ANIMAL MODELS FOR QUANTITATIVE GENETIC ANALYSIS IN RABBIT BREEDING PROGRAMS

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Abstract

This paper reviews the application of recently developed "animals models" for usage in rabbit breeding experimentation, in genetic evaluation programs and in timely adoption by industry. Animal models (AM) are relevant to single-trait breeding value estimation of meat and wool traits and include: 1) a full AM; 2) a full AM with repeated records; 3) a full AM for a maternally influenced trait with permanent environmental effects associated with the dam or litter, and 4) a reduced animal model (RAM) with maternal genetic and permanent environmental effects. These AM types are illustrated with numerical examples. The multiple-trait mixed model procedure will be briefly mentioned as another AM type relevant to rabbit breeding. Computer resource requirements necessary to implement AM analyses are discussed, as well. Breeding companies and seed stock suppliers adopting mixed model techniques using an AM will benefit directly through more efficient selection for rabbit meat or wool production. Ultimately, commercial and subsistence rabbit farmers throughout the world and consumers of rabbit products will benefit from this enhanced genetic merit.

Introduction

Domestic rabbit biology and management give rise to considerations that dictate how experiments should best be designed to yield valid and interpretable quantitative genetic results. To illustrate this contention: 1) rabbits are a litter bearing species (polytocous) and competition effects amongst siblings can be appreciable; 2) because of the short litter interval, confounding problems between individual doe, age of doe (parity) and time (season or month) effects are common in statistical analyses; 3) confounding between random sire, dam, litter and(or) progeny effects is often encountered; 4) maternal factors (e.g. uterine, nest quality, behavior and lactation) are generally pronounced, even for carcass traits because fryers are slaughtered at a relatively young age; 5) paternal half-sib estimates of heritability for growth and carcass traits typically are low to moderate, at best, even if standardization (fostering) or

statistical adjustment for litter size is made, and 6) sex effects are generally not important for traits measured during the pre-pubertal period. The basic challenge before rabbit geneticists is to appropriately account for these biological patterns to most accurately estimate genetic and environmental parameters for use in rabbit breeding programs.

In this paper, the animal model will be emphasized. This procedure has become popular in recent years for the primary purpose of genetic evaluation of animals. Adoption of Henderson's mixed model equations (MME) and procedures to derive best linear unbiased prediction (BLUP) of breeding value (BV) has resulted in technological breakthroughs in beef (Quaas and Pollak, 1980; Benyshek *et al.*, 1988) and dairy cattle (Misztal *et al.*, 1992) and swine (Hudson and Kennedy, 1985) genetic evaluation programs in the U.S., Canada and other industrialized nations. This breakthrough has been dependent upon enhanced computer capabilities (*e.g.* supercomputers). The animal model innovation has replaced many earlier genetic evaluation procedures. Utilizing BLUP procedures, the prospect exists for developing national, even international, rabbit genetic evaluation programs.

The objective of this paper is to describe relevant statistical designs and animal models, the application of which will enhance accuracy of breeding value prediction to accelerate genetic progress for the improvement of meat and wool production in rabbit breeding programs.

Mixed Model Methodologies

Breeding Value Prediction. Accurate determination of BV for a production trait in meat or wool rabbits is paramount to breeding program success. Genetic progress rests on the correlation between BV and phenotypic value, *ergo* heritability (h^2). Hence, accurate BV estimation is of utmost priority in progressive breeding programs. Conventionally, the formula: BV = h^2 (P_i - μ) has been used to predict BV based on animals with single records that belong to a contemporary group (where P_i - μ is the deviation of the phenotypic record of the ith animal from the population or contemporary group mean). The method of choice is to estimate breeding value of animals by BLUP (Henderson, 1973, 1977a, 1988). A BLUP procedure can be used to predict BV and adjust for model fixed effects (*e.g.* age group, season and sex) simultaneously.

Accuracy of BV estimation can be further enhanced by incorporation of the inverse of Wright's additive numerator relationship matrix (A^{-1}) into a mixed model analysis, as previously demonstrated by Henderson (1973). In addition, inverse matrices accounting for dominance (D^{-1}) and epistatic (I^{-1}) relationships can be constructed based on the A^{-1} matrix to estimate non-additive genetic effects, as well as dominance and epistatic variances (Henderson, 1977b; Kennedy and Sorenson, 1988; Lin and Lee, 1989;

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Hoeschele, 1991). These relationship matrices efficiently utilize available pedigree information in BV (genetic effect) solutions, and as well accounts for genetic trend. A relationship matrix could contain animals with records, sires and dams with progeny records that contribute to genetic relationships, and also common ancestors that have no records (base animals). Estimation of BV could be obtained not only for sires, dams and base animals (Henderson, 1977a), but also for young animals without progeny records ("interim expected progeny differences") on the basis of their genetic relationships (Wilson and Willham, 1988).

Accounting for inbreeding effects by regression in animal models minimizes the likelihood of confounding between selection and inbreeding effects in populations undergoing selection (Quaas and Pollak, 1980; Kennedy et al., 1988). Inbreeding coefficients for each animal can be calculated from available pedigree information using the method by Quaas (1976). In addition, under a multiple-trait mixed model (i.e. multivariate model) the effects of sequential culling in traits and(or) selection bias can be corrected (Henderson, 1975).

Numerical Example. To illustrate usage of a relatively simple animal model type (sire evaluation under a sire model for a single trait – average daily gain [ADG]), an example is provided by the usual matrix notation for a general mixed linear model, written as:

$$y = X\beta + Zs + e \qquad\qquad [1]$$

where y is an observational vector, β is a vector of an unknown fixed effect (mu), X and Z are known matrices relating records to mu and sire effects, s is a vector of unknown random sire effects (direct additive genetic transmitting ability [breeding value]) ~ $(0, A\sigma^2_s,$ where A is the numerator relationship matrix among sires), and e is a vector of unknown random effects ~ $(0, R\sigma^2_e,$ where R is assumed to be an identity matrix). Solutions to obtain best linear unbiased estimates (BLUE) of fixed effects and BLUP of random effects using MME:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\alpha \end{bmatrix}^{-1} \begin{bmatrix} X'y \\ Z'y \end{bmatrix} = \begin{bmatrix} \hat{\mu} \\ \hat{s} \end{bmatrix} \qquad [2]$$

where α represents the ratio of known variances (σ^2_e/σ^2_s), which is equivalent to $(4-h^2)/h^2$. (For this problem assume that $h^2 = .25$ and $\alpha = 15$). For simplicity, BV for ADG will be estimated for three non-inbred sires, each with 3 progeny records (k). (Maternal effects are ignored.) Grand and sire means equal 40.0, 41.2, 42.6 and 36.2 g, respectively. Further, sire 1 and 2 are full-sibs, sire 1 and 3 are half-sibs and sire 2 and 3 are half-sibs. (Relationships of mates and base animals being ignored.) The additive genetic relationship matrix (A), its inverse (A^{-1}) and αA^{-1} are shown:

$$
\mathbf{A} = \begin{bmatrix} 1.00 & .50 & .25 \\ .50 & 1.00 & .25 \\ .25 & .25 & 1.00 \end{bmatrix} \qquad \mathbf{A}^{-1} = \begin{bmatrix} 1.3636 & -.6364 & -.1818 \\ -.6364 & 1.3636 & -.1818 \\ -.1818 & -.1818 & 1.0909 \end{bmatrix}
$$

$$
\alpha\mathbf{A}^{-1} = \begin{bmatrix} 20.4545 & -9.5454 & -2.7272 \\ -9.5454 & 20.4545 & -2.7272 \\ -2.7272 & -2.7272 & 16.3636 \end{bmatrix}
\tag{3}
$$

The mixed model equations [2] can now be set up and solved:

$$
\begin{bmatrix} 9 & 3 & 3 & 3 \\ 3 & 3 + 20.4545 & 0 + -9.5454 & 0 + -2.7272 \\ 3 & 0 + -9.5454 & 3 + 20.4545 & 0 + -2.7272 \\ 3 & 0 + -2.7272 & 0 + -2.7272 & 3 + 16.3636 \end{bmatrix}^{-1}
\begin{bmatrix} 360.0 \\ 123.6 \\ 127.8 \\ 108.6 \end{bmatrix}
=
\begin{bmatrix} \hat{\mu} \\ \hat{s}_1 \\ \hat{s}_2 \\ \hat{s}_3 \end{bmatrix}
\tag{4}
$$

The solution vector yields BLUE of $\hat{\mu}$ = 39.95 g, and BLUP of BV for sire 1 = .26 g, sire 2 = .39 g, and sire 3 = -.49 g. Instead, if sires were unrelated the BV's would sum to zero, whereas this property does not exist when sire relationships are prevalent, as will be observed in some later problems in this paper. A general formula is provided for calculating BLUP of BV (or expected progeny difference [EPD]) when sires are related, as follows:

$$
\hat{s}_i = \left(\frac{1}{Z_{ii} + a^{ii}\alpha} \right) \left(\sum_k Y_i. - Z_{ii}\hat{\mu} \right) - \left(\frac{1}{Z_{ii} + a^{ii}\alpha} \right) \left(\sum_{j \neq i} a^{ij}\hat{s}_j\alpha \right)
\tag{5}
$$

where $\sum Y_i.$ represents the sum of k progeny records ($Z_{ii}y$) on the ith sire, and a^{ii} and a^{ij} denote the inverse additive genetic relationships of the individual sire and of the sire to its relatives, respectively. Instead, if sires had been assumed to be unrelated then the simple BLUP solution of EPD for sires:

$$
\hat{s}_i = \left(\frac{k_i}{k_i + \alpha} \right) (\overline{Y}_i. - \hat{\mu})
\tag{6}
$$

If progeny were grouped by age, sex and sire breed, for example, then mu with the appropriate generalized least squares class means would be inclusive in Equation 6.

