

## **ESTIMATES OF COMPONENTS OF VARIANCE AND COVARIANCE FOR CARCASS TRAITS IN RABBITS USING AN ANIMAL MODEL**

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### **Abstract**

Variance and covariance components for genetic and environmental effects on carcass traits were estimated from an experimental rabbit population comprised of four sire breed (SB) groups using univariate, restricted maximum likelihood (REML) with derivative and derivative-free REML (DFREML) methods. Derivative REML estimates of variance components using the GLMM package were for independent sire within SB, dam within sire, litter within dam, and residual random effects. Models used with DFREML were animal models including direct and maternal genetic effects with numerator relationships, litter effects, and residual effects. Carcass trait heritabilities for direct genetic effects were similar between corresponding full models (i.e. sires, dams and litters represented) where numerator relationships through sires were either ignored (GLMM) or accounted for (DFREML). In animal models using DFREML, direct genetic variances were inflated when maternal genetic effects were ignored. In animal models containing direct and maternal genetic effects the inclusion or exclusion of the litter effect had little impact on other variance components. Inclusion of numerator relationships through dams effectively decreased heritabilities for direct genetic effects and increased heritabilities for maternal genetic effects for most carcass traits. Inclusion of covariance between direct and maternal genetic effects resulted in relative shifts in direct and maternal genetic variances, but not in litter variances, in models where numerator relationships through both sires and dams were included. Estimates of genetic correlations suggest possible antagonisms between direct and maternal genetic effects particularly for preslaughter, carcass and total lean weight traits. These results with different models demonstrate model sensitivity according to choice of animal model.

### **Introduction**

Development of sound rabbit breeding programs depends upon accurate knowledge of genetic and environmental parameters. To date, limited U.S. studies have been reported

(Harvey *et al.*, 1961; Rollins and Casady, 1960, 1967; Rollins *et al.*, 1963; McReynolds, 1974; Vogt, 1979; Lukefahr *et al.*, 1983a,b, 1984; Johnson *et al.*, 1988). None of these reports, however, utilized restricted maximum likelihood (REML) methods with mixed models for variance component estimation under an animal model.

More specifically, the restricted maximum likelihood (REML) method (Patterson and Thompson, 1971) is routinely used by animal breeders to obtain variance components for random effects from mixed models, whereby loss of degrees of freedom due to model fixed effects and selection bias is accounted for (e.g. Searle, 1987). One alternative REML algorithm is derivative-free REML, or DFREML (Smith and Graser, 1986; Graser *et al.*, 1987; Meyer, 1989). For univariate models with one random factor, this application requires only a 1-dimensional search for variance components, thus reducing computational time and costs (Graser *et al.*, 1987). Further, computational efficiency of DFREML allows for a larger number of equations than derivative REML so that additional random effects (e.g. maternal and common environmental effects) can be incorporated with numerator relationships (e.g. Meyer, 1991).

The experimental objectives were to compare a derivative REML method (General Linear Mixed Models [GLMM], Blouin and Saxton, 1990) without numerator relationships for a litter in dam in sire model and DFREML using an individual animal model with direct genetic and maternal genetic effects with numerator relationships and non-genetic effects to estimate variance and covariance components and heritability and genetic correlations for carcass traits in rabbits.

#### Materials and Methods

**Population Background.** A total of 219 rabbit fryers representing four sire breed groups were involved in the experiment which occurred from July 1989 to February 1990. Sire breeds of medium-sized mature weight classification included Californian, Champagne D'Argent, New Zealand White and Palomino (American Rabbit Breeders Association, 1984). Bucks from these breeds were randomly sampled from commercial herds in the southeastern United States, except for the New Zealand White for which the Alabama A&M University randomly mating population was used. The New Zealand White was the dam resource used in this study because of the breed's commercial popularity. Hence, four sire breed groups - three two-breed crossbreds and one purebred - were produced. Comparisons among the four groups have been reported previously (Roberts and Lukefahr, 1992; Lukefahr *et al.*, 1992). Of relevance to the models for analyses, individual heterosis levels for carcass traits in rabbits are generally low (Bednarz and Frindt, 1975; Lukefahr *et al.*, 1983c; Brun and Ouhayoun, 1989).

