COMPARISON OF ANIMAL MODELS FOR ESTIMATION OF (CO)VARIANCE COMPONENTS AND GENETIC PARAMETERS OF REPRODUCTIVE, GROWTH AND SLAUGHTER TRAITS OF CALIFORNIAN AND NEW ZEALAND RABBITS RAISED UNDER TROPICAL CONDITIONS.[1]

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Abstract - In order to compare different animal models, the methodology of mixed models under animal models was used to predict (co)variance components of 23 traits related to reproduction traits of 1,456 litters and growth and slaughter traits of 3,845 Californian and New Zealand White rabbits raised in south-eastern Brazil. The (Co)variance components, obtained by four different models in single trait analysis, were used to estimate genetic parameters. The four animal models considered as random effects only the animal direct genetic effects (model 1), the animal direct and permanent effects of litters or common effects of does as permanent environment effects(model 2), the animal direct and maternal genetic effects, uncorrelated to each other, and permanent environmental effects (model 3), and as in model 3, but with correlated animal direct and maternal effects (model 4). All the model considered the fixed effects of contemporary groups, parity, sex and the covariates level of inbreeding of litters or rabbits and litter sizes, where applied. The models were compared based on likelihood ratio test and the « best » model is proposed for each trait. Permanent environmental effects were important for all traits and should be considered in animal models that analyse reproductive, growth and slaughter traits of rabbits of these two breeds. Maternal genetic effects were not important to reproductive traits, but significantly affected growth and slaughter traits, and were more important for New Zealand White than for Californian rabbits. As models 1,2,3 and 4 gave different estimates for genetic parameters, total heritabilities were calculated for all traits. Total heritabilities were low for reproductive traits (from 0 to .14), and moderate for growth (from .03 to .36) and slaughter traits (.02 to .23). Although New Zealand White and Californian rabbits perform similarly, the results showed that the genetic parameters for these two breeds are different and should not be analyzed together. The models chosen for each trait serve as guides for proposition of animal models in single or multi trait analysis of rabbit data.

INTRODUCTION

As rabbits can be fed with rough forages and do not compete directly with humans for grains, they can be a very important source of high quality animal protein in developing countries. However the knowledge of genetics of rabbit breeds, including two of the most used ones, New Zealand White and Californian, under tropical conditions is not well established and more studies are needed (FERRAZ, 1993; FERRAZ & ELER, 1994). In selection programs applied to rabbit production, reproductive, growth and slaughter traits can be considered. However, the larger the number of traits, the smaller the genetic gain obtained in each trait. The decision about which trait has to be considered depends not only on the economics involved, but also on genetic parameters of the traits and the « practical » importance of trait. The definition is taken by the geneticist and the breeder, always considering market reasons.

Studies on genetic parameters of several traits of rabbits have been made by some authors. KHALIL *et al* (1986) made an important review article on this subject. However, the studies of parameters estimated for populations raised under tropical or subtropical conditions are not very many. Several other studies have been conducted more recently, the majority using mixed models, like BASELGA & CAMACHO (1990), CAMACHO & BASELGA (1990), SANTACREU & BLASCO (1991), BASELGA *et al.*(1992), FERRAZ *et al.*(1992), LUKEFAHR *et al.* (1992), FERRAZ (1993), FERRAZ & ELER. (1994), LUKEFAHR *et al.* (1994).

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[1] Research partially supported by Fundação de Amparo à Pesquisa do estado de São Paulo - FAPESP and Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq, Brasil.

Best Linear Unbiased Predictors - BLUP, under methodology of mixed models is becoming the preferred method of estimation for animal breeders (HENDERSON, 1988). REML co(variance) component estimation is also becoming the most commonly used algorithm in such estimations.

The objectives of this study were to compare different animal models used to estimate genetic parameters of eight reproductive, nine growth and six slaughter traits of Californian and New Zealand White rabbits raised under subtropical conditions in south-eastern Brazil, using single trait analysis with mixed models methodology, under animal models, not only to have a better knowledge of genetics of those breeds in subtropics but also trying to choose the « best » models for each one of the traits that can be used as selection criteria.

MATERIAL AND METHODS

Data came from records of 1,456 litters (for reproductive traits), 3,845 rabbits (for growth traits) and 2,195 carcasses (for slaughter traits) of Californian and New Zealand White rabbits, born between 1988 and 1992. Table 1 shows the distribution of data between the breeds.