Restricted Maximum Likelihood (REML) Algorithms. Solutions to the above equations assume a priori knowledge of variance component values. If the observational components of variance are not known, estimation by REML (Patterson and Thompson, 1971) has become a popular method used by animal breeders. According to Henderson (1988), "a remarkable property of REML is that, under certain restrictions, it estimates free of bias due to selection the parameters needed in mixed-model evaluation of animals in a population undergoing selection." Derived by iterative procedures, REML variance component estimates can, in turn, be applied to derive BLUE of the fixed (contemporary group) effects employing MME (Henderson, 1973; Weigel et al., 1991). REML also takes into

account the degrees of freedom involved in estimation of fixed effects, including μ (Searle, 1987).

Other popular REML algorithms include derivative-free, or DFREML (Graser *et al.*, 1987; Meyer, 1988), and expectation maximization, or EMREML (Dempster *et al.*, 1977). The DFREML method has the advantage that only a 1-dimensional search for variance components is required, without inversion of the mixed model coefficient matrix, thereby reducing computational time and costs. Also, computational efficiency of DFREML allows for a larger number of equations than derivative REML so that additional random effects (*e.g.* dam and litter effects) can be incorporated with numerator relationships (Meyer, 1991). The EMREML method has the appealing property that convergence is guaranteed if positive variance estimates are used, even in cases where other iterative techniques have problems with negative or zero estimates (Henderson, 1984).

Computer Software for Animal Models. To date, there is limited availabilty of personal computer (PC) packages that utilize Henderson's MME that yield BLUE and BLUP solutions for fixed and random effects under an animal model. To date, two popular PC packages incorporate the numerator additive genetic relationship matrix (A^{-1}) into the MME (Meyer, 1988; Harvey, 1990). These programs can consider both non-inbred and inbred animals. If Meyer's DFREML package is supplemented with a fortran compiler and a sparse matrix program (George *et al.*, 1980), computational memory and time requirements can be reduced substantially for the DF-type algorithm, as discussed by Boldman and Van Vleck (1991). A rich variety of animal models can be investigated using the DFREML package. Harvey's LSMLMW and MIXMDL program (PC-2 version) includes two model types for BLUP estimation under an animal model. A maximum of only 150 animals (sires) can be evaluated in the same analysis, and only one random effect (usually direct genetic effects) can be accommodated in either model (*i.e.* maternal genetic or permanent environmental effects cannot be considered).

Another package includes the General Linear Mixed Models (GLMM) program developed by Blouin and Saxton (1990) which utilizes Henderson's MME to solve for BLUE and BLUP for fixed and random model effects. However, to date, the program does not incorporate the A^{-1} matrix, although the next version should (D. C. Blouin, personal communication). The General Linear Model (GLM) routine of SAS (1985) does not presently utilize mixed model techniques, although the forthcoming version (6.07) will have this capability (via PROC MIXED) to yield BLUE and BLUP estimates, although random effects (*e.g.* animals, sires or dams) are assumed to be uncorrelated (G. Hassan, personal communication).

Mixed models of particular relevance to prediction of breeding value in rabbit populations include full and reduced animal models (AM and RAM) for animal, animal with repeated records, and maternally-influenced trait data. Examples of these models will be provided in this paper. Due to page space limitations, only in the conclusions section will mention be made of multiple-trait models.

Full Animal Model. A full animal model (AM) considers all the additive genetic variation (σ^2_a) among animals based on relationships. A single-trait analysis for annual wool yield will be conducted under a full AM. Prediction of additive genetic value will be estimated for eleven animals produced in two year-season of birth groups and representing both sexes. (Maternal and(or) permanent environmental effects and non-additive genetic effects are assumed to be absent in this analysis.) Wool yield will be analyzed using software by Harvey (1990). The data set is given:

animal	sire	dam	ys	sex	wool yield (g)	deviation from mean (g)*
2	0**	1	1	M	1146	−6
3	0**	0**	1	M	1080	−72
12***	2	1	2	F	1230	78
13	4	6	2	F	1022	−130
14	4	8	2	F	1196	44
15	4	9	2	F	1040	−112
16	4	10	2	F	1132	−20
17	7	11	2	M	1220	68
18	7	8	2	M	1090	−62
19	7	11	2	F	1216	64
20	7	5	2	M	1300	148

*Simple mean for annual wool production is 1152 g.
**A "0" identification code represents an unknown parent.
***Inbreeding coefficient for animal 12 equals .25.

The following mixed model is assumed:

$$y = X\beta + Zd + Wx + e \qquad [7]$$

where y is an observational vector of animal records (expressed as deviations from the simple mean), β is a vector of unknown fixed mu and year-season (ys) group effects, d is a vector of random direct genetic effects ~ $(0, A\sigma^2_a$, where A is the numerator relationship matrix among animals), x is a vector of unknown fixed sex group effects, and e is a vector of unknown random environmental effects ~ $(0, R\sigma^2_e$, where R is assumed to be an identity matrix). The X, Z and W are incidence matrices of zeros and ones relating records to the appropriate ys, d and x groups, respectively. The mixed model equations are shown using matrix notation:

$$
\begin{bmatrix}
X'X & X'W & X'Z \\
W'X & W'W & W'Z \\
Z'X & Z'W & Z'Z + A^{-1}\alpha
\end{bmatrix}^{-1}
\begin{bmatrix}
X'y \\
W'y \\
Z'y
\end{bmatrix}
=
\begin{bmatrix}
\hat{\mu} \\
\hat{ys} \\
\hat{x} \\
\hat{d}
\end{bmatrix}
\qquad [8]
$$

The general X matrix is first computed. Columns and rows 1, 2 and 3 pertain to mu, the first year-season class and the first sex class, respectively, after imposing usual zero-sums restrictions to improve computational efficiency. (Negative one values being

assigned to second ys and sex classes.) Remaining columns and rows represent all 11 animals corresponding to coded year-season and sex classes. The general X (coefficient matrix), and y and general X'y (containing subvectors X'y, W'y and Z'y) matrices are shown:

$$
X = \begin{bmatrix}
1 & 1 & -1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 1 & -1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & -1 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & -1 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & -1 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & -1 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
1 & -1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
1 & -1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{bmatrix}
\quad
y = \begin{bmatrix}
-6 \\
-72 \\
78 \\
-130 \\
44 \\
-112 \\
-20 \\
68 \\
-62 \\
64 \\
148
\end{bmatrix}
\quad
X'y = \begin{bmatrix}
0 \\
-156 \\
-152 \\
-6 \\
-72 \\
78 \\
-130 \\
44 \\
-112 \\
-20 \\
68 \\
-62 \\
64 \\
148
\end{bmatrix}
\qquad [9]
$$

The complete A^{-1} numerator relationship matrix (20 x 20 dimension) is computed in Harvey's program for 9 base animals without records that contribute relationships to the 11 animals with records. Inbreeding is accounted for using the procedure of Quaas (1976). To reduce the number of equations, Henderson (1976) demonstrated how to eliminate the A^{-1} elements for base animals:

$$
A^{-1}_{22} = B_{22} - \begin{bmatrix} B'_{12} & B^{-1}_{11} \end{bmatrix} \begin{pmatrix} B_{12} \end{pmatrix} \qquad [10]
$$

where A^{-1}_{22} is the A^{-1} for animals with records only. The B_{22} contains the A^{-1} elements for these animals prior to elimination of the A^{-1} elements of the base animals (via absorption into the equations for animals with records). The B^{-1}_{11} is the inverse of A^{-1} block involving base animals and B_{12} contains the A^{-1} elements involving base animals and animals with records (Harvey, 1990). These matrices are symbolized by:

$$
A^{-1} = \begin{bmatrix} A_{11} & A_{12} \\ A'_{12} & A_{22} \end{bmatrix}^{-1} = \begin{bmatrix} B_{11} & B_{12} \\ B'_{12} & B_{22} \end{bmatrix} \qquad [11]
$$

