1+f_f+r)/2$ |
|---------------|----------------------|---------------------|-----------------------|---------------|
| Male Parent | r | $1 + f_m$ | r | $(1+f_m+r)/2$ |
| Selfed | $1 + f_f$ | r | $1 + \frac{1+f_f}{2}$ | $(1+f_f+r)/2$ |
| Crossed | $\tfrac{1+f_f+r}{2}$ | $\frac{1+f_m+r}{2}$ | $\frac{1+f_f+r}{2}$ | 1 + r/2 |

 $= 1 - \frac{1}{4}((1+s^2)(1+f_f) + 2sr(1-s) + (1-s)^2(1+f_m))$

Let s be the proportion selfed. The contribution of the female parent is then $(s + \frac{1}{2}(1-s))\boldsymbol{a}_f = \frac{1+s}{2}\boldsymbol{a}_f$. The contribution from the male parent is $\frac{1-s}{2}\boldsymbol{a}_m$. The diagonal element will be $s(1+\frac{1+f_f}{2})+(1-s)(1+r/2)=1+\frac{s(1+f_f)+(1-s)r}{2}$. Thus, the non zero elements of \boldsymbol{p}_w are $\left(\frac{1+s}{2},\frac{1-s}{2}\right)$ and $q_w^{-1} = 1 + \frac{s(1+f_f)+(1-s)r}{2} - \left(\frac{1+s}{2},\frac{1-s}{2}\right) \left(\begin{array}{c}1+f_f & r\\ r & 1+f_m\end{array}\right) \left(\begin{array}{c}\frac{1+s}{2}\\ \frac{1-s}{2}\end{array}\right)$

Now this expression for
$$q_w$$
 involves the covariance between the parents which
previously cancelled out and which is not easily available from the existing
algorithm. However, we expect that if the plant is outcrossed, the male parent

is not known. We could therefore nominate a degree of relationship for seeds collected in the wild, or just assume the male parent is unrelated.

As a starting point, ASReml assumes that if the male parent is unknown, there is proportional selfing but if the male parent is identified, that a controlled mating has occurred. This complicates the algorithm because in the former case, the nonzero element of \boldsymbol{p} is $\frac{1}{2}(1+s)$ while in the other case, there are two values of $\frac{1}{2}$

The following results from ASReml !METHOD 0 !SELF 0.3 !GIV !DIAG for the pedigree displayed at the bottom.

```
1 1.0000
   2 0.0000 1.0000
   3 0.0000 0.0000 1.
   4 1.0000 0.0000 0. 1.5000
   5 0.6500 0.0000 0. 0.9750 1.2250
   6 0.0000 0.6500 0. 0.0000 0.0000 1.1500
   7 0.5000 0.3250 0. 0.7500 0.4875 0.5750 1.0000
   8 0.3250 0.3250 0. 0.4875 0.6125 0.5750 0.5312 1.0000
   9 0.4125 0.3250 0. 0.6188 0.5500 0.5750 0.7656 0.7656 1.2656
  10 0.2681 0.2112 0. 0.4022 0.3575 0.3737 0.4977 0.4977 0.8227 1.1898
                3.00000
     1
           1
     2
           2
                1.58076
     3
           3
                              -2.00000
                1.00000
                           1
     4
           4
               3.45533
     5
           4
              -1.09937
                           5
                                2.30672
     6
           2 -0.893471
                           4
                              0.740741
                                               0.615385
                                                                2.73070
                                            5
                                                            6
     7
              -1.48148
                               -1.48148
                                            7
           4
                           6
                                                3.46296
     8
           5
              -1.23077
                              -1.23077
                                                                2.96154
                           6
                                           7
                                               0.500000
                                                            8
     9
           7
              -1.00000
                           8
                               -1.00000
                                                2.64492
                                           9
    10
           9 -0.992189
                          10
                                1.52644
Identity
          Female Male Inbreeding
                                     DiagofAinverse
                       0.0000
     1
           0
                  0
                                    3.0000
     2
           0
                  0
                       0.0000
                                    1.5808
     З
           0
                  0
                       0.0000
                                    1.0000
     4
           1
                  1
                      0.50000
                                    3.4553
     5
           4
                  0
                      0.22500
                                    2.3067
           2
     6
                  0
                      0.15000
                                    2.7307
     7
           4
                  6
                       0.0000
                                    3.4630
           5
     8
                  6
                       0.0000
                                    2.9615
     9
           7
                  8
                      0.26562
                                    2.6449
    10
           9
                  0
                      0.18984
                                    1.5264
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```

7 Inbred lines

In this situation, after a cross is made, it is selfed a large number of times to produce an inbred line. The procedure is basically as before except that the inbreeding is always 1.

For the non-zero elements of \boldsymbol{p}_i being $\frac{1}{2}$ and $\frac{1}{2}$, $\boldsymbol{A}_i = \begin{pmatrix} \boldsymbol{A}_1 & \boldsymbol{A}_1 \boldsymbol{p}_i \\ \boldsymbol{p}'_i \boldsymbol{A}_1 & 2 \end{pmatrix}$ and $\boldsymbol{A}_i^{-1} = \begin{pmatrix} \boldsymbol{A}_1^{-1} + \boldsymbol{p}_i q_i \boldsymbol{p}'_i & -\boldsymbol{p}_i q_i \\ -\boldsymbol{p}_i q_i & q_i \end{pmatrix}$ where $q_i^{-1} = 2 - \boldsymbol{p}'_i \boldsymbol{A}_1 \boldsymbol{p}_i = 1 - \frac{1}{2} a_{mf}$. This

 $\begin{pmatrix} -\boldsymbol{p}_i q_i & q_i \end{pmatrix}$ last term comes about from $2 - \begin{pmatrix} \frac{1}{2} & \frac{1}{2} \end{pmatrix} \begin{pmatrix} 2 & a_{mf} \\ a_{mf} & 2 \end{pmatrix} \begin{pmatrix} \frac{1}{2} \\ \frac{1}{2} \end{pmatrix}$

The special cases are that where no parents are known, $p_i = (0)$ so that $q_i^{-1} = 2$ and if only one parent is known, p_i contains a single $\frac{1}{2}$ so that $q_i^{-1} = 2 - \frac{1}{2}2\frac{1}{2} = 1.5$

The following results are from ASReml using the pedigree file displayed below with qualifiers !METHOD 0 !INBRED 1.0 !GIV !DIAG where the !INBRED qualifier implies inbred lines. Note that 'selfing' is not permitted in the pedigree with inbred lines as it will generate a singularity.

```
1 2.0000
 2 0.0000 2.0000
 3 0.0000 0.0000 2.00000
 4 1.0000 0.0000 1.0000 2.0000
 5 0.0000 1.0000 1.0000 0.5000 2.0000
 6 0.5000 0.5000 1.0000 1.2500 1.2500 2.0000
 7 0.7500 0.2500 1.0000 1.6250 0.8750 1.6250 2.0000
 8 1.3750 0.1250 0.5000 1.3125 0.4375 1.0625 1.3750 2.0000
 9 1.0625 0.1875 0.7500 1.4687 0.6562 1.3437 1.6875 1.6875 2.0000
10 0.7812 0.3437 0.8750 1.3594 0.9531 1.6719 1.6562 1.3750 1.6719 2.0
   1
             1.15000
         1
   2
         2
            0.750000
   3
         1
           0.250000
                        2 0.250000
                                            1.00000
                                        3
   4
         1 -0.500000
                        3 -0.500000
                                        4
                                            2.00000
  5
         2 -0.500000
                        3 -0.500000
                                        4
                                          0.333333
                                                            1.33333
                                                       5
   6
         4
             0.00000
                        5 -0.666667
                                        6
                                            2.76190
  7
           0.400000
                           -1.33333
                                          -1.33333
                                                       7
                                                           3.86667
         1
                        4
                                        6
  8
         1 -0.800000
                        7
                            0.00000
                                        8
                                            2.40000
  9
         6 0.761905
                        7 -1.60000
                                        8 -1.60000
                                                       9
                                                           3.96190
  10
         6 -1.52381
                        9 -1.52381
                                        0
                                            3.04762
```

| Identit | y Female | Male | Inbreeding | DiagofAinverse |
|---------|----------|------|------------|----------------|
| 1 | 0 | 0 | 1.0000 | 1.1500 |
| 2 | 0 | 0 | 1.0000 | 0.75000 |
| 3 | 0 | 0 | 1.0000 | 1.0000 |
| 4 | 1 | 3 | 1.0000 | 2.0000 |
| 5 | 2 | 3 | 1.0000 | 1.3333 |
| 6 | 4 | 5 | 1.0000 | 2.7619 |
| 7 | 6 | 4 | 1.0000 | 3.8667 |
| 8 | 7 | 1 | 1.0000 | 2.4000 |
| 9 | 8 | 7 | 1.0000 | 3.9619 |
| 10 | 9 | 6 | 1.0000 | 3.0476 |
| Thu 16/ | 09/2004 | | | |

For example, the coefficient 3.0476 = 1/(1 - 43/64) where $43/64 = \frac{1}{2}a_{96}$ The calculation of thes relationship required development of a recursive routine which works as follows. Define three vectors \boldsymbol{H} to hold the index of the higher numbered parent, \boldsymbol{L} to hold the index of the other parent, and \boldsymbol{c} to hold the contributions to relationship. Initialise $a_{69} = 0$, k = 1, $H_1 = 9$, and $L_1 = 6$.