Litter management, housing and diets were similar to those described by Ozimba and Lukefahr (1991) and Lukefahr and Ozimba (1991). At 70 d of age, 1 to 4 fryers per litter were randomly sampled for slaughter. Fryers were separated from feed and water

approximately 24 h prior to actual slaughter at 71, 72 or 73 d of age, and were sacrificed by sudden cervical dislocation.

**Carcass Trait Definitions.** Preslaughter, hot carcass and adjusted total lean weights were recorded. Hot carcass weight did not include head, giblets (heart, liver and kidneys) or abdominal fat. Dressing percentage was calculated as hot carcass plus abdominal fat plus giblet weights divided by preslaughter weight, times 100. Adjusted total lean weight was twice the hand-deboned, total lean tissue weight separated from one longitudinally split carcass half. Total lean weight and lean-to-bone ratio were indicators of cutability. The remaining carcass half was divided into retail cuts: forequarter (forelegs and rack), loin and hindquarter (hindlegs and rump) primals, each expressed as a percentage of carcass weight, as described by Lukefahr *et al.* (1989). Pelt and visceral weights were expressed as a percentage of preslaughter weight. Abdominal fat weight was expressed as a percentage of hot carcass weight. Overall means were preslaughter and hot carcass weights (1.86 and .93 kg), dressing, pelt, visceral and abdominal fat percentages (54.6, 11.7, 16.9 and 2.39%), forequarter, loin and hindquarter cut percentages (42.0, 21.6 and 38.3%), total lean weight (.74 kg) and lean-to-bone ratio (4.19).

**Statistical Procedures.** Numbers of records, sires, dams and litters by sire breed group are provided in Table 1. The hierarchical design involved sampling of 8 or 9 bucks per sire breed with 1 to 2 New Zealand White does being randomly assigned to each buck, each doe contributing 1 or 2 litters (i.e. repeat matings if 2 litters were produced) with 1 to 4 fryers per litter being randomly sampled for slaughter, for a total of 219 fryers involved in the experiment. Despite the limited data, more suitable rabbit data sets are not available.

Table 1. Number of sires, dams, litters and fryers by sire breed.

Sire breed	Sires	Dams <sup>a</sup>	Litters	Fryers
Californian	9	16	24	54
Champagne D'Argent	8	11	19	52
New Zealand White	9	15	22	57
Palomino	8	16	26	56
Total	34	58	91	219

<sup>a</sup> All dams were of the New Zealand White breed.

Data were blocked for environmental contemporary effects of month of birth (8 classes) and age at slaughter (3 classes), in addition to an adjustment by linear regression for litter size at weaning. The sire breed x contemporary effects interaction and sex effects (females vs males) were not included in the final model based on non-significant results observed in preliminary analyses (Roberts and Lukefahr, 1992; Lukefahr *et al.*, 1992).

Original analyses were with the expectation-maximization (EM) algorithm of the General Linear Mixed Models (GLMM) statistical package by Blouin and Saxton (1990) for a model including previously described fixed effects and independent random effects of sire within breed, dam within sire, litter within dam, and random residual effects. The EM algorithm of Dempster *et al.* (1977) has the desirable property of guaranteed positive estimates in cases where other iterative techniques may yield negative or zero estimates. Numerator relationships among sires and dams cannot be accommodated in GLMM so that the numerator relationship matrix among sires and dams is implied to be an identity matrix.

Several animal models were employed to determine the effect of deleting parts of the model and to compare with the model without relationships. The full animal model included direct genetic and maternal effects, permanent environmental effects within litter and a residual effect. Numerator relationships were included for all animals with records, their parents and some grandparents that provided collateral relationships to augment the mixed model equations (Henderson, 1977). The derivative-free REML (DFREML) software package developed by Meyer (1988) was used.

The models in addition to fixed effects were:

- 1) direct genetic effects with numerator relationships and a fixed covariate for milk production (e.g. total 21-d litter weight) to account for some maternal and litter effects,
- 2) direct genetic effects with numerator relationships and independent litter effects,
- 3) direct genetic effects with numerator relationships and independent maternal (dam) effects without relationships,
- 4) direct genetic effects with numerator relationships, and independent maternal (dam) and litter effects,
- 5) direct and maternal genetic effects with numerator relationships and litter effects but no covariance between direct and maternal effects,
- 6) direct and maternal genetic effects with numerator relationships and litter effects and covariance between direct and maternal effects.