Table 1 : Distribution of data used for estimation of genetic parameters, between Californian and New Zealand White breeds

Item	Californian	New Zealand White
Reproductive traits (# of litters)	662	794
Growth traits (rabbits)	2,010	1,835
Slaughter traits	1,149	1,046
number of sires	42	56
number of dams	161	180
number of animal in pedigree for reproductive traits	744	746
number of animals in pedigree for growth and slaughter traits	2,138	1,968

Animals raised at the Rabittery of the Campus of University of Sao Paulo, located in Pirassununga (22°S and 47°W, 750 m above sea level). Average temperatures were around 22.5°C from January to March, 19°C from April to June (decreasing each month) and from July to September (increasing each month) and 22°C from October to December. Sunlight time was similar to temperature. They were lodged in metal cages and fed a commercial pelleted feed (18% crude protein and 17% fibre guaranteed). Reproduction started after 130 days of age.

Traits controlled to be analyzed were

1. Reproductive traits

Reproduction data for each doe and parturition were recorded: litter size at birth total (LSB) and alive (LSBA), litter size at 21 days of age (LS21), litter size at weaning (LSW), litter weights at birth (LWB), 21 days (LW21) and weaning (LWW) and mortality from birth to weaning (MORT).

2. Growth traits

Animal were weekly weighed from weaning to 11 weeks, and the traits were: weaning weight (WW), weights at 5, 6, 7, 8, 9, 10 and 11 weeks (W5, W6, W7, W8, W9, W10, W11), besides average daily gain, from weaning to 10 weeks of age (ADG).

3. Slaughter traits

At slaughter, each animal was individually weighed before and after slaughter (it's parts), given the traits: weight at slaughter (WS), carcass weight (CW), viscera weight (VW), head weight (HEAD), skin weight (SKIN) and carcass yield (CY).

Inbreeding coefficients for litters and does were calculated using a modification of K. Meyer's program DFNRM, made by L.D. Van Vleck (1991, personal communication). Pedigree information was used as far it existed. Data was analyzed by mixed model methodology under animal model, in single trait analysis. using the software DFREML (MEYER 1988), modified by BOLDMAN and VAN VLECK (1991) for use of Sparspak, a sparse matrix solver, according to suggested procedures described by FERRAZ (1992). Parameters estimated were heritability for direct and maternal effects, total heritability (as proposed by DICKERSON, 1970). Analysis were done according to the general model:

$$y = X\beta + Za + Zm + Zc + e, \text{ where:}$$

y = vector of dependent variable, the observations; X = incidence matrix of fixed effects; β = vector of fixed effects, including sex (for growth and slaughter traits), parity, year and trimester (for reproductive traits), contemporary groups (for growth and slaughter traits), linear and quadratic effects of covariable level of inbreeding of does and rabbits, linear effects of covariable age at weaning (for weaning traits), linear and quadratic effects of litter size at weaning and linear effects of age at slaughter (for slaughter traits); Z = incidence matrix for random effects; a = vector of random animal direct genetic effects; m = vector of random animal maternal genetic effects; c = vector of random permanent environmental effects of does (for reproductive traits) or common effects of litters (for growth and slaughter traits); e = vector of random errors, NID $(0, \sigma^2)$.

The difference among the models refers to the number of random effects considered. Model 1 considered only the animal direct genetic effect, Model 2 the animal direct genetic effect and the permanent environmental effect of doe or common effect of litters, Model 3 also considered the effects included in Model 2 plus the animal maternal genetic effect, uncorrelated with the direct effect and Model 4 considered all the effects included in Model 3, but in this case the animal direct and maternal genetic effects were considered correlated. To compare animal models, it was used a property of mixed model that the higher the likelihood function, the more model explain data. Likelihood function is higher when new parameters are included in the model. So, to go from model 1 to model 2, model 2 to model 3 and model 3 to model 4, one parameter was added each time.

To compare if the difference between the values of the likelihood function of two models is significant, it was used the methodology described by RAO (1973) and MOOD et al. (1974). This method is based in the fact that that difference $-2[\log\Lambda_i - \log\Lambda_{i'}]$ has Qui squared distribution, where Λ_i and $\Lambda_{i'}$ are the values of likelihood function, after the convergence criteria of the iterative process has been reached (in this case the variance of the function in the last 5 evaluations should not be larger than 1×10^{-9}) in the different models. The number of degrees of freedom of this comparison is equal to the number of parameters that were added to the model (one in the case of the comparisons made here). Significance was tested not only at level of $P<0,05$, but also a « practical » significance, based on variation of values of genetic parameters was considered in the choice of the « best » model.