While k > 0,

if H_k equals L_k , add c_k to a and decrement k.

else identify sire and dam of H_k (s and d) and replace (H_k, L_k, c_k) with $(\max(s, L_k), \min(s, L_k, \frac{1}{2}c_k)$ and $(H_{k+1}, L_{k+1}, c_{k+1})$ with $(\max(d, L_k), \min(d, L_k, \frac{1}{2}c_k))$ (but omit operations if s and/or d are 0, adjusting k accordingly).

| H,L,c | k=1 k | x=2 k=3 | k=4 | k=5 | k=6 | a |
|-------|---------|----------|----------|------------|----------|-------|
| | 9,6,1 | | | | | |
| | 8,6,1/2 | 7,6,1/2 | | | | |
| | 8,6,1/2 | 6,4,1/4 | 6,6,1/4 | | | |
| | 8,6,1/2 | 5,4,1/8 | 4,4,1/8 | | | 1/4 |
| | 8,6,1/2 | 4,3,1/16 | 4,2,1/16 | 5 | | 3/8 |
| | 8,6,1/2 | 4,3,1/16 | 3,2,1/32 | 2,1,1/32 | | 3/8 |
| | 8,6,1/2 | 3,3,1/32 | 3,1,1/32 | 2 | | 3/8 |
| | 7,6,1/4 | 6,1,1/4 | | | | 13/32 |
| | 7,6,1/4 | 4,1,1/8 | 5,1,1/8 | | | 13/32 |
| | 7,6,1/4 | 4,1,1/8 | 2,1,1/16 | 3,1,1/16 | | 13/32 |
| | 7,6,1/4 | 1,1,1/16 | 3,1,1/16 | 5 | | 13/32 |
| | 6,6,1/8 | 6,4,1/8 | | | | 15/32 |
| | 6,6,1/8 | 4,4,1/16 | 5,4,1/16 | ; | | 15/32 |
| | 6,6,1/8 | 4,4,1/16 | 4,2,1/32 | 2 4,3,1/32 | | 15/32 |
| | 6,6,1/8 | 4,4,1/16 | 4,2,1/32 | 2 3,3,1/64 | 3,1,1/64 | 15/32 |
| | 6,6,1/8 | 4,4,1/16 | 1,2,1/64 | 3,2,1/64 | | 31/64 |
| | 6,6,1/8 | | | | | 35/64 |
| | | | | | | 43/64 |

While the ASReml syntax allows for an inbreeding coefficient less that one to be specified, the algebra has not been worked through for that case.

8 Mixed Model equations

If \boldsymbol{y} denotes the $n \times 1$ vector of observations, the linear mixed model can be written as

$$y = X\tau + Zu + e \tag{1}$$

where $\boldsymbol{\tau}$ is the $p \times 1$ vector of fixed effects, \boldsymbol{X} is an $n \times p$ design matrix of full column rank which associates observations with the appropriate combination of fixed effects, \boldsymbol{u} is the $q \times 1$ vector of random effects, \boldsymbol{Z} is the $n \times q$ design matrix which associates observations with the appropriate combination of random effects, and \boldsymbol{e} is the $n \times 1$ vector of residual errors.

The model (1) is called a linear mixed model or linear mixed effects model. It is assumed

$$\begin{bmatrix} \boldsymbol{u} \\ \boldsymbol{e} \end{bmatrix} \sim N\left(\begin{bmatrix} \boldsymbol{0} \\ \boldsymbol{0} \end{bmatrix}, \begin{bmatrix} \boldsymbol{G}(\boldsymbol{\gamma}) & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{R}(\boldsymbol{\phi}) \end{bmatrix} \right)$$
(2)

where the matrices G and R are functions of parameters γ and ϕ , respectively.

Details of the AI algorithm for REML estimation can be found in several places including Gilmour et al. (1995). It revolves around the mixed model equations derived from the objective function

$$\log f_{oldsymbol{Y}}(oldsymbol{y} \mid oldsymbol{u} \;;\; oldsymbol{ au}, oldsymbol{R}) + \log f_{oldsymbol{U}}(oldsymbol{u} \;;\; oldsymbol{G})$$
 .

which is the log-joint distribution of $(\boldsymbol{Y}, \boldsymbol{u})$. Differentiating with respect to $\boldsymbol{\tau}$ and \boldsymbol{u} leads to the mixed model equations (Robinson, 1991) which are given by

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \hat{\boldsymbol{\tau}} \\ \tilde{\boldsymbol{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\boldsymbol{y} \\ \mathbf{Z}'\mathbf{R}^{-1}\boldsymbol{y} \end{bmatrix}.$$
 (3)

These can be written as

$$C\tilde{eta} = W'R^{-1}y$$

where $\boldsymbol{C} = \boldsymbol{W}' \boldsymbol{R}^{-1} \boldsymbol{W} + \boldsymbol{G}^*, \ \boldsymbol{\beta} = [\boldsymbol{\tau}' \ \boldsymbol{u}']' \ \text{and} \ \boldsymbol{G}^* = \begin{bmatrix} \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} \ \boldsymbol{G}^{-1} \end{bmatrix}.$

The solution of (3) requires values for the variance parameters γ and ϕ . In practice we replace γ and ϕ by their REML estimates $\hat{\gamma}$ and $\hat{\phi}$.

The AI algorithm uses the trace($(\partial C) \ C^{-1}$) when calculating the score and uses Y'PY as the the Average Information matrix where y'Py is the usual residual sum of squares and Y is a matrix of working variables, one for each variance parameter, given by either (∂R) $R^{-1}e$ for parameters of Ror $Z(\partial G) \ G^{-1}u$ for parameters of G.

Y'PY is formed by an absorption process (Gilmour et al 1995) which is quite efficient when C is sparse provided a judicious ordering is used. The other part of the process requires calculation of trace($(\partial C) C^{-1}$). We only need the elements of C^{-1} which correspond to non-zero elements in C when calculating this trace since the derivative ∂C is zero for all zero elements of C. There is a therefore a huge advantage in forming as few extra elements as possible when forming the required elements of C^{-1} . This is controlled by the order in which the equations are processed.

The AI algorithm requires space for C^{-1} and for working variables and their cross-products. ASReml uses the same memory to form the mixed model equations, absorb them and then hold the (partial) inverse.

For convenience, we have described the situation where both R and G are positive definite but we in fact also allow special cases where G is singular or negative definite (for example Thompson et al 2003).

9 Discussion

10 Acknowledgements

11 References

Gilmour, A.R., Thompson, R. and Cullis, B.R. (1995). Average Information, an efficient algorithm for REML estimation in linear mixed models. *Biometrics* **51**, 1440-50.

Gilmour, A.R., Cullis, B.R., Gogel, B.J., Welham, S.J. and Thompson, R. (2002). ASREML User Guide. VSN International, Hemel Hempstead, United

Kingdom. http://www.asreml.co.uk

Derivation of the Reduced Animal Model

Consider an animal model analysis which can be represented by the model

$$y = Xeta + Zu + e$$

$$\operatorname{Var}\begin{pmatrix}\boldsymbol{u}\\\boldsymbol{e}\end{pmatrix} = \begin{pmatrix}\sigma_A^2\boldsymbol{A} & 0\\ 0 & \sigma_E^2\boldsymbol{I}\end{pmatrix}$$

Letting $\gamma = \sigma_A^2/\sigma_E^2$; $\lambda = 1./\gamma$, the mixed model equations can be represented by

$$egin{pmatrix} oldsymbol{X'X} & oldsymbol{X'Z} \ oldsymbol{Z'X} & oldsymbol{Z'Z}+\lambda oldsymbol{A}^{-1} \end{pmatrix} egin{pmatrix} oldsymbol{eta} \ oldsymbol{u} \end{pmatrix} = egin{pmatrix} oldsymbol{X'y} \ oldsymbol{Z'y} \end{pmatrix}$$

Now order the data file and pedigree file so that the last p rows relate to pprogeny with own data but no descendents in the data or pedigree file.

Represent the data/design as

and $\mathbf{A}^{-1} = \begin{pmatrix} \mathbf{A}_a^{-1} + \mathbf{A}_a^{-1} \mathbf{B} \mathbf{Q} \mathbf{B}' \mathbf{A}_a^{-1} & -\mathbf{A}_a^{-1} \mathbf{B} \mathbf{Q} \\ -\mathbf{Q} \mathbf{B}' \mathbf{A}_a^{-1} & \mathbf{Q} \end{pmatrix}$ noting that in this case of

a relationship matrix, Q is diagona

The elements of Q are calculated from the inbreeding coefficients of the parents as $1/(1 - (a_{jj} + a_{kk})/4)$ where $a_{jj} = 1 + i_j$ and $a_{kk} = 1 + i_k$ and the relationship matrix coefficients for the parents, with inbreeding coefficients i_j and i_k respectively. The elements of $\mathbf{B}'\mathbf{A}^{-1}$ are all zero except cells ij and ikare 0.5.