The solution for A^{-1}_{22} representing the 11 animals with records:

$$
\begin{bmatrix}
1.6969 & .0000 & -.7272 & .0000 & .0000 & .0000 & .0000 & .0000 & .0000 & .0000 & .0000 \\
.0000 & 1.0000 & .0000 & .0000 & .0000 & .0000 & .0000 & .0000 & .0000 & .0000 & .0000 \\
-.7272 & .0000 & 1.4545 & .0000 & .0000 & .0000 & .0000 & .0000 & .0000 & .0000 & .0000 \\
.0000 & .0000 & .0000 & 1.1456 & -.2072 & -.1877 & -.1877 & -.0080 & .0584 & -.0080 & -.0106 \\
.0000 & .0000 & .0000 & -.2072 & 1.2430 & -.2072 & -.2072 & .0478 & -.3506 & .0478 & .0637 \\
.0000 & .0000 & .0000 & -.1877 & -.2072 & 1.1456 & -.1877 & -.0080 & .0584 & -.0080 & -.0106 \\
.0000 & .0000 & .0000 & -.1877 & -.2072 & -.1877 & 1.1456 & -.0080 & .0584 & -.0080 & -.0106 \\
.0000 & .0000 & .0000 & -.0080 & .0478 & -.0080 & -.0080 & 1.3865 & -.1673 & -.6135 & -.1514 \\
.0000 & .0000 & .0000 & .0584 & -.3506 & .0584 & .0584 & -.1673 & 1.2271 & -.1673 & -.2231 \\
.0000 & .0000 & .0000 & -.0080 & .0478 & -.0080 & -.0080 & -.6135 & -.1673 & 1.3865 & -.1514 \\
.0000 & .0000 & .0000 & -.0106 & .0673 & -.0106 & -.0106 & -.1514 & -.2231 & -.1514 & 1.1315
\end{bmatrix} \qquad [12]
$$

Heritability of .40 for wool yield is arbitrarily assumed. Multiplication of the above A^{-1}_{22} matrix by the scalar, α ($\alpha = \sigma^2_e/\sigma^2_a$ = $(1 - h^2)/ h^2 = 1.5$), yields products that are added to the $Z \times Z$ ($Z'Z$) block of coefficients for animals. The completed coefficent matrix required to obtain solutions to obtain BLUE of fixed effects and BLUP of random effects is given [Equation 13]:

$$
\begin{bmatrix}
11 & -7 & 1 & 1.000 & 1.000 & 1.000 & 1.000 & 1.000 & 1.000 & 1.000 & 1.000 & 1.000 & 1.000 & 1.000 \\
-7 & 11 & -5 & 1.000 & 1.000 & -1.000 & -1.000 & -1.000 & -1.000 & -1.000 & -1.000 & -1.000 & -1.000 & -1.000 \\
1 & -5 & 11 & -1.000 & -1.000 & 1.000 & 1.000 & 1.000 & 1.000 & 1.000 & -1.000 & -1.000 & 1.000 & -1.000 \\
1 & 1 & -1 & 3.545 & .000 & -1.091 & .000 & .000 & .000 & .000 & .000 & .000 & .000 & .000 \\
1 & 1 & -1 & .000 & 2.500 & .000 & .000 & .000 & .000 & .000 & .000 & .000 & .000 & .000 \\
1 & -1 & 1 & -1.091 & .000 & 3.182 & .000 & .000 & .000 & .000 & .000 & .000 & .000 & .000 \\
1 & -1 & 1 & .000 & .000 & .000 & 2.718 & -.311 & -.282 & -.282 & -.012 & .088 & -.012 & -.016 \\
1 & -1 & 1 & .000 & .000 & .000 & -.311 & 2.865 & -.311 & -.311 & .072 & -.526 & .072 & .096 \\
1 & -1 & 1 & .000 & .000 & .000 & -.282 & -.311 & 2.718 & -.282 & -.012 & .088 & -.012 & -.016 \\
1 & -1 & 1 & .000 & .000 & .000 & -.282 & -.311 & -.282 & 2.718 & -.012 & .088 & -.012 & -.016 \\
1 & -1 & -1 & .000 & .000 & .000 & -.012 & .072 & -.012 & -.012 & 3.080 & -.251 & -.920 & -.227 \\
1 & -1 & -1 & .000 & .000 & .000 & .088 & -.526 & .088 & .088 & -.251 & 2.841 & -.251 & -.335 \\
1 & -1 & 1 & .000 & .000 & .000 & -.012 & .072 & -.012 & -.012 & -.920 & -.251 & 3.080 & -.227 \\
1 & -1 & -1 & .000 & .000 & .000 & -.016 & .096 & -.016 & -.016 & -.227 & -.335 & -.227 & 2.697 \\
\end{bmatrix}
$$

Inversion of the latter matrix and multiplication to the general $X'y$ vector (from Equation 9), yields the solutions: BLUE for mu = 1128.43, ys (class 1) = -41.73, ys (class 2) = 41.73, sex class 1 = -21.62, sex class 2 = 21.62; and BLUP of direct BV for animal 2 = 20.69, animal 3 = -11.33, animal 12 = 32.70, animal 13 = -51.98, animal 14 = -2.63, animal 15 = -45.98, animal 16 = -15.32, animal 17 = 18.18, animal 18 = -23.97, animal 19 = 27.99 and animal 20 = 40.46 g, respectively. Equation 14 below is the BV prediction formula from this analysis ($Z_{ii} = 1$, since each animal has a record):

$$
\hat{d}_i = \left(\frac{1}{Z_{ii} + a^{ii}\alpha} \right) \left(Y_i - \hat{\mu} - \hat{y}s_i - \hat{x}_m \right) - \left(\frac{1}{Z_{ii} + a^{ii}\alpha} \right) \left(\sum_{j \neq i} a^{ij} \hat{d}_j \alpha \right)
$$

where $\hat{d}$ is estimated direct BV for wool yield of the ith animal based to its own record and the contribution of its relatives, and adjusted for fixed effects (mu and appropriate ys and x class means).

Animal Model with Repeated Records. The last trait problem will again be used with the additional consideration of repeatability for the case when more than one record is available on animals. Angora rabbits have repeated records based on, for example, annual or seasonal shearing-related traits. Maternal genetic effects as would be associated with the same dam, and(or) environmental effects as would be associated with the same litter, are presumed to be absent in this model. Further, for simplicity here, sex differences will be ignored as well as additive genetic relationships among animals. The mixed model as shown previously from Equation 7 is rewritten as follows:

$$y = Xys + Z_1 d + Z_2 pe + e \tag{15}$$

The model terms are as defined previously, except that ys is a vector of unknown fixed effects due to year-season (2 classes) as contemporary groups, and pe is an unknown vector of random permanent environmental effects (if non-additive genetic effects are absent) ~ (0, $I\sigma^2_{pe}$, where I is an identity matrix). Random effects, d , pe and e, are further assumed to be uncorrelated. The MME for this problem:

$$\begin{bmatrix} X'X & X'Z_1 & X'Z_2 \\ Z'_1X & Z'_1Z_1 + A^{-1}\alpha_1 & Z'_1Z_2 \\ Z'_2X & Z'_2Z_1 & Z'_2Z_2 + I\alpha_2 \end{bmatrix}^{-1} \begin{bmatrix} X'y \\ Z'_1y \\ Z'_2y \end{bmatrix} = \begin{bmatrix} \hat{ys} \\ \hat{d} \\ \hat{pe} \end{bmatrix} \quad [16]$$

The data set involves 5 animals with records as listed below:

animal	ys	record no.	wool yield (g)*	breeding value solution ($\hat{d}$)	producing ability solution ($\hat{p}$)**
1	1	1	1228	-7.1111	-10.6667
1	1	2	1272		
2	1	1	1282	7.1111	10.6667
3	2	1	1194	-3.3676	-5.0515
3	2	2	1240		
4	2	1	1252	37.2353	55.8529
4	2	2	1286		
4	2	3	1338		
5	2	1	1124	-33.8676	-50.8015
5	2	2	1188		

*Simple mean for wool production is 1240.4 g.
**Estimated producing ability (EPA) equals the sum of BLUP for additive genetic merit (BV) and permanent environmental effects.