An additive genetic model was assumed since there are no known reports that suggest dominance and epistatic effects for carcass traits in rabbits. Heritability estimates obtained from the sire (s), dam in sire (d), and litter in dam (l) model were calculated as  $4(\sigma_a^2)/\sigma_T^2$ , where  $\sigma_T^2$  is total phenotypic variance ( $\sigma_T^2 = \sigma_a^2 + \sigma_d^2 + \sigma_l^2 + \sigma_e^2$ ). Expectations for variance components were assumed as follows:  $\sigma_s^2 = 1/4\sigma_a^2$ ;  $\sigma_d^2 = 1/4\sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_{me}^2$ ;  $\sigma_l^2 = \sigma_p^2$ , and  $\sigma_e^2 = 1/2\sigma_a^2 + \sigma_e^2$ , where  $\sigma_a^2$  is the direct additive genetic variance,  $\sigma_m^2$  is the maternal additive genetic variance,  $\sigma_{am}$  is the covariance between direct and maternal additive genetic effects (presumably between carcass traits and milk production),  $\sigma_{me}^2$  is the variance of permanent maternal environmental effects,  $\sigma_p^2$  is variance of permanent environmental effects within litter, and  $\sigma_e^2$  is residual environmental variance. Alternatively, heritability estimates obtained under an animal model were calculated as  $\sigma_a^2/\sigma_T^2$ , where expectation for total phenotypic variance varied depending on the specific model, as described above.

Additive genetic relationships among sires of the same breed, among New Zealand White dams, between sires and dams (both of New Zealand White breeding), and among base animals (without records) in all three groups were computed. Pedigree analyses revealed that only 16 of 389 animals were inbred. Specifically, none of the New Zealand White sires were half- or full-siblings to one another; however, such relationships were quite common among New Zealand White dams, and between sires and dams of New Zealand White breeding (sire-daughter relationships were prevalent in the latter case, as well). Further, only two Californian sires were related as full-sibs. Several Champagne D'Argent sires were connected through full-sib, sire-son, uncle-nephew or full- and half-cousin relationships, and several Palomino sires were connected through uncle-nephew or half-cousin relationships.

## Results and Discussion

**Derivative REML Results.** REML variance component estimates for carcass traits obtained from the derivative method, and without taking genetic relationships into account, are shown in Table 2. Sire variances were proportionately higher for traits expressed on an actual weight than traits expressed as percentages. Preslaughter, hot carcass and total lean weights were lowly to moderately heritable, estimates being .10, .08 and .15, respectively. One French report by Rouvier (1970) estimated paternal half-sib heritabilities of .13, .11 and .21 for preslaughter, hot carcass and total lean tissue weights involving comparable medium-sized breeds, in agreement with present results. Earlier domestic studies by Rollins and Casady (1960), Harvey *et al.* (1960) and McReynolds (1974) reported heritabilities of individual 56-d market weight of .06, .13 and .30, respectively, for New Zealand White rabbits. In addition, the litter component of variance was approximately three-times larger in magnitude than the dam component of variance for preslaughter, hot carcass and total lean weights, suggestive of environmental effects peculiar to litters being more important than maternal genetic or environmental effects common to all progeny of a dam across litters.

Heritability estimates for carcass traits expressed as percentages of preslaughter or hot carcass weights were either .00 or .01, except for hindquarter percentage ( $h^2 = .48$ ). These small heritabilities may partially reflect greater relative influence of common maternal and

Table 2. REML estimates of variance components and heritability from GLMM for preslaughter and carcass yield traits in rabbits.

Item <sup>a</sup>	Trait <sup>b</sup>					
	PSW	HCW	DP	PELT	VISC	ABF
s	.02	.02	.00	.00	.00	.00
(h <sup>2</sup> )	(.10)	(.08)	(.01)	(.01)	(.01)	(.00)
d	.15	.16	.09	.20	.26	.11
l	.47	.48	.38	.14	.19	.41
ε	.36	.34	.53	.66	.55	.48
σ <sup>2</sup> <sub>T</sub>	.07	.02	5.90	1.27	5.02	.77

Table 2 (continued). REML estimates of variance components and heritability from GLMM for carcass primal and lean yield traits in rabbits.