The mixed model equations are then represented by

$$egin{pmatrix} oldsymbol{X}_a'oldsymbol{X}_a+oldsymbol{X}_p'oldsymbol{X}_a&oldsymbol{X}_a'&oldsymbol{X}_a&oldsymbol{X}_p'\ oldsymbol{Z}_a'oldsymbol{X}_a&oldsymbol{Z}_a'oldsymbol{Z}_a+\lambdaoldsymbol{A}_a^{-1}+\lambdaoldsymbol{A}_a^{-1}oldsymbol{B}oldsymbol{Q}oldsymbol{B}'oldsymbol{A}_a^{-1}&-\lambdaoldsymbol{A}_a^{-1}oldsymbol{B}oldsymbol{Q}\ oldsymbol{X}_p&-\lambdaoldsymbol{Q}oldsymbol{B}'oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{X}_p&-\lambdaoldsymbol{Q}oldsymbol{B}'oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{X}_p&-\lambdaoldsymbol{Q}oldsymbol{B}'oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{A}_p^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{A}_p^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{A}_p^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{B}'oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{A}_p^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{B}'oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{B}'oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{B}'oldsymbol{A}_p^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{B}'oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{B}'oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{B}'oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{Q}\ oldsymbol{B}'oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{B}\ oldsymbol{B}'oldsymbol{B}'\ oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{A}\ oldsymbol{A}'oldsymbol{B}'oldsymbol{B}'oldsymbol{B}'oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{B}\ oldsymbol{B}'oldsymbol{B}'\ oldsymbol{A}_a^{-1}&oldsymbol{I}+\lambdaoldsymbol{B}\ oldsymbol{B}'oldsymbol{B}'oldsymbol{B}'oldsymbol{B}'oldsymbol{B}'oldsymbol{A}'\ oldsymbol{B}'oldsymbol{B}'oldsymbol{A}'\ oldsymbol{B}'oldsymbol{B}'oldsymbol{B}'oldsymbol{B}'\ oldsymbol{B}'oldsymbol{B}'oldsymbol{B}'oldsymbol{B}'oldsymbol{B}'oldsymbol{A}'\ oldsymbol{B}'oldsymbol{B}'oldsymbol{B}'oldsymbol{B}'\ oldsymbol{B}'oldsymbol{B}'\ oldsymbol{B}'oldsymbol{B}'oldsymbol{B}'oldsymbol{$$

$$egin{pmatrix} eta\ u_a\ u_p \end{pmatrix} = egin{pmatrix} X_a' vec y_a + X_p' y_p\ Z_a' y_a\ y_p \end{pmatrix}$$

Absorbing the progeny equations gives

$$\begin{pmatrix} \boldsymbol{X}_{a}^{\prime}\boldsymbol{X}_{a} + \boldsymbol{X}_{p}^{\prime}[\boldsymbol{I} - (\boldsymbol{I} + \lambda\boldsymbol{Q})^{-1}]\boldsymbol{X}_{p} & \boldsymbol{X}_{a}^{\prime}\boldsymbol{Z}_{a} + \boldsymbol{X}_{p}^{\prime}(\boldsymbol{I} + \lambda\boldsymbol{Q})^{-1}\lambda\boldsymbol{Q}\boldsymbol{B}^{\prime}\boldsymbol{A}_{a}^{-1} \\ \boldsymbol{Z}_{a}^{\prime}\boldsymbol{X}_{a} + \lambda\boldsymbol{A}_{a}^{-1}\boldsymbol{B}\boldsymbol{Q}(\boldsymbol{I} + \lambda\boldsymbol{Q})^{-1}\boldsymbol{X}_{p} \boldsymbol{Z}_{a}^{\prime}\boldsymbol{Z}_{a} + \lambda\boldsymbol{A}_{a}^{-1} + \lambda\boldsymbol{A}_{a}^{-1}\boldsymbol{B}\boldsymbol{Q}[\boldsymbol{I} - (\boldsymbol{I} + \lambda\boldsymbol{Q})^{-1}\lambda\boldsymbol{Q}]\boldsymbol{B}^{\prime}\boldsymbol{A}_{a}^{-1} \end{pmatrix} \times \\ \begin{pmatrix} \boldsymbol{\beta} \\ \boldsymbol{u}_{a} \end{pmatrix} = \begin{pmatrix} \boldsymbol{X}_{a}^{\prime}\boldsymbol{y}_{a} + \boldsymbol{X}_{p}^{\prime}[\boldsymbol{I} - (\boldsymbol{I} + \lambda\boldsymbol{Q})^{-1}]\boldsymbol{y}_{p} \\ \boldsymbol{Z}_{a}^{\prime}\boldsymbol{y}_{a} + \lambda\boldsymbol{A}_{a}^{-1}\boldsymbol{B}\boldsymbol{Q}(\boldsymbol{I} + \lambda\boldsymbol{Q})^{-1}\boldsymbol{y}_{p} \end{pmatrix}$$

Let $\boldsymbol{W}_p = \boldsymbol{I} - (\boldsymbol{I} + \lambda \boldsymbol{Q})^{-1} = (\boldsymbol{I} + \lambda \boldsymbol{Q} - \boldsymbol{I})(\boldsymbol{I} + \lambda \boldsymbol{Q})^{-1} = \lambda \boldsymbol{Q}(\boldsymbol{I} + \lambda \boldsymbol{Q})^{-1}$

$$\lambda \boldsymbol{Q}[\boldsymbol{I} - (\boldsymbol{I} + \lambda \boldsymbol{Q})^{-1}\lambda \boldsymbol{Q}] = \lambda \boldsymbol{Q}(\boldsymbol{I} + \lambda \boldsymbol{Q})^{-1}[\boldsymbol{I} + \lambda \boldsymbol{Q} - \lambda \boldsymbol{Q}] = \boldsymbol{W}_{p}$$

giving

$$egin{aligned} &egin{aligned} &egin{aligne$$

At this point, let $\boldsymbol{Z}_p = \boldsymbol{B}' \boldsymbol{A}_a^{-1}$ and the equations become

$$egin{aligned} &oldsymbol{X}_a'oldsymbol{X}_a+oldsymbol{X}_p'oldsymbol{W}_poldsymbol{X}_p &oldsymbol{X}_a'oldsymbol{Z}_a+oldsymbol{X}_p'oldsymbol{W}_poldsymbol{Z}_p \ &oldsymbol{Z}_a'oldsymbol{X}_a+oldsymbol{Z}_p'oldsymbol{W}_poldsymbol{X}_p &oldsymbol{Z}_a'oldsymbol{Z}_a+\lambdaoldsymbol{A}_a^{-1}+oldsymbol{Z}_p'oldsymbol{W}_poldsymbol{Z}_p \ &oldsymbol{U}_a'oldsymbol{U}_a+oldsymbol{X}_p'oldsymbol{W}_poldsymbol{X}_p &oldsymbol{Z}_a'oldsymbol{Z}_a+\lambdaoldsymbol{A}_a^{-1}+oldsymbol{Z}_p'oldsymbol{W}_poldsymbol{Z}_p \ &oldsymbol{U}_a'oldsymbol{U}_a+oldsymbol{X}_p'oldsymbol{W}_poldsymbol{Z}_a+\lambdaoldsymbol{A}_a^{-1}+oldsymbol{Z}_p'oldsymbol{W}_poldsymbol{Z}_p \ &oldsymbol{U}_a'oldsymbol{U}_a+oldsymbol{X}_p'oldsymbol{W}_poldsymbol{U}_p \ &oldsymbol{U}_a'oldsymbol{U}_a+oldsymbol{X}_p'oldsymbol{W}_poldsymbol{U}_p \ &oldsymbol{U}_a'oldsymbol{U}_a+oldsymbol{Z}_p'oldsymbol{W}_poldsymbol{U}_p \ &oldsymbol{U}_a'oldsymbol{U}_a+oldsymbol{Z}_p'oldsymbol{W}_poldsymbol{U}_p \ &oldsymbol{U}_a'oldsymbol{U}_p'oldsymbol{$$

So, we have a reduced set of equations formed in the normal way with respect to the parental data, and with weights \boldsymbol{W}_p and a special design matrix (\boldsymbol{Z}_p) for the offspring data.

The weights are derived from the diagonal of the inverse of the A matrix and the special design matrix is from the parent/offspring block of the A-inverse.

Consider a six animal pedigree

201 101 102 202 101 102 301 201 202 302 201 202

The A-inverse (obtained from ASReml using the !GIV qualifier) is

| | 101 | 102 | 201 | 202 | 301 | 302 |
|-----|-----|-----|-----|-----|-----|-----|
| 101 | 2 | | | | | |
| 102 | 1 | 2 | | | | |
| 201 | -1 | -1 | 3 | | | |
| 202 | -1 | -1 | 1 | 3 | | |
| 301 | 0 | 0 | -1 | -1 | 2 | |
| 302 | 0 | 0 | -1 | -1 | 0 | 2 |
| | | | | | | |

So
$$\boldsymbol{Q} = \begin{pmatrix} 2 & 0 \\ 0 & 2 \end{pmatrix}; \boldsymbol{W}_p = \lambda \boldsymbol{Q} (\boldsymbol{I} + \lambda \boldsymbol{Q})^{-1}$$

 Z_a is defined in **ASReml** as id.Parent, Z_p is defined as and(sire.Proj.Half) and(Half.dam.Proj) where Half is a variate with values all 0.5 and the and() function overlays the design matrix.

So, to use the reduced animal model, we need to augment the data file by the weights. The !DIAG qualifier used on the whole pedigree will write the Q values to ainverse.dia. Alternatively, the Q values can be worked out from the inbreeding coefficients of the parents.