The above data set was analyzed using GLMM software (Blouin and Saxton, 1990), although DFREML or SAS (6.07 version) could be used for this problem. Since animal relationships were ignored, the A^{-1} matrix turns out to be an identity matrix, I. In GLMM, a no intercept (mu) model may be chosen as used in this example. The completed mixed model coefficient matrix, and the general $X'y$ (containing $X'y$, Z'_1y and Z'_2y) and the solution (ys, d and pe) vectors computed to solve the MME are given [Equation 17]:

$$\begin{bmatrix} 3 & 0 & 2 & 1 & 0 & 0 & 0 & 2 & 1 & 0 & 0 & 0 \\ 0 & 7 & 0 & 0 & 2 & 3 & 2 & 0 & 0 & 2 & 3 & 2 \\ 2 & 0 & 2+\alpha_1 & 0 & 0 & 0 & 0 & 2 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1+\alpha_1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 2 & 0 & 0 & 2+\alpha_1 & 0 & 0 & 0 & 0 & 2 & 0 & 0 \\ 0 & 3 & 0 & 0 & 0 & 3+\alpha_1 & 0 & 0 & 0 & 0 & 3 & 0 \\ 0 & 2 & 0 & 0 & 0 & 0 & 2+\alpha_1 & 0 & 0 & 0 & 0 & 2 \\ 2 & 0 & 2 & 0 & 0 & 0 & 0 & 2+\alpha_2 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1+\alpha_2 & 0 & 0 & 0 \\ 0 & 2 & 0 & 0 & 2 & 0 & 0 & 0 & 0 & 2+\alpha_2 & 0 & 0 \\ 0 & 3 & 0 & 0 & 0 & 3 & 0 & 0 & 0 & 0 & 3+\alpha_2 & 0 \\ 0 & 2 & 0 & 0 & 0 & 0 & 2 & 0 & 0 & 0 & 0 & 2+\alpha_2 \end{bmatrix}^{-1} \begin{bmatrix} 3782 \\ 8622 \\ 2500 \\ 1282 \\ 2434 \\ 3876 \\ 2312 \\ 2500 \\ 1282 \\ 2434 \\ 3876 \\ 2312 \end{bmatrix} = \begin{bmatrix} 1264.22 \\ 1223.74 \\ -7.11 \\ 7.11 \\ -3.37 \\ 37.24 \\ -33.87 \\ -3.56 \\ 3.56 \\ -1.68 \\ 18.62 \\ -16.93 \end{bmatrix}$$

The α_1 and α_2 values relate to heritability (h^2) and repeatabilty (r) estimates, where $\alpha_1 = \sigma^2_e/\sigma^2_a = (1-r)/h^2$ and $\alpha_2 =$

$\sigma^2_e/\sigma^2_{pe} = (1-r)/(r-h^2)$, respectively. Using arbitrary values of heritability of .4 and repeatabilty of .6, α_1 and α_2 values of 1 and 2 are calculated. Of relevance, if these parameters change with age, as reported by Garcia and Magofke (1982) and Jaitner et al. (1988), then a multivariate analysis under an animal model approach might be preferable whereby each available record is regarded as a different trait. Two excellent review papers on genetics and(or) breeding programs for Angora wool production are by Yadav and Dempfle (1988) and Rochambeau and Thebault (1990).

BLUE for ys first and second classes are 1264.22 and 1223.74 g. BLUP solutions for direct BV and estimated producing ability (EPA) for wool yield, adjusted for ys effects, are shown above with the data. EPA is a function of an animal's additive genetic merit plus a permanent environmental and(or) non-additive genetic value. Animal relationships were ignored, so BLUP solutions for BV and EPA sum to zero within each ys class, as expected. Basic formulas for direct BV (d) and EPA (p) prediction from this analysis are given:

$$\hat{d}_i = \left(\frac{n_i h^2}{1+(n_i-1)r}\right) (\bar{y}_i. - \hat{y}s_j) \quad \text{and} \quad \hat{p}_i = \left(\frac{n_i r}{1+(n_i-1)r}\right) (\bar{y}_i. - \hat{y}s_j) \qquad [18]$$

These formulas are also the selection index for the ith animal with n records for estimating additive genetic merit and producing ability, adjusted for BLUE of the jth ys effect (Van Vleck, 1988).

The animal with repeated records model could also be used for genetic evaluation of does for reproductive performance (litter size or weight at weaning). The MME would be set-up based on h^2 and r parameter estimates (either known or derived iteratively prior to computing BV and EPA solutions), additive genetic relationships and number of records per doe. Recent papers (Estany et al., 1988a; Baselga et al., 1992; Blasco et al., 1992 Ferraz et al., 1992a; Rochambeau et al., 1992), all published in World Rabbit Congress proceedings, describing similar models have discussed BLUP applications for doe evaluation and(or) selection/culling purposes.

<u>Animal Model for a Maternally Influenced Trait</u>. Of relevance to meat rabbit breeding, this AM type considers a growth trait that is influenced by direct genetic effects, maternal genetic effects (chiefly milk production), and also permanent environmental differences common to contemporary littermates (presumably due to maternal environmental, competition and(or) pen effects) at the time of measurement. In addition, direct and maternal genetic effects may be correlated; in other words, a genetic covariance may exist. Failure to take into account such factors can lead to serious bias in BV estimation, thus realized genetic progress could prove disappointing. Van Vleck (1990a) outlined procedures for BV prediction under an AM with maternal effects which accounted for a covariance between direct and maternal additive genetic effects, as well as permanent environmental effects.

To illustrate, a 70-day body weight analysis under this AM type will be performed using observational components of (co)variance reported by Lukefahr et al. (1992b) as obtained from the DFREML method (Meyer, 1988). The simulated data set is shown:

animal	sire	dam	ys	sex	lsw	bw, g*	direct breeding value	maternal breeding value	permanent environmental deviation
1	0**	0**	–	M	–	–	11.3053	-15.9504	–
2	1	0**	–	F	–	–	6.4750	.3583	–
3	1	2	1	M	6	2139	50.8289	-91.6427	.3300
4	0**	2	1	F	8	1781	-14.5425	15.7706	–
5	1	4	2	F	5	2256	41.4494	-86.1944	.2358
6	1	4	2	F	5	1936	-25.8624	48.3798	.2358
7	3	4	2	F	7	1977	18.3426	-38.3348	-.3569
8	3	4	2	M	7	1843	-6.9868	12.3055	-.3569
9	3	2	2	F	6	2192	61.2806	-110.8760	.7474
10	3	2	2	M	6	2123	48.2378	-84.7996	.7474
11	1	2	2	M	4	1855	-41.1159	92.1794	-.6263

*Simple mean for 70-day body weight (bw) is 2011.33 g.
**A "0" identification code represents an unknown parent.
Codes: ys = year-season class; lsw = litter size weaned (mean lsw = 6 kits).

For this example, an additive genetic model will be assumed since non-additive genetic (heterosis) effects on body weight may possibly be of minor importance (Carregal, 1980; Baselga et al., 1982; Lukefahr et al., 1983a,b; Brun and Ouhayoun, 1989; Krogmeier and Dzapo, 1991). Body weight records from the above table will be adjusted for litter size, as conducted in other genetic variance component analysis rabbit studies (McReynolds, 1974; Lukefahr et al., 1988, 1992a,b; Moura et al., 1991; Ferraz et al., 1992a). An adjustment for inbreeding effects by regression will not be made in this example. Ferraz et al. (1992b) included inbreeding effects as covariates using an animal model for analysis of production traits in rabbits. Further, permanent maternal environmental effects on body weight will be assumed to be absent between siblings from non-contemporary litters. The sex effect will also be ignored in this example, because sex differences for body weight are generally not important in young rabbits. The mixed model is rewritten from Equation 15, as follows:

$$y = X\beta + Z_1d + Z_2m + Z_3pe + e \qquad [19]$$

where y is an observational vector, β is a vector of unknown fixed effects due to year-season of birth as contemporary groups (and includes the linear covariate of lsw with records deviated from the lsw mean of 6 kits), X, Z_1, Z_2 and Z_3 are known incidence matrices relating records to the appropriate fixed and random effect classes, d is an unknown vector of random direct genetic effects ~ $(0, A\sigma^2_a$ and $A\sigma_{am}$, where A is the numerator relationship matrix among animals), m is an unknown vector of random maternal genetic effects ~ $(0, A\sigma^2_m$ and $A\sigma_{am}$, where A is the same numerator relationship matrix), and pe is an unknown vector of random permanent environmental effects ~ $(0, I\sigma^2_{pe}$, where I is an identity matrix). Random effects, d and m are correlated, whereas the random pe

effect is assumed to be uncorrelated with d, m and e effects. The MME for this analysis (Equation 20):

$$
\begin{bmatrix}
X'X & X'Z_1 & X'Z_2 & X'Z_3 \\
Z'_1X & Z'_1Z_1 + A^{-1}\alpha_{11} & Z'_1Z_2 + A^{-1}\alpha_{12} & Z'_1Z_3 \\
\text{Symmetric} & & Z'_2Z_2 + A^{-1}\alpha_{22} & Z'_2Z_3 \\
& & & Z'_3Z_3 + I\alpha_{33}
\end{bmatrix}^{-1}
\begin{bmatrix}
X'y \\
Z'_1y \\
Z'_2y \\
Z'_3y
\end{bmatrix}
=
\begin{bmatrix}
\hat{\beta} \\
\hat{d} \\
\hat{m} \\
\hat{pe}
\end{bmatrix}
$$

The $X'X$, $X'Z_1$, $X'Z_2$ and $X'Z_3$ matrices are shown (Equation 21):

$X'X$

$$
\begin{bmatrix}
2 & 0 & 2 \\
0 & 7 & -2 \\
2 & -2 & 12
\end{bmatrix}
$$

$X'Z_1$

$$
\begin{bmatrix}
0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\
0 & 0 & 0 & 2 & -1 & -1 & 1 & 1 & 0 & 0 & -2
\end{bmatrix}
$$

$X'Z_2$

$$
\begin{bmatrix}
0 & 2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 3 & 0 & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{bmatrix}
$$