Item <sup>a</sup>	Trait <sup>b</sup>				
	FQR	LOIN	HQR	LEAN	LBR
s	.00	.00	.12	.04	.00
(h <sup>2</sup> )	(.00)	(.00)	(.48)	(.15)	(.00)
d	.00	.01	.01	.13	.13
l	.14	.20	.04	.43	.01
ε	.86	.79	.84	.40	.86
σ <sup>2</sup> <sub>T</sub>	3.30	3.43	1.84	.01	.67

<sup>a</sup> Symbols: s, d, l, and ε are sire, dam in sire, litter in dam and residual variance component estimates, respectively, all components being expressed as a proportion of total phenotypic variance ( $\sigma^2_T = \sigma^2_s + \sigma^2_d + \sigma^2_l + \sigma^2_\epsilon$ ). Heritability was estimated as  $4(\sigma^2_s)/\sigma^2_T$ .

<sup>b</sup> Trait abbreviations: PSW = preslaughter wt, kg; HCW = hot carcass wt, kg; DP = dressing percentage; PELT = pelt percentage; VISC = visceral percentage; ABD = abdominal fat percentage; FQR = forequarter cut percentage; LOIN = loin cut percentage; HQR = hindquarter cut percentage; LEAN = total lean wt, kg, and LBR = lean to bone ratio.

litter effects, small sample size, or some combination thereof. The rabbit fryer is a young animal at slaughter relative to market cattle, hogs and lambs; hence, common maternal and litter effects may be substantial. Limited European reports (Fl'ak *et al.*, 1978; Varewyck *et al.*, 1986), however, tend to indicate that certain percentage carcass traits may be moderately to highly heritable.

**Derivative-Free (DF) REML Results.** DFREML estimates of (co)variance components for carcass traits with six alternative animal models for preslaughter and carcass yield traits (Table 3) and for carcass primal and lean yield traits (Table 4) are presented. Model 1 represented direct genetic effects with numerator relationships and a fixed covariate for milk production to account for some maternal and litter effects. Direct genetic effects with numerator relationships and independent litter effects were represented in Model 2. Generally, variances for direct genetic effects (heritability) appeared to be biased upwardly in both models in the absence of maternal genetic effects, yielding unreasonably high estimates of heritability, especially for preslaughter, hot carcass and total lean weights or carcass traits expressed on a percentage basis from the preslaughter weight.

Model 3 included direct genetic effects with numerator relationships and independent maternal (dam) effects without relationships, whereas Model 4 included direct genetic effects with numerator relationships, and maternal (dam) effects without relationships and litter effects. The effect of either ignoring or including the litter effect (permanent environmental effects), resulted in little or no change in estimates of direct and maternal genetic variances as proportions of total phenotypic variance.

In addition, REML estimates obtained from GLMM (Table 2) were most comparable to DFREML estimates from Model 4 (Tables 3 and 4), except that numerator relationships can not be considered with the GLMM procedure. In general, heritabilities tended to be similar for GLMM and DFREML methods whether or not numerator relationships were taken into account, possibly because most sires within sire breed were neither closely related nor inbred in our experiment. However, estimates of the litter variance from GLMM were consistently and proportionately larger across traits than those obtained from DFREML, indicating either less confounding between dam and litter effects as compared to maternal genetic and litter effects for GLMM and DFREML methods, or that permanent environmental effects were not modelled quite the same between methods, respectively.

Direct and maternal genetic effects with numerator relationships and litter effects but no covariance between direct and maternal effects were included in Model 5. Comparison of Models 4 and 5 results was made to study the impact of ignoring numerator relationships for the maternal genetic effect. Heritabilities for direct genetic effects were effectively reduced at the gain of heritabilities for maternal genetic effects for preslaughter and carcass yield traits, while little change occurred for carcass primal and lean yield traits. A plausible explanation for the change in heritability is that the number and degree of genetic relationships through dams and between New Zealand White sires and dams, as well as relationships through base animals, were generally greater than were genetic relationships through sires within sire

Table 3. Derivative-free (DF) REML estimates of variance and covariance components for preslaughter and carcass yield traits in rabbits.