Extension to Maternal Grandsire model

Consider we have an existing relationship matrix and its inverse involving MGS (row 1) and SIRE (row 2) represented by

$$\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}^{-1} = \begin{pmatrix} a^{11} & a^{12} \\ a^{21} & a^{22} \end{pmatrix}$$

. Add rows for an unrelated **MGD** (row 3) and their progeny **DAM** (row 4).

$$\begin{pmatrix} a^{11} + q_d/4 \ a^{12} \ 0 + q_d/4 \ 0 - q_d/2 \\ a^{21} \ a^{22} \ 0 \ 0 \\ 0 + q_d/4 \ 0 \ 1 + q_d/4 \ 0 - q_d/2 \\ 0 - q_d/2 \ 0 \ 0 - q_d/2 \ 0 + q_d \end{pmatrix}$$

where $q_d = 1/(1 - (a_{11} + a_{33})/4)$ and $a_{33} = 1$ so that $q_d = 4/(3 - a_{11})$.

We no longer require \mathbf{MGD} so absorb row 3 to give

$$\begin{pmatrix} a^{11} + 1/(4 - a_{11}) & a^{12} & -2/(4 - a_{11}) \\ a^{21} & a^{22} & 0 \\ -2/(4 - a_{11}) & 0 & 4/(4 - a_{11}) \end{pmatrix}$$

since

$$q_d[1 - q_d/4/(1 + q_d/4)] = q_d[1 - 1/(3 - a_{11})/[(3 - a_{11} + 1)/(3 - a_{11})])$$

= $q_d[1 - 1/(4 - a_{11})] = 4/(4 - a_{11})$

Adding the progeny of SIRE and DAM as new row 4 gives

$$\begin{pmatrix} a^{11} + 1/(4 - a_{11}) & a^{12} & -2/(4 - a_{11}) & 0 \\ a^{21} & a^{22} + q_p/4 & 0 + q_p/4 & -q_p/2 \\ -2/(4 - a_{11}) & 0 + q_p/4 & 4/(4 - a_{11}) + q_p/4 & -q_p/2 \\ 0 & -q_p/2 & -q_p/2 & q_p \end{pmatrix}$$

where $q_p = 1/(1 - (a_{22} + a_{44})/4)$ and $a_{44} = 1$ since its dam was unknown so that $q_p = 4/(3 - a_{22})$.

Finally, we absorb \mathbf{DAM} (row 3).

Let

$$D = 1/[4/(4 - a_{11}) + q_p/4]$$

= 1/[4/(4 - a_{11}) + 1/(3 - a_{22})]
= (4 - a_{11})(3 - a_{22})/(4(3 - a_{22}) + 4 - a_{11})
= (4 - a_{11})(3 - a_{22})/(16 - 4a_{22} - a_{11})

Cell 1, 1 becomes

$$a^{11} + \frac{1}{(4-a_{11})} - \frac{4D}{(4-a_{11})^2} = a^{11} + \frac{(1-4(3-a_{22}))}{(16-4a_{22}-a_{11})} / \frac{(4-a_{11})}{(4-a_{11})^2} = \frac{1}{(4-a_{11})^2} - \frac{1}{(4-a_{11})^2} - \frac{1}{(4-a_{11})^2} \frac{$$

$$= a^{11} + 1/(16 - 4a_{22} - a_{11})$$

Cell 2, 1=Cell 1, 2 becomes $a^{21} + 2D/(4 - a_{11})/(3 - a_{22}) = a^{21} + 2/(16 - 4a_{22} - a_{11}).$

Cell 2, 2 becomes

$$a^{22} + q_p/4 - Dq_p^2/16 = a^{22} + (1 - (4 - a_{11})/(16 - 4a_{22} - a_{11}))/(3 - a_{22})$$

= $a^{22} + 4/(16 - 4a_{22} - a_{11})$

Cell 4, 1 (1, 4) becomes $-2Dq_p/2/(4 - a_{11}) = -4/(16 - 4a_{22} - a_{11}).$

Cell 4, 2 (2, 4) becomes

$$-q_p/2 + Dq_p^2/8 = -2(1 - (4 - a_{11})/(16 - 4a_{22} - a_{11}))/(3 - a_{22})$$

= -8/(16 - 4a_{22} - a_{11}).

Cell 4, 4 becomes

$$q_p - Dq_p^2/4 = q_p(1 - Dq_p/4) = 16/(16 - 4a_{22} - a_{11}).$$

Let $Q_p = 16/(16 - 4a_{22} - a_{11})$ and the matrix becomes

$$\begin{pmatrix} a^{11} + Q_p/16 \ a^{12} + Q_p/8 \ -Q_p/4 \\ a^{21} + Q_p/8 \ a^{22} + Q_p/4 \ -Q_p/2 \\ -Q_p/4 \ -Q_p/2 \ Q_p \end{pmatrix}$$

For non inbred parents, $a_{11} = a_{22} = 1$ and $Q_p = 16/11$

Consequently, we can also use the RAM method with a maternal grandsire pedigree by using the model terms

 Z_a is defined in ASReml as id.Parent, Z_p is defined as and (Half.sire*Proj) and (mgs.Proj,0.25)

and using weights for the progeny records calculated using $Q_p = 16/(16 - 4a_{22} = a_{11} = 16/(11 - 4i_s - i_{mgs})$.

Estimating the variance parameters under the RAM model

As formulated, the RAM model cannot be used to estimate the variance ratio because **ASReml** cannot handle the differential of the weight with respect to the variance ratio. It can however be estimated by putting the extra progeny variance into an extra variance component. It is not obvious that this would provide any computational advantage over using the IAM since the original order (number of) of equations is retained.

The expanded equations become

$$egin{aligned} egin{aligned} egin{aligne} egin{aligned} egin{aligned} egin{aligned} egin$$

noting that λ appears in two places. The extra random effect is then the deviation of the animal's BLUP from its midparent value.

An example

Following is a data file (anim.ped) generated in S-Plus containing 4 generations. We then show an **ASReml** job which fits the full animal model and estimates the variance components, and an **ASReml** job which fits the reduced animal model to estimated the BLUP values.

The first 70 lines of anim.ped relate to Parents, the remaining 70 lines relate to progeny without descendents. The first three columns contain the full pedigree. The column ramid is like animal except that it is zero for the progeny lines. The progeny variable is 0 for parents, 1 for progeny (it could be created from the ramid column via transformation). ibv is the inbreeding associated with the animal (times 32 to make it an integer) and is there just for interest. The progeny rows of Q contain the diagonal of the inverse of the full A inverse for these animals.