$X'Z_3$

$$
\begin{bmatrix}
1 & 0 & 0 & 0 & 0 \\
0 & 2 & 2 & 2 & 1 \\
0 & -2 & 2 & 0 & -2
\end{bmatrix}
$$

The transpose of the general $X'y$ matrix (subvectors $X'y$, Z'_1y, Z'_2y and Z'_3y), referred to as the right-hand sides of the normal equations, is given (Equation 22):

$X'y$: 3920 14182 -520 Z'_1y: 0 0 2139 1781 2256 1936 1977 1843 2192 2123 1855

Z'_2y: 0 10090 0 8012 0 0 0 0 0 0 0 Z'_3y: 2139 4192 3820 4315 1855

The Z'_1Z_1 animal block matrix (11 x 11) is an identity matrix of 0's and 1's, where a 1 value is assigned to each diagonal position since each animal has a record (except for animals 1 and 2). The Z'_1Z_2 animal x dam block matrix (11 x 11) assigns a 1 value at the animal row by dam column position if the given animal has a known dam. The Z'_1Z_3 matrix of 0's and 1's (11 x 5) assigns a 1 value at the animal row by litter column position if the given animal is from a known litter. The Z'_2Z_2 dam block matrix (11 x 11) codes values of 5 and 4 (number of progeny per dam) in the appropriate diagonal position for dams 2 and 4, respectively, all other values being zero. The Z'_2Z_3 matrix (11 x 5) codes values of 1 or 2 (number of contemporary littermates) in the appropriate dam row (2 or 4) by litter column position, other values being zero. The Z'_3Z_3 litter block matrix (5 x 5) is an identity matrix with a value for the sibling number per litter assigned to the corresponding diagonal cell for each of 5 contemporary litters. Except for Z'_1Z_1, these incidence matrices are shown for clarity:

Z'_1Z_2	Z'_1Z_3	Z'_2Z_2	Z'_2Z_3	Z'_3Z_3
0 0 0 0 ... 0	0 0 0 0 0	0 0 0 0 ... 0	0 0 0 0 0	1 0 0 0 0
0 0 0 0	0 0 0 0 0	0 5 0 0	1 0 0 2 1	0 2 0 0 0
0 1 0 0	1 0 0 0 0	0 0 0 0	0 0 0 0 0	0 0 2 0 0
0 1 0 0	0 0 0 0 0	0 0 0 4	0 2 2 0 0	0 0 0 2 0
0 0 0 1	0 1 0 0 0	. . . .	. . . . .	0 0 0 0 1
0 0 0 1	0 1 0 0 0	. . . .	. . . . .	
0 0 0 1	0 0 1 0 0	. . . .	. . . . .	
0 0 0 1	0 0 1 0 0	. . . .	. . . . .	
0 1 0 0	0 0 0 1 0	. . . .	. . . . .	
0 1 0 0	0 0 0 1 0	. . . .	. . . . .	
0 1 0 0 ... 0	0 0 0 0 1	0 0 0 0 ... 0	0 . . . 0	[23]

The A^{-1} (upper diagonal) and A (lower diagonal) relationship matrices (accounting for some inbreeding) that pertain to the 11 x 11 animal (Z'_1Z_1), dam (Z'_2Z_2) and animal x dam (Z'_1Z_2) blocks of the coefficient matrix are provided below (Equation 24):

```
3.3333   .3333 -1.0000  1.0000 -1.0000 -1.0000   .0000   .0000   .0000   .0000 -1.0000
         3.8095  .1429  -.6667   .0000   .0000   .0000   .0000 -1.1429 -1.1429 -1.0000
1.0000          4.2857  1.1429   .0000   .0000 -1.1429 -1.1429 -1.1429 -1.1429   .0000
 .5000  1.0000          3.4762 -1.0000 -1.0000 -1.1429 -1.1429   .0000   .0000   .0000
 .7500   .7500  1.2500          2.0000   .0000   .0000   .0000   .0000   .0000   .0000
 .2500   .5000   .3750  1.0000          2.0000   .0000   .0000   .0000   .0000   .0000
 .6250   .5000   .5625   .6250  1.1250          2.2857   .0000   .0000   .0000   .0000
 .6250   .5000   .5625   .6250   .6250  1.1250          2.2857   .0000   .0000   .0000
 .5000   .6250   .8125   .6875   .5938   .5938  1.1875          2.2857   .0000   .0000
 .5000   .6250   .8125   .6875   .5938   .5938   .7500  1.1875          2.2857   .0000
 .6250   .8750  1.0000   .4375   .5313   .5313   .7188   .7188  1.3750          2.0000
 .6250   .8750  1.0000   .4375   .5313   .5313   .7188   .7188   .9375  1.3750
 .7500   .7500   .7500   .3750   .5625   .5625   .5625   .5625   .7500   .7500  1.2500
```

The DFREML observational components of (co)variance for pre-slaughter body weight at approximately 70 days of age, obtained by iteration, were: $\sigma^2_a = 13{,}428$ ($h^2_d = .16$); $\sigma^2_m = 72{,}173$ ($h^2_m = .86$); $\sigma_{am} = -26{,}855$ ($r_{am} = -.87$); $\sigma^2_{pe} = 0$, and $\sigma^2_\epsilon = 25{,}177$ (Lukefahr et al., 1992b). The genetic components are derived through additive genetic relationships. These parameter estimates are biased to some degree due, in part, to the small sample population size of 219 rabbit fryers from 4 sire breeds, 34 sires, 58 dams and 91 litters used in the experiment. To solve for the α values for this example:

$$\begin{bmatrix} \sigma^2_a & \sigma_{am} \\ \sigma_{am} & \sigma^2_m \end{bmatrix}^{-1} \sigma^2_\epsilon = \begin{bmatrix} \alpha_{11} & \alpha_{12} \\ \alpha_{21} & \alpha_{22} \end{bmatrix} = \begin{bmatrix} 7.329 & 2.727 \\ 2.727 & 1.364 \end{bmatrix} \qquad [25]$$

The α_{33} is the ratio of $\sigma^2_\epsilon / \sigma^2_{pe} = 299.726$ (σ^2_{pe} was arbitrarily assigned a value that was .1% of total variance to illustrate this source of variation in the MME). Following multiplication of the A^{-1} to each of three α scalar matrices (corresponding to α_{11}, α_{12} and α_{22}) separately, the resulting product matrices are then added to the corresponding values in the appropriate block of the coefficient matrix. The final form of the four blocks: $Z'_1Z_1 + A^{-1}\alpha_{11}$, $Z'_2Z_2 + A^{-1}\alpha_{22}$, $Z'_1Z_2 + A^{-1}\alpha_{12}$ and $Z'_3Z_3 + I\alpha_{33}$, are shown below:

$Z'_1Z_1 + A^{-1}\alpha_{11}$ (upper diagonal) and $Z'_2Z_2 + A^{-1}\alpha_{22}$ (lower diagonal) [Symmetric]:

```
24.430   2.443  -7.329   7.329  -7.329  -7.329    .000    .000    .000    .000  -7.329
        27.920   1.047  -4.886    .000    .000    .000    .000  -8.376  -8.376  -7.329
 4.547          32.410   8.376    .000    .000  -8.376  -8.376  -8.376  -8.376    .000
  .455  10.196          26.477  -7.329  -7.329  -8.376  -8.376    .000    .000    .000
-1.364    .195   5.846          15.658    .000    .000    .000    .000    .000    .000
 1.364   -.909   1.559   8.742          15.658    .000    .000    .000    .000    .000
-1.364    .000    .000  -1.364   2.278          17.752    .000    .000    .000    .000
-1.364    .000    .000  -1.364    .000   2.728          17.752    .000    .000    .000
  .000    .000  -1.559  -1.559    .000    .000   3.118          17.752    .000    .000
  .000    .000  -1.559  -1.559    .000    .000    .000   3.118          17.752    .000
  .000  -1.559  -1.559    .000    .000    .000    .000    .000   3.118          15.658
  .000  -1.559  -1.559    .000    .000    .000    .000    .000    .000   3.118
-1.364  -1.364    .000    .000    .000    .000    .000    .000    .000    .000   2.728
```

$Z'_1Z_2 + A^{-1}\alpha_{12}$ (Non-symmetric):

```
 9.090    .909  -2.727   2.727  -2.727  -2.727    .000    .000    .000    .000  -2.727
  .909  10.389    .390  -1.818    .000    .000    .000    .000  -3.117  -3.117  -2.727
-2.727   1.390  11.687   3.117    .000    .000  -3.117  -3.117  -3.117  -3.117    .000
 2.727   -.818   3.117   9.480  -2.727  -2.727  -3.117  -3.117    .000    .000    .000
-2.727    .000    .000  -1.727   5.454    .000    .000    .000    .000    .000    .000
-2.727    .000    .000  -1.727    .000   5.454    .000    .000    .000    .000    .000
  .000    .000  -3.117  -2.117    .000    .000   6.233    .000    .000    .000    .000
  .000    .000  -3.117  -2.117    .000    .000    .000   6.233    .000    .000    .000
  .000  -2.117  -3.117    .000    .000    .000    .000    .000   6.233    .000    .000
  .000  -2.117  -3.117    .000    .000    .000    .000    .000    .000   6.233    .000
-2.727  -1.727    .000    .000    .000    .000    .000    .000    .000    .000   5.454
```

$Z'_3Z_3 + I\alpha_{33}$ (Symmetric):

```
300.726    .000    .000    .000    .000
       301.726    .000    .000    .000
              301.726    .000    .000
                     301.726    .000
                            300.726
```
[26]

The completed (augmented) mixed model coefficient matrix does not require inversion when using DFREML. Instead, the Gaussian elimination method is employed to obtain solutions directly (hence, derivative-free), whereby the likelihood function is evaluated explicitly in each round of iteration until the maximum (with respect to the (co)variance components) is located upon convergence (Boldman and Van Vleck, 1991). Improved computational efficiency is realized if a sparse matrix package is supplied (George et al., 1980). The procedures and steps are quite involved, however, and as such it would not be appropriate to review these measures in this paper. The reader is referred to papers, in particular, by Meyer (1988, 1989) for a comprehensive understanding of this program.