Item <sup>a</sup>	Trait <sup>b</sup>					
	PSW	HCW	DP	PELT	VISC	ABF
1 <sup>c</sup>						
a	1.00	1.00	.60	.68	.73	.74
$\sigma^2_T$	.06	.02	5.20	1.35	5.05	.76
2						
a	1.00	1.00	.77	.67	.75	.78
p	.00	.00	.00	.00	.00	.03
$\sigma^2_T$	.07	.02	6.22	1.35	5.15	.84
3						
a	.17	.08	.00	.11	.00	.00
m	.52	.57	.37	.24	.41	.40
$\sigma^2_T$	.08	.03	5.84	1.27	5.02	.76
4						
a	.18	.07	.00	.11	.00	.00
m	.52	.57	.37	.24	.41	.40
p	.00	.00	.00	.00	.00	.00
$\sigma^2_T$	.08	.03	5.84	1.27	5.02	.76



Table 3 (continued). Derivative-free (DF) REML estimates of variance and covariance components for preslaughter and carcass yield traits in rabbits (Cont.)

Item <sup>a</sup>	Trait <sup>b</sup>					
	PSW	HCW	DP	PELT	VISC	ABF
5						
a	.00	.00	.03	.39	.12	.05
m	.62	.62	.36	.12	.33	.36
p	.00	.00	.00	.00	.00	.03
$\sigma^2_T$	.08	.03	5.91	1.31	5.06	.80
6						
a	.16	.01	.03	.33	.13	.05
m	.86	.69	.37	.03	.17	.38
am	-.32	-.08	-.01	.11	.15	-.02
( $r_p$ )	(-.87)	(-1.00)	(-.08)	(1.00)	(1.00)	(-.13)
p	.00	.00	.00	.00	.01	.02
$\sigma^2_T$	.08	.03	5.91	1.29	5.02	.79

<sup>a</sup> Symbols: a is direct additive genetic variance ( $h^2_d$ ); m is maternal additive genetic variance ( $h^2_m$ ); am is covariance between direct and maternal additive genetic effects, and p is permanent environmental effects within litter, all components being expressed as a proportion of total phenotypic variance ( $\sigma^2_T$ ).

<sup>b</sup> Trait abbreviations: PSW = preslaughter wt, kg; HCW = hot carcass wt, kg; DP = dressing percentage; PELT = pelt percentage; VISC = visceral percentage, and ABD = abdominal fat percentage.

<sup>c</sup> Animal models: 1 = direct genetic effects with numerator relationships and a fixed covariate for milk production to account for some maternal and litter effects; 2 = direct genetic effects with numerator relationships and independent litter effects; 3 = direct genetic effects with numerator relationships and independent maternal effects without relationships; 4 = direct genetic effects with numerator relationships, and independent maternal (dam) without relationships and litter effects; 5 = direct and maternal genetic effects with numerator relationships and litter effects, but no covariance between direct and maternal effects, and 6 = direct and maternal genetic effects with numerator relationships and litter effects and covariance between direct and maternal effects.

Table 4. Derivative-free (DF) REML estimates of variance and covariance components for carcass primal and lean yield traits in rabbits.

Item <sup>a</sup>	Trait <sup>b</sup>				
	FQR	LOIN	HQR	LEAN	LBR
1 <sup>c</sup>					
a	.17	.10	.19	1.00	.16
$\sigma^2_T$	3.29	3.06	1.73	.05	.65
2					
a	.14	.19	.19	1.00	.23
p	.00	.09	.14	.00	.00
$\sigma^2_T$	3.28	3.65	2.03	.05	.67
3					
a	.14	.00	.22	.18	.00
m	.00	.18	.04	.48	.14
$\sigma^2_T$	3.28	3.46	1.83	.06	.67
4					
a	.14	.00	.15	.18	.00
m	.00	.15	.02	.48	.14
p	.00	.09	.14	.00	.00
$\sigma^2_T$	3.28	3.72	2.03	.06	.67

Table 4 (continued). Derivative-free (DF) REML estimates of variance and covariance components for carcass primal and lean yield traits in rabbits.