| animal | sir | e d | lam | ram | id | у | pro | ogeny | 'i | .bv | Q |
|--------|-----|-----|-----|------|-----|-----|------|-------|----|-----|---|
| 11 1 | 4 | 11 | 10. | 390 | 885 | 747 | 754 | 16 | 0 | 0 | 0 |
| 12 1 | 5 | 12 | 11. | 110 | 465 | 739 | 224 | 10 | 0 | 0 | 0 |
| 13 2 | 6 | 13 | 11. | 777 | 955 | 272 | 2657 | 71 | 0 | 0 | 0 |
| 14 2 | 4 | 14 | 8.6 | 5741 | 538 | 043 | 8638 | 3 | 0 | 0 | 0 |
| 15 2 | 7 | 15 | 7.9 | 9189 | 037 | 803 | 8010 |)2 | 0 | 0 | 0 |
| 16 3 | 5 | 16 | 9.7 | 165 | 542 | 929 | 673 | 33 | 0 | 0 | 0 |
| 17 3 | 8 | 17 | 10. | 890 | 447 | 376 | 5775 | 59 | 0 | 0 | 0 |
| 18 3 | 9 | 18 | 9.6 | 5120 | 768 | 058 | 332 | 25 | 0 | 0 | 0 |
| 19 3 | 6 | 19 | 10. | 522 | 782 | 070 | 686 | 56 | 0 | 0 | 0 |
| | | | | | | | | | | | |

| 67 | 14 | 30 | 67 | 9.43485295607768 | 0 | 0 | 0 |
|-----|----|----|-----|------------------|---|---|--------|
| 68 | 16 | 23 | 68 | 9.75749335918498 | 0 | 0 | 0 |
| 69 | 14 | 23 | 69 | 9.49082318556744 | 0 | 4 | 0 |
| 70 | 11 | 22 | 70 | 10.180415181553 | 0 | 4 | 0 |
| 71 | 14 | 28 | 71 | 10.5015621557079 | 0 | 0 | 0 |
| 72 | 15 | 28 | 72 | 9.38552780572869 | 0 | 0 | 0 |
| 73 | 12 | 25 | 73 | 10.0811885517726 | 0 | 0 | 0 |
| 74 | 20 | 24 | 74 | 9.98029685584483 | 0 | 0 | 0 |
| 75 | 18 | 27 | 75 | 10.3921923488348 | 0 | 4 | 0 |
| 76 | 12 | 21 | 76 | 11.2095368426887 | 0 | 4 | 0 |
| 77 | 14 | 30 | 77 | 11.4028159057297 | 0 | 0 | 0 |
| 78 | 16 | 27 | 78 | 9.03775130221661 | 0 | 8 | 0 |
| 79 | 18 | 22 | 79 | 11.3811226071947 | 0 | 0 | 0 |
| 80 | 18 | 25 | 80 | 7.8124711265838 | 0 | 0 | 0 |
| 81 | 37 | 54 | 0 | 9.41301907943905 | 1 | 2 | 2.1333 |
| 82 | 32 | 56 | 0 | 10.9478210963465 | 1 | 1 | 2.0000 |
| 83 | 43 | 51 | 0 | 10.4108227824721 | 1 | 1 | 2.0000 |
| 84 | 38 | 63 | 0 | 9.50198191412658 | 1 | 2 | 2.2857 |
| 85 | 49 | 56 | 0 | 10.1836742661691 | 1 | 2 | 2.0000 |
| 86 | 36 | 67 | 0 | 9.43561878646791 | 1 | 6 | 2.1333 |
| 87 | 39 | 54 | 0 | 8.96051177807472 | 1 | 1 | 2.0000 |
| 88 | 37 | 57 | 0 | 10.6006629223889 | 1 | 2 | 2.1333 |
| 89 | 40 | 61 | 0 | 10.8951841890337 | 1 | 1 | 2.0000 |
| 90 | 31 | 59 | 0 1 | 1.6171466747894 | 1 | 2 | 2.1333 |
| 91 | 34 | 71 | 0 | 8.82615618148376 | 1 | 2 | 2.1333 |
| 92 | 48 | 75 | 0 | 10.0784745397543 | 1 | 0 | 2.1333 |
| 93 | 39 | 62 | 0 | 10.1091215894326 | 1 | 2 | 2.0000 |
| 94 | 44 | 73 | 0 | 10.0999858381977 | 1 | 5 | 2.1333 |
| 95 | 32 | 74 | 0 | 8.91637153793524 | 1 | 5 | 2.0000 |
| 96 | 49 | 74 | 0 | 9.98534429588077 | 1 | 1 | 2.0000 |
| 97 | 42 | 80 | 0 | 9.72385207966892 | 1 | 1 | 2.1333 |
| 98 | 50 | 74 | 0 | 10.4435420931982 | 1 | 1 | 2.0000 |
| 99 | 40 | 51 | 0 | 10.1924373987657 | 1 | 3 | 2.0000 |
| 100 | 46 | 57 | 0 | 9.61540429177981 | 1 | 4 | 2.0000 |
| 101 | 49 | 69 | 0 | 10.2832108644091 | 1 | 3 | 2.1333 |
| 102 | 44 | 51 | 0 | 10.7724842239921 | 1 | 2 | 2.1333 |
| 103 | 40 | 53 | 0 | 9.84204430655675 | 1 | 1 | 2.0000 |
| 104 | 39 | 57 | 0 | 7.91867388041925 | 1 | 1 | 2.0000 |
| 105 | 36 | 62 | 0 | 10.1864922259464 | 1 | 2 | 2.1333 |
| 106 | 44 | 80 | 0 | 10.3704117751821 | 1 | 1 | 2.1333 |
| 107 | 43 | 64 | 0 | 10.4920572539863 | 1 | 2 | 2.0000 |
| 108 | 42 | 72 | 0 | 8.36290471333196 | 1 | 0 | 2.1333 |
| 109 | 45 | 79 | 0 | 10.2650472908691 | 1 | 5 | 2.0000 |
| 110 | 42 | 56 | 0 | 10.2986886395126 | 1 | 5 | 2.1333 |
| 111 | 44 | 80 | 0 | 10.6009452530656 | 1 | 1 | 2.1333 |
| 112 | 38 | 74 | 0 | 8.67042728685292 | 1 | 0 | 2.2857 |
| 113 | 40 | 72 | 0 | 11.0634565743273 | 1 | 1 | 2.0000 |

| 114 | 31 | 61 | 0 | 8.89534464048755 | 1 | 2 | 2.0000 |
|-----|----|----|-----|------------------|---|----|--------|
| 115 | 49 | 71 | 0 | 10.8962430535315 | 1 | 3 | 2.0000 |
| 116 | 39 | 62 | 0 | 9.18754090244638 | 1 | 2 | 2.0000 |
| 117 | 46 | 66 | 0 | 10.8691783663719 | 1 | 1 | 2.0000 |
| 118 | 36 | 77 | 0 | 10.2807432360335 | 1 | 6 | 2.1333 |
| 119 | 39 | 56 | 0 | 9.10687842385982 | 1 | 1 | 2.0000 |
| 120 | 46 | 52 | 0 | 11.8720666576208 | 1 | 3 | 2.1333 |
| 121 | 47 | 72 | 0 | 10.1850603552501 | 1 | 2 | 2.0000 |
| 122 | 46 | 54 | 0 | 9.6558797999729 | 1 | 2 | 2.0000 |
| 123 | 32 | 57 | 0 | 9.22850429171406 | 1 | 3 | 2.0000 |
| 124 | 45 | 66 | 0 8 | 3.15136825542446 | 1 | 2 | 2.0000 |
| 125 | 46 | 73 | 0 | 7.88941183740888 | 1 | 2 | 2.0000 |
| 126 | 39 | 53 | 0 | 9.01615309035975 | 1 | 2 | 2.0000 |
| 127 | 31 | 55 | 0 | 10.3523192574918 | 1 | 2 | 2.2857 |
| 128 | 43 | 79 | 0 | 10.2148135862004 | 1 | 1 | 2.0000 |
| 129 | 44 | 76 | 0 8 | 3.50957680401474 | 1 | 10 | 2.2857 |
| 130 | 32 | 54 | 0 | 9.53000303131414 | 1 | 5 | 2.0000 |
| 131 | 44 | 52 | 0 | 9.33721586426789 | 1 | 7 | 2.2857 |
| 132 | 36 | 78 | 0 | 8.48635421527905 | 1 | 0 | 2.4615 |
| 133 | 31 | 77 | 0 | 11.3329385837141 | 1 | 3 | 2.0000 |
| 134 | 37 | 56 | 0 | 10.4134913778961 | 1 | 0 | 2.1333 |
| 135 | 46 | 70 | 0 | 9.56323081820872 | 1 | 2 | 2.1333 |
| 136 | 47 | 61 | 0 | 9.730332323743 | 1 | 2 | 2.0000 |
| 137 | 50 | 79 | 0 | 8.65562598882075 | 1 | 1 | 2.0000 |
| 138 | 35 | 54 | 0 | 9.97523579491704 | 1 | 1 | 2.0000 |
| 139 | 34 | 79 | 0 | 8.2347003348346 | 1 | 2 | 2.1333 |
| 140 | 49 | 60 | 0 | 10.2526254965016 | 1 | 3 | 2.1333 |
| 141 | 46 | 69 | 0 | 9.72524883824503 | 1 | 0 | 2.1333 |
| 142 | 34 | 70 | 0 | 10.2568000361074 | 1 | 0 | 2.2857 |
| 143 | 32 | 69 | 0 | 10.2691991448205 | 1 | 2 | 2.1333 |
| 144 | 44 | 79 | 0 | 7.99985920710376 | 1 | 3 | 2.1333 |
| 145 | 45 | 51 | 0 | 10.1699822966765 | 1 | 2 | 2.0000 |
| 146 | 31 | 61 | 0 | 9.35249803893117 | 1 | 2 | 2.0000 |
| 147 | 50 | 80 | 0 | 9.2115314170863 | 1 | 2 | 2.0000 |
| 148 | 42 | 63 | 0 | 10.7952258148718 | 1 | 0 | 2.1333 |
| 149 | 39 | 57 | 0 | 9.8647096375117 | 1 | 1 | 2.0000 |
| 150 | 45 | 80 | 0 | 10.4279842491734 | 1 | 8 | 2.0000 |

The first job fits the animal model (estimating the variance component).

Analysis by animal model animal !P sire !P dam !P ramid Y anim.ped !skip 1 !make !diag anim.ped !skip 1 !extra 3 Y~ mu !r anim An extract from the .asr file follows. ASReml 1.57 [04 Dec 2003] Analysis by animal model 16 Jan 2004 14:46:52.155 64.00 Mbyte Windows anim Folder: C:\data\proj\agbu animal !P sire !P dam !P Reading pedigree file anim.ped : skipping 1 lines PEDIGREE [anim.ped] has 150 identities, 547 Non zero elements QUALIFIERS: !SKIP 1 !Evec{X}TRA 3 Reading anim.ped FREE FORMAT skipping 1 lines Univariate analysis of Y 140 records of Using 140 read Model term Size Minimum Mean Maximum #zero #miss 3.000 1 animal !P 150 80.24 150.0 0 0 2 sire !P 150 2.000 25.43 50.00 0 0 3 dam !P 150 1.000 43.07 80.00 0 0 4 ramid 11.00 22.75 80.00 70 0 5 Y 7.812 9.944 0 0 Variate 11.87 6 mu 1 Forming 151 equations: 1 dense. Initial updates will be shrunk by factor 0.316 1 LogL=-53.3627 S2= 0.70623 139 df 0.1000 1.000 2 LogL=-53.3585 S2= 0.70315 139 df 0.1060 1.000 3 LogL=-53.3550 S2= 0.69912 1.000 139 df 0.1140 4 LogL=-53.3538 S2= 0.69537 139 df 0.1216 1.000 5 LogL=-53.3538 S2= 0.69485 139 df 0.1226 1.000 6 LogL=-53.3538 S2= 0.69479 139 df 0.1228 1.000 7 LogL=-53.3538 S2= 0.69478 139 df 0.1228 1.000 S2= 0.69478 8 LogL=-53.3538 139 df 0.1228 1.000 1.0000 Final parameter values 0.12278 Degrees of Freedom and Stratum Variances 67.43 0.844141 1.8 1.0 71.57 0.694780 0.0 1.0 % C Source Model terms Gamma Component Comp/SE 150 150 0.122781 0.853059E-01 0.80 0 P animal 5.98 Variance 140 139 1.00000 0.694780 0 P Analysis of Variance NumDF DenDF F-incr F-adj Prob 6 mu 1 2.6 5366.78 NA NA

| 6 mu | E | stimate | Standard Error | T-value | T-prev |
|-----------------|--------|--------------|----------------|---------|--------|
| | 1 | 9.97036 | 0.136099 | 73.26 | |
| 1 animal | | | 150 effects : | fitted | |
| Finished: 16 Ja | n 2004 | 14:46:53.737 | LogL Converge | d | |

The **!DIAG** qualifier caused the elements of Q to be written to ainverse.dia from whence they were copied into the data file. The Q values can also be worked out directly (not within **ASReml**) from the inbreeding coefficients of the parents. For example, **81** has parents **37** and **54** with inbreeding coefficients of 4/32 and 0/32 respectively. $q_{81} = 1/(1 - (1 + 4/32 + 1 + 0/32)/4) =$ 32/(16 - 1) = 2.13333. For non inbred parents, the coefficient is 2. **84** has parents **38** and **63** with inbreeding coefficients of 8/32 and 0/32 respectively. $q_{84} = 1/(1 - (1 + 8/32 + 1 + 0/32)/4) = 32/(16 - 2) = 2.28571$.