The solution set to the mixed model coefficent matrix (Equation 26) is shown with the tabulated observation data above. Generalized least squares means (g) for first and second ys classes and the litter size covariate are 1988.573, 1989.629 and -47.2395, respectively. For animals (parents) with progeny records but without their own individual record (e.g. animals 1 and 2), BLUP of direct BV (d_i) for growth is derived through records on their respective relatives and adjustment for mates, d_j. Individual direct BV is also adjusted based on the relationship between direct and maternal components (presumably between growth and milk production), m_j (relatives and mates), and m_i (individual maternal BV). In this case, the formula for direct BV prediction is as follows (Note: The a^{ii}, a^{ij}, a^{is} and a^{iD} values are from the A^{-1} matrix, whereas the $a^{ii}\alpha_{11}(\alpha_{12}$ or $\alpha_{22})$, $a^{ij}\alpha_{11}(\alpha_{12}$ or $\alpha_{22})$, $a^{is}\alpha_{11}(\alpha_{12})$, $a^{iD}\alpha_{11}(\alpha_{12})$ and $a^{ik}\alpha_{12}$ values are from the coefficient matrix.):

$$\hat{d}_i = -\left(\frac{1}{a^{ii}}\right)\left(\sum_{j \neq i} a^{ij}\hat{d}_j\right) - \left(\frac{\alpha_{12}}{a^{ii}\alpha_{11}}\right)\left(\sum_{j \neq i} a^{ij}\hat{m}_j\right) - \left(\frac{\alpha_{12}}{\alpha_{11}}\right)(\hat{m}_i)$$

[27]

Direct BV for animals (parents) with information of their own individual record and also progeny records (e.g. animals 3 and 4) would have the prediction formula as given:

$$\hat{d}_i = \left(\frac{1}{1+a^{ii}\alpha_{11}}\right) \left(y_i - \hat{y}s_i - \hat{b}(lsw_o - \overline{lsw}) - \hat{pe}_{litter}\right) - \left(\frac{\alpha_{11}}{1+a^{ii}\alpha_{11}}\right)\left(\sum_{j\neq i}a^{ij}\hat{d}_j\right)$$

$$- \left(\frac{\alpha_{12}}{1+a^{ii}\alpha_{11}}\right)\left(\sum_{j\neq i}a^{ij}\hat{m}_j\right) - \left(\frac{1+a^{iD}\alpha_{12}}{1+a^{ii}\alpha_{11}}\right)(\hat{m}_D) - \left(\frac{a^{ii}\alpha_{12}}{1+a^{ii}\alpha_{11}}\right)(\hat{m}_i) \qquad [28]$$

The formula for maternal BV for base animals or male parents (e.g. animals 1 and 3):

$$\hat{m}_i = - \left(\frac{1}{a^{ii}}\right)\left(\sum_{j\neq i}a^{ij}\hat{m}_j\right) - \left(\frac{\alpha_{12}}{a^{ii}\alpha_{22}}\right)\left(\sum_{j\neq i}a^{ij}\hat{d}_j\right) - \left(\frac{\alpha_{12}}{\alpha_{22}}\right)(\hat{d}_i) \qquad [29]$$

Maternal BV prediction for female parents with progeny records (k):

$$\hat{m}_i = \left(\frac{1}{k+a^{ii}\alpha_{22}}\right) \left(\sum_l\sum_k y_k - \hat{y}s_i - \hat{b}(lsw_o - \overline{lsw}) - \hat{pe}_{litter}\right) - \left(\frac{\alpha_{22}}{k+a^{ii}\alpha_{22}}\right)\left(\sum_{j\neq i}a^{ij}\hat{m}_j\right)$$

$$- \left(\frac{\alpha_{12}}{k+a^{ii}\alpha_{22}}\right)\left(\sum_{j\neq i}a^{ij}\hat{d}_j\right) - \left(\frac{1}{k+a^{ii}\alpha_{22}}\right)\left(\sum_{x\neq i}1+a^{ik}\alpha_{12}\ [\hat{d}_k]\right) - \left(\frac{a^{ii}\alpha_{12}}{k+a^{ii}\alpha_{22}}\right)(\hat{d}_i) \qquad [30]$$

The EPA values for does 2 and 4 would be calculated from $.5\hat{d}_i + \hat{m}_i$, which yields 3.60 and 8.50 g, respectively. The permanent environmental (pe) effect does not enter into the EPA formula since this effect was not associated with the dam as in this example. In the last equation, the pe effect would consider the litter (not the dam) for the kth progeny record, in other words.

For animals (progeny) with individual records (first line) the direct BV formula (the second line is the direct BV contribution of parents, S and D; the third line is the adjustment for maternal BV relationship):

$$\hat{d}_i = \left(\frac{1}{1+a^{ii}\alpha_{11}}\right) \left(y_i - \hat{y}s_i - \hat{b}(lsw_o - \overline{lsw}) - \hat{pe}_{litter} \right)$$

$$- \left(\frac{1}{1+a^{ii}\alpha_{11}}\right) \left(a^{iS}\alpha_{11}\ [\ \hat{d}_S\ ] + a^{iD}\alpha_{11}\ [\hat{d}_D\ ] \right)$$

$$- \left(\frac{1}{1+a^{ii}\alpha_{11}}\right) \left([a^{iS}\alpha_{12}\ (\hat{m}_S)] + [1+a^{iD}\alpha_{12}\ (\hat{m}_D)] + [a^{ii}\alpha_{12}\ (\hat{m}_i)] \right) \qquad [31]$$

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Lastly, for animals (progeny) with individual records the maternal BV formula is shown (maternal BV being based on records from dams with progeny records):

$$\hat{m}_1 = .5\ (\hat{m}_S + \hat{m}_D) - \frac{\alpha_{12}}{\alpha_{22}}\ (\ -.5\hat{d}_S - .5\hat{d}_D + \hat{d}_1\ )$$

[32]

Of interest, the -.87 genetic correlation between direct and maternal genetic effects for approximate 70-day body weight as reported by Lukefahr *et al.* (1992b), is in contrast to the positive genetic correlation of 1.00 for the same character involving 1,731 fryers as documented by Ferraz *et al.* (1992a). Earlier reports (Rollins and Casady, 1960; Harvey *et al.*, 1961, Rollins *et al.*, 1963) implicated an additive genetic by general maternal effects covariance affecting 56-day market weights in New Zealand White rabbits. Obviously, more research in this area is urgently needed to incorporate unbiased genetic and environmental parameters into MME for accurate BV prediction. If an unreasonable genetic covariance is derived from an iterative REML solution, however, then it may be best to not include this biased parameter in the MME (assume independent animal and dam effects) until a reasonable estimate is obtained later (Benyshek *et al.*, 1988). Should a strong genetic antagonism actually exist, then selection for one or the other genetic components of a trait (Van Vleck, 1970), or selection within those populations for seemingly rare individuals with highest ranking positive direct and maternal BV's would be plausible approaches. Development of specialized dam and sire lines is another option (Moav, 1966; Dickerson, 1969), and usage of a restricted selection index is still another (Kempthorne and Nordskog, 1959; Xu and Muir, 1992).

Reduced Animal Model for a Maternally Influenced Trait. The reduced animal model (RAM) has become popular in recent years because of the computational efficiency advantage over obtaining solutions under a full animal model. In other words, the number of equations needed involve only those associated with fixed effects (year-season and litter size) and random parent and litter effects from the previous problem. Especially applicable to rabbits where progeny numbers may greatly exceed the number of parents, the RAM approach is appealing because of the reduction in computational requirements. Observations of progeny (non-parents) are basically absorbed into the equations for parents. BV solutions (direct and maternal) for progeny can be computed from a RAM analysis using straightforward back-solution procedures.