Item <sup>a</sup>	Trait <sup>b</sup>				
	FQR	LOIN	HQR	LEAN	LBR
5					
a	.14	.00	.19	.19	.00
m	.00	.14	.00	.49	.12
p	.00	.09	.14	.00	.00
$\sigma^2_T$	3.27	3.70	2.04	.06	.67
6					
a	.13	.00	.50	.44	.02
m	.00	.17	.30	.89	.07
am	.00	-.03	-.39	-.52	-.04
( $r_p$ )	(1.00)	(-1.00)	(-1.00)	(-.83)	(-1.00)
p	.00	.09	.04	.00	.00
$\sigma^2_T$	3.28	3.69	1.93	.06	.67

<sup>a</sup> Symbols: a is direct additive genetic variance ( $h^2_d$ ); m is maternal additive genetic variance ( $h^2_m$ ); am is covariance between direct and maternal additive genetic effects, and p is permanent environmental effects within litter, all components being expressed as a proportion of total phenotypic variance ( $\sigma^2_T$ ).

<sup>b</sup> Trait abbreviations: FQR = forequarter cut percentage; LOIN = loin cut percentage; HQR = hindquarter cut percentage; LEAN = total lean wt, kg, and LBR = lean to bone ratio.

<sup>c</sup> Animal models: 1 = direct genetic effects with numerator relationships and a fixed covariate for milk production to account for some maternal and litter effects; 2 = direct genetic effects with numerator relationships and independent litter effects; 3 = direct genetic effects with numerator relationships and independent maternal effects without relationships; 4 = direct genetic effects with numerator relationships, and independent maternal(dam) without relationships and litter effects; 5 = direct and maternal genetic effects with numerator relationships and litter effects, but no covariance between direct and maternal effects, and 6 = direct and maternal genetic effects with numerator relationships and litter effects and covariance between direct and maternal effects.

breed (and relationship structures were not the same). For all carcass traits, the relative litter variance was unaffected regardless of numerator relationships for maternal genetic effects.

Model 6 accounted for direct and maternal genetic effects with numerator relationships and covariance between direct and maternal effects and litter effects. Comparison of Models 5 and 6 results reflected the consequence of ignoring the covariance between direct and maternal genetic effects. Inclusion of the covariance in Model 6 had a marked effect on direct and maternal genetic variances but not on litter variance across carcass traits. Generally, heritabilities of the direct genetic effect and the maternal genetic effect either increased or remained unchanged.

Genetic correlations based on covariance between direct and maternal effects were large and negative for preslaughter, hot carcass and total lean weights, as well as for loin and hindquarter cut percentages (primal regions with the largest proportion of lean tissue) and total lean-to-bone ratio, suggestive of possible genetic antagonisms between carcass traits and milk production. Conversely, genetic correlations of 1.00 were obtained for pelt, visceral and forequarter cut percentages, traits where a decrease in performance is desirable. Genetic correlations approached zero for dressing percentage and abdominal fat percentage. The magnitude and signs of the genetic correlations are difficult to interpret, perhaps due, in part, to the number of parameters being estimated from a small data set. Previous rabbit carcass studies reporting similar genetic correlations are not available for comparison. Nonetheless, Model 6 is perhaps the more appropriate animal model for large data sets with suitable genetic relationship structures in similarly designed animal breeding experiments. Further research is needed to estimate genetic parameters from more and larger data sets using mixed model techniques to corroborate present findings and to advance knowledge on appropriate choice of animal models.

### Conclusions

Genetic and environmental parameters for carcass traits were estimated from a rabbit population using restricted maximum likelihood (REML) and derivative-free REML (DFREML) methods. Animal models using DFREML were employed to determine the effect of deleting certain parameters of the model and to compare with the model without relationships using REML. Heritabilities for direct genetic effects were similar between corresponding full models (i.e. sires, dams and litters represented) where numerator relationships through sires were either ignored (REML) or accounted for (DFREML). In animal models, the consequence of ignoring the maternal genetic effect or numerator relationships through dams, as well as the covariance between direct and maternal genetic effects, was pronounced. Genetic correlations suggest antagonisms between direct and maternal genetic effects, particularly for preslaughter, carcass and total lean weight traits. These results demonstrate that parameter estimates depend on the choice of animal model.

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