The job to estimate the effects using the reduced animal model is

```
Analysis by Reduced animal model
! From animal model, gamma = 0.122781
animal
sire !P !*V6
dam !P !*V6
ramid !P
Y
Progeny Parent !=1 !-Prog
Weight !/0.122781 !+1 !^-1 !+1 !+Parent
ram.ped !skip 1
anim.ped !skip 1 !MAvec{X}IT 1 !BLUP 2
Y !wt We ~ mu !r ramid .122781 , and(sire,0.5) and(dam,0.5)
```

This job uses the same data file but the pedigree file just contains the parents (the first 70 lines of anim.ped)

The sire and dam fields are multiplied by Progeny (V6) to anihilate the information in them in the parent records. ibv is overwritten by a created variable Parent which is the complement of Progeny and is subsequently used to give a weight of 1. to the parent records.

Q is converted to the weight using $-((Q/\gamma + 1)^{-1} - 1)$. Since Q was supplied as 0 for the parents, this generates 0 for the parental records hence we then added the Parent indicator variable to set the weight to 1 for the parental records.

Running this job gave

ASReml 1.57 [04 Dec 2003] Analysis by Reduced animal model 16 Jan 2004 20:10:44.768 64.00 Mbyte Windows ram! From animal model, gamma = 0.122781 Folder: C:\data\proj\agbu sire !P !*V6 dam !P !*V6 ramid !P Progeny Parent !=1 !-Prog Weight !/0.122781 !+1 !^-1 !-1 !*-1 !+Parent A-inverse retrieved from ainverse.bin PEDIGREE [ram.ped] has 80 identities, 271 Non zero elements QUALIFIERS: !SKIP 1 !MAvec{X}IT 1 !BLUP 2 Reading anim.ped FREE FORMAT skipping 1 lines Univariate analysis of Y 140 records of Using 140 read Model term Size Minimum Maximum #zero #miss Mean 1 animal 11.00 80.50 150.0 0 0 2 sire !P 80 31.00 20.43 50.00 70 0 3 dam !P 80 51.00 32.62 80.00 70 0 4 ramid !P 80 3.000 22.49 80.00 70 0 5 Y Variate 7.812 9.944 11.87 0 0 70 0 6 Progeny 1.000 0.5000 1.000 70 0 7 Parent 1.000 0.5000 1.000 8 Weight 0.9422 0.9721 1.000 0 0 Weight 9 mu 1 10 and(sire,0.5) 80 11 and(mgs, 0.5)80 Forming 81 equations: 1 dense. 1 LogL=-53.3538 S2= 0.69478 139 df Warning: The estimation was ABORTED because the !BLUP qualifier was specified. The Standard Errors of variance components (and solutions?) and derived quantities are wrong. Use !MAvec{X}IT 1 instead of !BLUP to get correct standard errors. . . . Standard Error Estimate T-value **T-prev**

| 9 mu | | | | | | | • |
|-----------|----|-----|------|--------------|--------------|--------|---|
| | | | 1 | 9.97036 | 0.136099 | 73.26 | |
| 4 ramid | | | | | 80 effects | fitted | |
| Finished: | 16 | Jan | 2004 | 20:10:45.899 | BLUP run don | e | |

Notice that the LogL, S2 and mu values agree with the full animal model results.

Furthermore, the BLUPS for the parents agree. The following shows some

values.

| | | anim.s | ln | ram.sln | |
|--------|----|-------------|--------|-------------|--------|
| mu | 1 | 9.970 | 0.1361 | 9.970 | 0.1361 |
| animal | 4 | 0.6236E-01 | 0.2705 | 0.6236E-01 | 0.2705 |
| animal | 1 | 0.2862E-01 | 0.2606 | 0.2862E-01 | 0.2606 |
| animal | 11 | 0.1169 | 0.2535 | 0.1169 | 0.2535 |
| animal | 5 | -0.1774 | 0.2681 | -0.1774 | 0.2681 |
| animal | 12 | -0.6694E-01 | 0.2497 | -0.6694E-01 | 0.2497 |
| animal | 6 | 0.2221 | 0.2737 | 0.2221 | 0.2737 |
| animal | 2 | -0.1436E-01 | 0.2607 | -0.1436E-01 | 0.2607 |
| animal | 13 | 0.2136 | 0.2643 | 0.2136 | 0.2643 |
| animal | 14 | -0.2214E-02 | 0.2482 | -0.2214E-02 | 0.2482 |
| animal | 7 | -0.2042 | 0.2755 | -0.2042 | 0.2755 |
| animal | 37 | -0.7297E-01 | 0.2714 | -0.7297E-01 | 0.2714 |
| animal | 54 | 0.2736E-01 | 0.2599 | 0.2736E-01 | 0.2599 |
| animal | 70 | 0.1271 | 0.2727 | 0.1271 | 0.2727 |
| animal | 71 | 0.8816E-01 | 0.2644 | 0.8816E-01 | 0.2644 |
| animal | 72 | -0.1188 | 0.2614 | -0.1188 | 0.2614 |
| animal | 73 | -0.1705E-01 | 0.2631 | -0.1705E-01 | 0.2631 |
| animal | 74 | -0.2541E-01 | 0.2601 | -0.2541E-01 | 0.2601 |
| animal | 75 | -0.1041 | 0.2768 | -0.1041 | 0.2768 |
| animal | 76 | -0.5544E-01 | 0.2693 | -0.5544E-01 | 0.2693 |
| animal | 77 | 0.1469 | 0.2615 | 0.1469 | 0.2615 |
| animal | 78 | -0.2678 | 0.2840 | -0.2678 | 0.2840 |
| animal | 79 | -0.1235E-01 | 0.2592 | -0.1235E-01 | 0.2592 |
| animal | 80 | -0.8484E-01 | 0.2598 | -0.8484E-01 | 0.2598 |
| animal | 81 | -0.5190E-01 | 0.2748 | | |
| animal | 82 | 0.1257 | 0.2744 | | |
| animal | 83 | 0.4467E-01 | 0.2753 | | |
| animal | 84 | -0.1789 | 0.2732 | | |
| animal | 85 | 0.6887E-01 | 0.2767 | | |

ASReml does not work out the Progeny breeding values but they can be obtained as follows. Animal 81 has parents 37 and 54 whose BLUPS are

| animal | 37 | -0.7297E-01 | 0.2714 |
|--------|----|-------------|--------|
| animal | 54 | 0.2736E-01 | 0.2599 |

and has residual of

| 71 | 9.9476 | -0.5345 | 1.000 |
|----|--------|---------|-------|
| | | | |

So its BLUP = 0.5(-.07297+.02736) + 1/(1+Q)(-.5345) where Q = 2.1333/.122781

= 17.37484

 $\mathrm{BLUP}=0.5(\text{-}.04561)$ -.02909 = -.02280-.02909 = -0.05189 which compares well with the animal model solution.

Further checking

Modifying pedigree of the last three animals, the last three lines of the data file now read

| 147 | 50 | 80 | 0 | 9.2115314170863 | 1 | 0 | 2 | 2.0000 |
|-----|----|----|---|------------------|---|---|---|--------|
| 148 | 42 | 0 | 0 | 10.7952258148718 | 1 | 2 | 0 | 1.3913 |
| 149 | 0 | 57 | 0 | 9.8647096375117 | 1 | 0 | 1 | 1.3333 |
| 150 | 0 | 0 | 0 | 10.4279842491734 | 1 | 0 | 8 | 1.0000 |

where the Q values have also been updated to reflected the changed pedigree (diagonal elements of A^{-1} .