The RAM method has been extended for analysis of traits influenced by maternal effects, such as weaning weight in beef cattle (Benyshek *et al.*, 1988; Johnson *et al.*, 1992). For postweaning performance traits in swine, Hudson (1984) and Hudson and Kennedy (1985) developed a RAM procedure to predict BV, although an additive genetic model was assumed in both papers. Van Vleck (1990b) outlined procedures for performing a RAM analysis for

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traits affected by direct and maternal genetic, covariance between direct and maternal genetic and permanent environmental effects.

Using the same previous data set with 4 parents (p = 1, 2, 3 and 4) and 7 non-parents (n = 5, 6, 7, 8, 9, 10 and 11) as analyzed under a full animal model, the MME for a RAM analysis (adapted from Quaas and Pollak [1980] and Benyshek et al., [1988]):

$$
\begin{bmatrix}
X'_pX_p + X'_nRX_n & X'_pZ_1 + \frac{1}{2}X'_nRZ_1^* & X'_pZ_2 + X'_nRZ_2^* & X'_pZ_3 + X'_nRZ_3^* \\
 & Z'_1Z_1 + \frac{1}{4}Z'_1^*RZ_1^* + A^{-1}_{pp}\alpha_{11} & Z'_1Z_2 + \frac{1}{2}Z'_1^*RZ_2^* + A^{-1}_{pp}\alpha_{12} & Z'_1Z_3 + \frac{1}{2}Z'_1^*RZ_2^* \\
\text{Symmetric} & & Z'_2Z_2 + Z'_2^*RZ_2^* + A^{-1}_{pp}\alpha_{22} & Z'_2Z_3 + Z'_2^*RZ_3^* \\
 & & & Z'_3Z_3 + Z'_3^*RZ_3^* + I\alpha_{33}
\end{bmatrix}
$$

$$
* \begin{bmatrix} \hat{\beta} \\ \hat{d}_p \\ \hat{m}_p \\ \hat{pe}_1 \end{bmatrix} = \begin{bmatrix} X'_pY_p + X'_nRY_n \\ Z'_1Y_p + \frac{1}{2}Z'_1^*RY_n \\ Z'_2Y_p + Z'_2^*RY_n \\ Z'_3Y_p + Z'_3^*RY_n \end{bmatrix}
$$

[33]

For this RAM analysis, there are 16 rather than 30 equations (2 fixed ys classes, 1 fixed covariate (lsw), 4 random direct and 4 random maternal genetic effects for parents, and 5 random permanent environmental effects for litters). For clarity, a series of matrices that are incorporated into the above RAM equations are as follows (Equation 34):

X_p	Y_p	X_n	Y_n
0 0 0	0	0 1 -1	2256
0 0 0	0	0 1 -1	1936
1 0 0	2139	0 1 1	1977
1 0 2	1781	0 1 1	1843
		0 1 0	2192
		0 1 0	2123
		0 1 -2	1855

A_{pp}

1.000	.500	.750	.250
.500	1.000	.750	.500
.750	.750	1.250	.375
.250	.500	.375	1.000

A^{-1}_{pp}

1.833	-.167	-1.000	.000
-.167	2.167	-1.000	-.667
-1.000	-1.000	2.000	.000
.000	-.667	.000	1.333

The Z_1, Z_1^*, Z_2, Z_2^*, Z_3 and Z_3^* matrices pertain to direct, maternal and litter random effects for parents and non-parents(*), respectively (Equation 35).

Z_1	Z_1^*	Z_2	Z_2^*	Z_3	Z_3^*
0 0 0 0	1 0 0 1	0 0 0 0	0 0 0 1	0 0 0 0 0	0 1 0 0 0
0 0 0 0	1 0 0 1	0 0 0 0	0 0 0 1	0 0 0 0 0	0 1 0 0 0
0 0 1 0	0 0 1 1	0 1 0 0	0 0 0 1	1 0 0 0 0	0 0 1 0 0
0 0 0 1	0 0 1 1	0 1 0 0	0 0 0 1	0 0 0 0 0	0 0 1 0 0
	0 1 1 0		0 1 0 0		0 0 0 1 0
	0 1 1 0		0 1 0 0		0 0 0 1 0
	1 1 0 0		0 1 0 0		0 0 0 0 1

The Z_1 (p x p) and Z_1^* (n x p) matrices contain pedigree codes (sire and dam) for the 4 parents (p) and 7 nonparents (n); Z_2 (p x p) and Z_2^* (n x p) matrices relate parents and nonparents to known dams (2 and 4), and Z_3 (p x 1) and Z_3^* (n x 1) matrices relate parents and nonparents to the 5 contemporary litters (1), respectively. In the case of the RAM, parent and nonparent matrices are subsets (inclusive of only parent or litter columns with parent or nonparent rows) of matrices Z_1, Z_2 and Z_3 as found for the full AM, as illustrated in the previous example. Likewise, the same α values are used for either a full AM or a RAM (Equation 25).

The R matrix (within-animal residual structure) is an identity matrix with zero off-diagonal elements and diagonal elements corresponding to the following formula for R_n, which is calculated separately for each nonparent with a body weight record:

$$R_n = \frac{1}{1 + D_n(\alpha_1^{-1})}$$

[36]

where D_n is $\frac{1}{2}$ if both parents are known and non-inbred, ¾ if only one parent is known and non-inbred, or if one or both of known parents are inbred than D_n equals $1/[2/(1 - f)]$ where f is the average of the inbreeding coefficients of the parents. Only one parent, 3, was inbred (F_3 = .25) in this example. If nonparents (progeny) are assumed to be non-inbred then D_n is simply $\frac{1}{2}$ or ¾, which improves computational ease (D_n for nonparents 5, 6 and 11 = .5 (parents non-inbred) and for nonparents 7, 8, 9 and 10 = .4375 (sire is inbred but not the dam). The α_1 is the ratio: σ^2_e/σ^2_a = 1.875. The R identity matrix for the 7 nonparents used in the RAM analysis is therefore:

$$
\begin{bmatrix}
.7894737 & .0000000 & .0000000 & .0000000 & .0000000 & .0000000 & .0000000 \\
.0000000 & .7894737 & .0000000 & .0000000 & .0000000 & .0000000 & .0000000 \\
.0000000 & .0000000 & .8108108 & .0000000 & .0000000 & .0000000 & .0000000 \\
.0000000 & .0000000 & .0000000 & .8108108 & .0000000 & .0000000 & .0000000 \\
.0000000 & .0000000 & .0000000 & .0000000 & .8108108 & .0000000 & .0000000 \\
.0000000 & .0000000 & .0000000 & .0000000 & .0000000 & .8108108 & .0000000 \\
.0000000 & .0000000 & .0000000 & .0000000 & .0000000 & .0000000 & .7894737
\end{bmatrix}
$$

[37]

The completed RAM mixed model coefficient matrix and solution vector are shown for convenience as subset matrices (Equation 38):

$X'_p X_p + X'_n R X_n$

2.000	.000	2.000
.000	5.612	-1.536
2.000	-1.536	10.358

$X'_p Z_1 + \frac{1}{2}X'_n R Z_1^*$

.000	.000	1.000	1.000
1.184	1.206	1.622	1.600
-1.579	-.789	.811	2.021

$X'_p Z_2 + X'_n R Z_2^*$

.000	2.000	.000	.000
.000	2.411	.000	3.201
.000	.421	.000	.043

$X'_p Z_3 + X'_n R Z_3^*$

1.000	.000	.000	.000	.000
.000	1.579	1.622	1.622	.789
.000	-1.579	1.622	.000	-1.579

$X'_p Y_p + X'_n R Y_n$

3920.000
11369.890
420.880

$\hat{\beta}$

1988.573
1989.629
-47.240

$Z'_1 Z_1 + \frac{1}{4}Z'_1 {}^*R Z_1^* + A^{-1}_{pp}\alpha_{11}$

```
14.029   -1.024   -7.329    .395
-1.024   16.482   -6.924  -4.886
-7.329   -6.924   16.469    .405
  .395   -4.886     .405  11.572
```

$Z'_1 Z_2 + \frac{1}{2}Z'_1 {}^*R Z_2^* + A^{-1}_{pp}\alpha_{12}$

```
 5.000   -.060   -2.727    .789
 -.455   7.114   -2.727  -1.818
-2.727   -.916    5.454    .811
  .000   -.818     .000   5.236
```

$Z'_1 Z_3 + \frac{1}{2}Z'_1 {}^*R Z_2^*$

```
 .000   .789   .000   .000   .395
 .000   .000   .000   .811   .395
1.000   .000   .811   .811   .000
 .000   .789   .811   .000   .000
```

$Z'_1 Y_p + \frac{1}{2}Z'_1 {}^*R Y_n$

```
2386.974
2481.561
5436.973
4984.386
```

$\hat{d}_p$

```
 11.305
  6.475
 50.829
-14.543
```

$Z'_2 Z_2 + Z'_2 {}^*R Z_2^* + A^{-1}_{pp}\alpha_{22}$

```
 2.501   -.227  -1.364   .000
 -.227   7.366  -1.364  -.909
-1.364  -1.364   2.728   .000
  .000   -.909    .000  5.019
```

$Z'_2 Z_3 + Z'_2 {}^*R Z_3^*$

```
 .000   .000   .000   .000   .000
1.000   .000   .000  1.622   .789
 .000   .000   .000   .000   .000
 .000  1.579  1.622   .000   .000
```

$Z'_2 Y_p + Z'_2 {}^*R Y_n$

```
    .000
8883.122
    .000
6406.771
```

$\hat{m}_p$

```
-15.950
   .358
-91.643
 15.771
```

$Z'_3 Z_3 + Z'_3 {}^*R Z_3^* + I\alpha_{33}$

```
300.726        0        0        0        0
      0  301.305        0        0        0
      0        0  301.348        0        0
      0        0        0  301.348        0
      0        0        0        0  300.516
```

$Z'_3 Y_p + Z'_3 {}^*R Y_n$

```
2139.000
3309.474
3097.297
3498.649
1464.474
```

$\hat{pe}_1$

```
 .330
 .236
-.357
 .747
-.626
```

The above mixed model coefficient matrix with solution sub-vectors for parents and litters serve only as a guide for proofing because of the rounding to only three decimal places. The DFREML package yields solutions only under a full individual AM, so for a RAM analysis the equations can be constructed (including inversion of the coefficient matrix) and solved using SAS (1985) or a spreadsheet computer program with matrix algebra capabilities.

Estimation of nonparent direct BV from back-solutions is based on an understanding of the following linear relationship:

$$y_n = .5\hat{d}_s + .5\hat{d}_D + \phi_n + \epsilon_n \qquad [39]$$

where y is the observation of the nth nonparent which is a function of the average gamete contribution of its parents (i.e. midparent direct BV), ϕ represents Mendelian sampling apart from midparent BV, and ϵ is the nonparent's environmental deviation from its own observation, y (inclusive of year-season, litter size, maternal, litter and residual effects in this example). Thus, direct BV is conceptually derived by both a midparental contribution plus a Mendelian sampling contribution, ergo a gametic model (Quaas and Pollak, 1980; Hudson, 1984).

Back-solutions for nonparent direct and maternal BV prediction, presumably for growth and milk (adapted after Benyshek et al., 1988):

$$\hat{d}_n = .5\ (\hat{d}_s + \hat{d}_D)$$

$$+ \left(\frac{1}{1 + \alpha_1 (D_n)^{-1}} \right)\ (Y_n - \hat{y}s_1 - \hat{b}(lsw_o - \overline{lsw}) - \hat{pe}_{litter} - \hat{m}_D - .5\hat{d}_s - .5\hat{d}_D)$$

$$\hat{m}_n = .5\ (\hat{m}_s + \hat{m}_D) + \frac{\alpha_1}{\alpha_2}\ (\hat{d}_n - .5\hat{d}_s - .5\hat{d}_D) \qquad\qquad [40]$$

Nonparent back-solution values are the same as those BV's listed with the tabulated data from the preceding full AM problem. All terms are as previously defined, except α_2 which is the ratio: $\sigma^2_e / \sigma_{am} = -.9375$.

Lastly, a recursive procedure to generate nonparent direct and maternal BV's can be computed using the equations as follows (modified after Van Vleck [1990b]):

$$\begin{bmatrix} \alpha_{11}^* & \alpha_{12}^* \\ \alpha_{21}^* & \alpha_{22}^* \end{bmatrix} \begin{bmatrix} Y_n - \hat{y}s_1 - \hat{b}(lsw_o - \overline{lsw}) - \hat{pe}_{litter} - \hat{m}_D \\ + \alpha_{11}(D_n)^{-1}(\hat{d}_s + \hat{d}_D)/2 + \alpha_{12}(D_n)^{-1}(\hat{m}_s + \hat{m}_D)/2 \\ \alpha_{12}(D_n)^{-1}(\hat{d}_s + \hat{d}_D)/2 + \alpha_{22}(D_n)^{-1}(\hat{m}_s + \hat{m}_D)/2 \end{bmatrix} = \begin{bmatrix} \hat{d}_n \\ \hat{m}_n \end{bmatrix}$$

$$[41]$$

where $(D_n)^{-1}$ is the inverse of D of the nth nonparent (e.g. $(D_n)^{-1} = (.5)^{-1} = 2.0000$ for nonparents 5, 6 and 11, and $(D_n)^{-1} = (.4375)^{-1} = 2.2857$ for nonparents 7, 8, 9 and 10. The α_{11}, α_{12} and α_{22} values are identical to those found in Equation 25. The α_{11}^*, α_{12}^* and α_{22}^* values would be computed based on individual nonparent D_n and population α values, written as:

$$\begin{bmatrix} 1 + (D_n)^{-1}\alpha_{11} & (D_n)^{-1}\alpha_{12} \\ (D_n)^{-1}\alpha_{21} & (D_n)^{-1}\alpha_{22} \end{bmatrix}^{-1} = \begin{bmatrix} \alpha_{11}^* & \alpha_{12}^* \\ \alpha_{21}^* & \alpha_{22}^* \end{bmatrix} \qquad [42]$$

where α_{11}^*, α_{12}^* ($\alpha_{12}^* = \alpha_{21}^*$) and α_{22}^* values of .2103, -.4205 and 1.2073 apply to nonparents 5, 6 and 11; whereas, corresponding values of .1890, -.3779 and 1.0763 apply to nonparents 7, 8, 9 and 10, respectively.

According to Hudson and Kennedy (1985), recent nonparents are of interest for estimation of herd genetic value, within herd genetic trend and for current selection decisions.

Other Special Topics and Conclusions

Several animal model types appropriate for mixed-model analyses for single-trait evaluation have been presented and discussed in this paper with numerical examples and using various statistical packages. Extension to a multiple-trait, mixed-model procedure has several appealing features for rabbit genetic evaluations beyond more efficient selection. For example, data consisting of correlated growth and carcass traits, growth and reproductive traits, wool quantity and quality traits, and between a trait measured in both sexes and a trait that is sex-limited, can be analyzed using a multiple trait model. This procedure has the advantages, in particular, that records on all animals are not required (because of trait correlations and relationships among animals), and adjustment is made for the effects of sequential selection/culling bias (Henderson and Quaas, 1976; Quaas and Pollak, 1980; Boldman et al., 1992).

The animal model procedure is also useful in determination of genetic, environmental and phenotypic trends or progress realized over several years (Henderson et al., 1959; Henderson, 1973; Schaeffer, 1974). This is possible when there is overlapping of generations in a population, whereby genetic ties exist due to certain animals that produce offspring over several generations. Of course, with artificial insemination this procedure is more easily facilitated. The weighted average of predicted breeding values is calculated on a within birth-year basis and then is regressed on birth year. Genetic trends for rabbit populations have previously been reported by Estany et al., 1988b, 1989; Baselga et al., 1992; Ferraz et al., 1992a; Rochambeau et al., 1992; Utrillas et al., 1992). Moreover, mixed animal models apply, as well, to crossbreeding (Fimland, 1975; Elzo and Famula, 1985; Komender and Hoeschele, 1989) and in selection experiments (Sorensen and Kennedy, 1984; Estany et al., 1989; Lamberson et al., 1991), whereby crossbreeding and selection parameters may be more accurately estimated and with improved precision.

Adoption of animal model techniques is not only presently feasible but is most appropriate for rabbit within-herd genetic evaluations for economic traits to maximize selection efficacy. As artificial insemination becomes more cost-effective, and later embryo transfer, it would be possible to produce sufficient genetic ties across herds. Hence, usage of multiple-herd sires and dams in cross-referencing programs could serve as a basis for selection from national, and with time global gene pools (Banos and Smith, 1991). Multibreed sire and dam evaluations are another prospect that would provide a basis for judicious selection of new breeds utilized in different environments. Preliminary research could test for breed and individual sire interactions across divergent environments (e.g. temperate and tropical) prior to global exchange of germplasm. Concurrently, conservation programs must be maintained.

On a within-country basis, a standardized system for genetic evaluations would need to be well defined initially. This would involve proper animal identification, collection and reporting procedures for major economic traits, and evaluation methodologies which utilize an animal model(s). Periodic summaries of qualifying sires and dams with EPD or probable breeding value (PBV) and associative repeatability information could be prepared and made available to commercial producers by breeding companies, test stations and seedstock suppliers which possess the genetic stocks. In addition, information on within-herd genetic progress, as well as herd-year-season environmental trends, could be furnished to progressive producers as a managerial tool. In only a limited number of countries, similar, albeit less ambitious, efforts may already be taking place.

Ideally, national rabbit genetic evaluation programs should first be formally established, and eventually extend to a global evaluation program. The World Rabbit Science Association could serve a leadership role in the design, implementation, monitoring and evaluation of this prospective rabbit genetic improvement proposition whereby state-of-the-art animal model applications would be highlighted.

In conclusion, commercial and subsistence producers would be the ultimate beneficiaries (not to mention consumers of rabbit meat) from the enhanced genetic merit achieved indirectly by utilization of the animal model innovation. Moreover, breeder reputation, profitability and nutritional quality of the human diet as associated with the genetic improvement would be enhanced.

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