Running the IAM on the revised data gave LogL=-53.2775, S2=0.68607 and gamma=0.138732. Selected BLUPS are

| animal | 31 | 0.1804 | 0.2715 |
|--------|-----|-------------|--------|
| animal | 42 | -0.5272E-01 | 0.2795 |
| animal | 50 | -0.9671E-01 | 0.2716 |
| animal | 57 | 0.1613E-02 | 0.2722 |
| animal | 61 | -0.2036E-01 | 0.2743 |
| animal | 80 | -0.1335 | 0.2739 |
| animal | 147 | -0.1579 | 0.2899 |
| animal | 148 | 0.4939E-01 | 0.2824 |
| animal | 149 | -0.1071E-01 | 0.2850 |
| animal | 150 | 0.5383E-01 | 0.2896 |

Re running the RAM job (referring to the modified data file and with gamma=0.138732) gave identical values for LogL, S2, gamma and the BLUPS. The BLUPS for the last 4 animals are given by

147: (-0.09671-.1335)/2 + (-.6595)/(1+2./.138732) = -.15788

148: (-0.05272+0.000)/2 + (0.8355)/(1+1.3913/.138732) = 0.049397

149: (0.00+.001613)/2 + (-.1222)/(1+1.3333/.138732) = -.01071077

150: (0.00+0.00)/2 + (0.4419)/(1+1./.138732) = 0.053837

Extension to Maternal Grandsire model

The machinery also works for the maternal grandsire model. Using the same

data file except for the Q column, we compare the results from a direct MGS analysis performed using

```
Analysis by animal model - Maternal grandsires pedigree
animal !P
sire !P
mgs !P
ramid Y
anim.mgs !skip 1 !mgs
anim.mgs !skip 1 !extra 3
Y ~ mu !r anim
```

and a RAM model analysis using

```
Analysis by Reduced animal model : Maternal grandsire pedigree
! From animal model, gamma = 0.245788
animal
sire !P !*V6
mgs !P !*V6
ramid !P
Y
Progeny Skip Parent !=1 !-Prog
Weight !/16 !*0.245788 !^-1 !V10=1 !+V9 !V9 !/V10 !+Parent
ram.ped !skip 1 !MGS !DIAG
anim.mgs !skip 1 !MAvec{X}IT 1 !BLUP 2
Y !wt We ~ mu !r ramid .245788 , and(sire,0.5) and(mgs,0.25)
```

As part of this exercise, I made **ASReml** report inbreeding coefficients as an extension of the !DIAG qualifier output. Previous versions printed the diagonal elements of A^{-1} to AINVERSE.DIA. The new version also prints the inbreeding coefficients. After an initial run of the second job to obtain the inbreeding coefficients, I calculated $11 - 4i_s - i_{mgs}$ for the progeny records and placed it in the 9th data field. Transformations then converted this to the weight.

Portion of the output from the IAM run follows:

ASReml 1.58 [20 Jan 2004]

| 8 LogL=-52.9871 | S2= 0. | 62605 | 139 df | 0.2458 | 1.000 | |
|-----------------|----------|-------|----------------|-----------|---------|-----|
| Source | Model | terms | Gamma | Component | Comp/SE | % C |
| animal | 290 | 290 | 0.245788 | 0.153877 | 1.06 | 0 P |
| Variance | 140 | 139 | 1.00000 | 0.626054 | 4.46 | 0 P |
| | Estimate | | Standard Erron | r T-value | T-prev | |
| 6 mu | 1 9.96 | 253 | 0.125665 | 79.28 | | |

Analysis by animal model

| 1 anima | L | | | | 290 | effects fitted |
|-----------|----|-----|------|--------------|------|----------------|
| Finished: | 28 | Jan | 2004 | 13:52:22.651 | LogL | Converged |

The RAM model gave equivalent results:

ASReml 1.58 [20 Jan 2004] Analysis by Reduced animal model 1 LogL=-52.9871 S2= 0.62605 139 df Estimate Standard Error **T-value** T-prev 10 mu 1 9.96253 0.125665 79.28 4 ramid 150 effects fitted Finished: 28 Jan 2004 13:53:21.165 BLUP run done

Following is a comparison of breeding values. **ASReml** fits the maternal gransire model at present by inserting a dummy DAM for each offspring. Given the algebra in chapter 1, it would be possible to modify the Ainverse algorithm to directly form the MGS Ainverse without inserting the dummy dams.

| Identity | IAM-solutio | ns | RAM_solutio | ns |
|-----------|-------------|--------|-------------|--------|
| 4 | 0.3351E-01 | 0.3818 | 0.3351E-01 | 0.3818 |
| 999999998 | 0.1122 | 0.3732 | 0.1122 | 0.3732 |
| 1 | 0.1314 | 0.3435 | 0.1314 | 0.3435 |
| 11 | 0.2491 | 0.3183 | 0.2491 | 0.3183 |
| 5 | -0.8852E-01 | 0.3812 | -0.8852E-01 | 0.3812 |
| 999999994 | -0.3013E-01 | 0.3726 | -0.3013E-01 | 0.3726 |
| 12 | 0.6950E-01 | 0.3145 | 0.6950E-01 | 0.3145 |
| 6 | 0.2155 | 0.3831 | 0.2155 | 0.3831 |
| 999999991 | 0.2758 | 0.3780 | 0.2758 | 0.3780 |
| 2 | -0.2119E-01 | 0.3390 | -0.2119E-01 | 0.3390 |
| 13 | 0.3514 | 0.3366 | 0.3514 | 0.3366 |
| 999999988 | -0.1295E-01 | 0.3709 | -0.1295E-01 | 0.3709 |
| 14 | -0.5668E-01 | 0.3090 | -0.5668E-01 | 0.3090 |
| 7 | -0.1837 | 0.3847 | -0.1837 | 0.3847 |
| | • • | | | |
| 77 | 0.2457 | 0.3399 | 0.2457 | 0.3399 |
| 999999855 | -0.1147 | 0.3707 | -0.1147 | 0.3707 |
| 78 | -0.2681 | 0.3473 | -0.2681 | 0.3473 |
| 999999853 | 0.1617 | 0.3706 | 0.1617 | 0.3706 |
| 79 | 0.1154 | 0.3389 | 0.1154 | 0.3389 |
| 999999851 | -0.9385E-01 | 0.3705 | -0.9385E-01 | 0.3705 |
| 80 | -0.2626 | 0.3390 | -0.2626 | 0.3390 |
| 999999849 | 0.3336E-01 | 0.3717 | | |
| 81 | -0.1087 | 0.3445 | -0.10864 | |
| 999999847 | 0.2351 | 0.3716 | | |
| 82 | 0.2383 | 0.3451 | 0.23831 | |
| 999999845 | 0.1202 | 0.3718 | | |
| 83 | 0.5213E-01 | 0.3463 | 0.05212 | |

| -0.1291 | 0.3721 | |
|-------------|--|---|
| -0.2099 | 0.3448 | -0.20990 |
| • • | • • | |
| -0.2627 | 0.3463 | -0.26271 |
| -0.3639E-01 | 0.3722 | |
| 0.7755E-01 | 0.3433 | 0.07754 |
| 0.9237E-01 | 0.3720 | |
| -0.2316 | 0.3438 | -0.23162 |
| -0.9452E-01 | 0.3708 | |
| 0.6621E-01 | 0.3499 | 0.06621 |
| | -0.1291 -0.2099 -0.2627 -0.3639E-01 0.7755E-01 0.9237E-01 -0.2316 -0.9452E-01 0.6621E-01 | -0.1291 0.3721 -0.2099 0.3448 -0.2627 0.3463 -0.3639E-01 0.3722 0.7755E-01 0.3433 0.9237E-01 0.3720 -0.2316 0.3438 -0.9452E-01 0.3708 0.6621E-01 0.3499 |

Again, ASReml does not work out the progeny values directly but they are easily obtained from the parental blups and the residual as BLUP=Sire/2+MGS/4+Res/(1+Q/0.245788).

| Peo | ligı | ree | Sire | MGS | Residual | 1/(16Q) | BLUP |
|-----|------|-----|---------|---------|----------|---------|----------|
| 81 | 37 | 54 | -0.1457 | 0.1480 | -0.5136 | 10.75 | -0.10864 |
| 82 | 32 | 56 | 0.05798 | 0.3324 | 0.8732 | 11. | 0.23831 |
| 83 | 43 | 51 | -0.1133 | 0.1673 | 0.4631 | 11. | 0.05212 |
| 84 | 38 | 63 | -0.2315 | -0.2120 | -0.2918 | 10.6875 | -0.20990 |
| | | | | | | | |
| 147 | 50 | 80 | -0.2291 | -0.2626 | -0.5708 | 11. | -0.26271 |
| 148 | 42 | 63 | 0.01169 | -0.2120 | 0.8798 | 10.75 | 0.07754 |
| 149 | 39 | 57 | -0.5885 | 0.1601 | 0.1564 | 11. | -0.23162 |
| 150 | 45 | 80 | 0.1288 | -0.2626 | 0.4667 | 11. | 0.06621 |

RAM estimation

The **ASReml** job to estimate the variance ratio using the RAM modelling is

```
Analysis by Reduced animal model
! From animal model, gamma = 0.122781
animal
sire !P !*V6
dam !P !*V6
ramid !P
Y
Progeny #Skip Parent !=1 !-Prog Weight !/0.122781 !+1 !^-1 !-1 !+Parent
ram.ped !skip 1
ram.giv # Diagonal matrix containing Q
anim.ped !skip 1 !VCC
```

Y ~ mu !r ramid .122781 , and(sire,0.5) and(dam,0.5) uni(Prog,1,70)
0 0 1
uni 1
uni 0 GIV1 .122781
+ 2 7

which produced the following results:

ASReml 1.58 [20 Jan 2004] Analysis by Reduced animal model 02 Feb 2004 14:52:33.287 64.00 Mbyte Windows rame ! From animal model, gamma = 0.122781 Folder: C:\data\proj\agbu sire !P !*V6 dam !P !*V6 ramid !P Reading pedigree file ram.ped : skipping 1 lines 80 identities, PEDIGREE [ram.ped] has 271 Non zero elements Reading ram.giv skipping 0 header lines Inverse G structure of 70 rows having 70 non zero cells read from ram.giv QUALIFIERS: !SKIP 1 ! VCC Reading anim.ped FREE FORMAT skipping 1 lines Univariate analysis of Y 140 records of 140 read Using Model term Size Minimum Mean Maximum #zero #miss 1 animal 11.00 80.50 150.0 0 0 2 sire 31.00 20.43 50.00 70 0 !P 80 3 dam !P 51.00 70 0 80 32.62 80.00 70 4 ramid !P 80 3.000 22.49 80.00 0 5 Y Variate 7.812 9.944 11.87 0 0 6 Progeny 1.000 0.5000 1.000 70 0 7 mu 1 8 and(sire,0.5) 80 9 and (dam, 0.5)80 70 0.5000 70 10 uni(Prog,1,70) 1.000 1.000 0 70 ram.giv 0.1228 Structure for uni(Prog,1,70) has 70 levels defined 1 dense. 151 equations: Forming Initial updates will be shrunk by factor 0.316 For setting constraints, the variance parameters are numbered 2 to 7 1 LogL=-53.3538 S2= 0.69478 139 df 2 LogL=-53.3538 S2= 0.69478 139 df Source Model Component Comp/SE % C terms Gamma 0 P 2 0.853063E-01 0.80 ramid 80 80 0.122782

| Variance | 140 | 139 | 1.00000 | 0.694780 | 5.98 | 0 P | |
|--------------------|--------------|--------|----------------|--------------|--------|-----|---|
| uni(Prog,1,70) | ram.giv | 70 | 0.122782 | 0.853063E-01 | 0.00 | 0 C | 2 |
| 7 mu | Estimate | | Standard Error | T-value | T-prev | | |
| 7 ma | 1 9.970 |)36 | 0.136099 | 73.26 | | | |
| 4 ramid | | | 80 effects | fitted | | | |
| 10 uni(Prog,1,70) | | | 70 effects | fitted | | | |
| Finished: 02 Feb 2 | 2004 14:52:3 | 84.419 | LogL Converge | ed | | | |

Simulated Tree example

This exercise was stimulated by a comparison of Treeplan with ASReml in which ASReml took 30 times longer than Treeplan and this was attributed to the use of the reduced animal model.

Following are results from ASReml using a simulated data set with size and structure somewhat like that used in the comparison with Treeplan. In particular, we have 71000 progeny of 500 parents (randomly allocated to progeny). For the exercise, parents are unrelated. The progeny have been allocated to 71 groups of 1000 each. For the exercise, there is no data on parents.

The following table compares 6 runs. The greatest amount of time is taken forming the A-inverse matrix (about 126 seconds) for the IAM-1 run. Runs IAM-2 and IAM-3 used the A-inverse formed when IAM-1 was run. It took 13 seconds to read the data and set up the design matrix (the data was held as a .csv file). IAM-4 uses a different subroutine to form the A-inverse.

The default in ASReml is to seek to find an optimum equation order to use. This process took 8 seconds but was omitted in IAM-3 as the natural order of equations [groups, parents, progeny] is ideal.

With RAM, we trade a smaller system of equations with a more complex design matrix. The reduced size of the Ainverse matrix means that little time is taken forming A-inverse (0.04 seconds?) but it takes a little (2s) longer to set up the design matrix. The more complex design matrix means it takes a little longer to form the SSP which is now much more dense. Processing it is now a second longer although finding the order is much quicker.

Writing the solutions is slightly faster because BLUPS for the PROGENY are not reported.

| Process | IAM-1 | IAM-2 | IAM-3 | IAM-4 | RAM-1 | RAM-2 |
|-----------------|---------|--------|--------|--------|--------|--------|
| Getting Started | 129.406 | 13.179 | 13.079 | 21.451 | 15.152 | 15.112 |
| R&Gformed | 0.150 | 0.150 | 0.160 | 0.180 | 0.030 | 0.030 |
| SSP formed | 0.070 | 0.070 | 0.070 | 0.060 | 0.591 | 0.631 |

| 0.090 | 0.090 | 0.090 | 0.090 | 0.010 | 0.000 |
|---------|--|---|--|--|--|
| 8.372 | 8.412 | - | - | 0.881 | 0.901 |
| 5.308 | 5.298 | 4.336 | 4.306 | 6.219 | 6.219 |
| 0.120 | 0.090 | 0.090 | 0.080 | 0.080 | 0.080 |
| 5.5 | 5.5 | 5.5 | 5.5 | 3.0 | 3.0 |
| 156.104 | 36.172 | 26.929 | 40.919 | 28.501 | 29.853 |
| | 0.090 8.372 5.308 0.120 5.5 156.104 | 0.090 0.090 8.372 8.412 5.308 5.298 0.120 0.090 5.5 5.5 156.104 36.172 | 0.090 0.090 0.090 8.372 8.412 - 5.308 5.298 4.336 0.120 0.090 0.090 5.5 5.5 5.5 156.104 36.172 26.929 | $\begin{array}{cccccccccccccccccccccccccccccccccccc$ | $\begin{array}{cccccccccccccccccccccccccccccccccccc$ |

The bottom line is that for this size problem, there appears little advantage to RAM except the cost of forming the large A-inverse matrix for IAM. Even allowing for this, the difference is 5-fold, not 30-fold.

The A-inverse is formed using, by default, a subroutine obtained from Robin. I had not optimised it but to calculate inbreeding it has a loop across all remaining animals. This searching for animals who are descendants of the current animal is the expensive process. In version 1.58 I have added a test which checks whether there are any offspring first. Using it, the 'Getting started' time reduced to 21.75 seconds (i.e. 8 seconds to form the A-inverse). There is another A-inverse routine in ASReml invoked by the !OLD qualifier which does not handle genetic groups but did have the pre-test for calculating contributions to inbreeding. Using it, 'Getting started' took 21.541 seconds (i.e. it took about 8 seconds to form the A-inverse). Unfortunately, the old code did not handle 'selfing' properly which my test pedigree had some 150 cases of. This is also now fixed in 1.58.

The preceding results were obtained with version 1.57 (1.58). Below is a comparison of various versions of ASReml running the model as in IAM-1.

| Version | | Elapsed time | |
|---------|-----------|--------------|-------------|
| | | AIM-1 | RAM-1 |
| Jul | 1999 | 173.74 | 25.85 |
| Nov | 2001 | 157.92 | 19.92,15.20 |
| Sep | 2003[110] | 156.94 | 32.25,28.24 |
| Dec | 2003[157] | 151.60 | 30.92 |
| Feb | 2004[158] | 37.24 | 29.35 |

These timings were obtained on an ACER Travelmate with 504 MB RAM and a 1000 MHz processor. Ir is evident PC timings are somewhat variable (10I have not explored at the moment. The Nov 2001 version seems to be reading the data file much faster, probably reflecting less options for decoding the data.

The IAM runs require more memory than the RAM models. If the test machine had less RAM (e.g. 64MB rather than 504 MB), then paging would slow the analysis. The RAM model needed S3 (64MB) but the IAM model needed S4 (128MB) to run. If the IAM model omitted the !BLUP 2 qualifier and had !MAXIT 1 instead, the elapsed time would be increased 5s because of the

extra processing involved.

Discussion and Conclusion

In chapter 1, I have outlined some matrix results supporting the use of **AS-Reml** for fitting a Reduced Animal model. Chapter 2 provides an example with inbreeding.

RAM is fitted in **ASReml** using two particular features of the program, weights and the and() model function. Both of these features are discussed in the 1999 ASReml Reference manual. The only things that is a little tricky is the working out of the appropriate weights for the RAM analysis and the backsolving for the BLUPs of the absorbed progeny.

The former is based on the diagonal elements of the Ainverse, and without inbreeding, these values are 1 if no parent is known, 4/3 if one parent is known, 16/11 if sire and maternal grandsire is known, 2 if both parents known. With inbreeding, they can be calculated from the parental inbreeding values or taken from the A-inverse that includes the progeny. The !DIAG qualifier reports the latter.

I understand some European colleagues have used the and() function in models similar to RAM.

It is not possible as things stand to directly estimate the genetic variances using the RAM model because the variance ratio is used in the weights and the weights are not differentiated with respect to the ratio. It can of course be done if the reidual is split into the genetic and residual components and this is shown.

ASReml has benefitted from a review of the A-inverse algorithm to speed it up. However, in a sparse matrix implementation, there is little advantage in using the RAM model per se.

I am interested in understanding what additional time costs can be identified which made the Treeplan comparison so much faster than the ASReml run, given I have identified only 20 percent of the difference within ASReml.