RESULTS AND DISCUSSION

The definition of the correct model is a need, because the more complex the model, the larger the time needed for solution. This is even more important in multi-trait analysis, because CPU time is a function of n^3, where n is the number of variance and covariance components to be estimated. If you go from a Model 1 to Model 4 in a single trait analysis, the number of parameters to be estimated goes from one (the variance component for the animal direct genetic effect) to three (animal direct and maternal genetic effect and the covariance between them), and CPU time will be close to 9 times larger. In a two-trait analysis, the number of variance components goes from three (both direct effects and their covariance) to nine and CPU time will be increased in the order of $9^3/3^3$ or 27 times larger. This « rule » is only a guide to estimate the processing time, but it depends of course on several factors, like the genetic relationship among animals, established in A matrix (the relationship matrix) and it's inverse, A^{-1}, The case will be even worse for three or four-trait analysis. With the right models defined in single-trait analysis, a great time waste can be avoid.

The Qui-squared value and it's significance for the likelihood ratio test for each trait is given in Table 2. The analysis of that Table shows that models affect differently the results, depending if the traits are reproductive or growth and slaughter. For both breeds, common environmental effects of litters strongly affected the estimation of (co)variance components for growth and slaughter traits, but very few reproductive traits were affected by permanent environmental effects of does. That can be explained by the age of animals when measures occur. Rabbits are animal that grow very fast and there is an interval of only around 50 days between weaning and slaughter, and in this interval the effects of litters still exist. These results show that is very important to include permanent environmental effects when (co)variances are estimated with rabbit data.

When comparing Model 3 with Model 2, which difference is the inclusion of maternal genetic effects, only LSB and LSBA for reproductive traits, WW and CY had the influence of such source of variation in Californian rabbits. However, no reproductive traits and all growth traits (but ADG) and WS, CW, VW were affected by genetic maternal effects in New Zealand White rabbits. That is very important, because the inclusion of genetic maternal effects sometimes is confounded with permanent environmental effects of does and hard to separate or explain. In Californian rabbits, maternal effects can be excluded of animal models in the majority of traits. The differences between Models 4 and 3, that means the correlation between direct and maternal genetic effects were not detected in any one of the 23 traits analyzed in both Californian and New Zealand White rabbits, what is also very important to avoid CPU time wasting.

Table 2 : Qui-squared value (1 degree of freedom) for likelihood ratio test used to compare different animal models used for (co)variance components estimation in 23 traits of rabbits

	Californian Comparison between Models			New Zealand White Comparison between Models		
Trait	**2-1**	**3-2**	**4-3**	**2-1**	**3-2**	**4-3**
LSB	3.42	65.7*	1.50	4.8*	0.72	0.13
LSBA	5.6*	69.9*	0.68	2.07	1.79	0.10
LS21	3.76	0.00	0.40	0.68	0.00	0.18
LSW	3.46	0.00	0.62	1.59	0.00	0.11
LWB	1.04	0.16	0.04	5.1*	0.17	0.27
LW21	0.98	0.36	0.00	1.41	0.00	0.00
LWW	0.10	0.04	1.48	1.72	0.00	-0.13
MORT	4.66*	0.40	-0.16	4.7*	0.00	-0.84
WW	317.8*	5.2*	0.28	391.5*	4.7*	0.15
W5	257.5*	3.58	0.22	285.5*	6.5*	0.17
W6	49.3*	1.82	-1.04	183.4*	6.7*	0.22
W7	179.6*	0.00	0.22	163.0*	4.7*	0.22
W8	161.6*	0.04	0.62	83.3*	8.1*	2.12
W9	112.1*	0.00	0.54	128.0*	7.9*	0.14
W10	57.0*	0.06	0.70	61.3*	8.4*	0.38
W11	26.0*	0.00	0.46	84.2*	4.9*	1.44
ADG	3.8*	0.00	0.08	30.8*	1.64	0.06
WS	50.0*	0.10	0.58	49.5*	4.7*	2.58
CW	54.32*	0.02	0.66	48.6*	8.1*	0.42
VW	1471.2*	0.00	0.52	26.5*	4.6*	0.86
HEAD	15.1*	0.00	0.18	15.4*	0.00	-0.16
SKIN	40.1*	0.00	0.70	53.9*	2.44	0.56
CY	13.9*	4.1*	0.10	14.0*	1.48	-0.72

* - statistically significant at $P<0.05$ (critical value for 1 d.f = 3.84)

Table 3 presents the values of total heritability, that considers heritabilities for direct and maternal effects and also their correlation. The values in bold face refers to models chosen as « best ». Those values are very important in the choice of « best » models, because if no statistical difference has been detected by the likelihood ratio test, but total heritability changes in what can be considered a « practical » difference, a more complex model can be considered « better » than the one detected by the statistical test. The analysis of this table explains why a model other than the one chosen by the likelihood test was considered the « best » model, as shown in bold face in Table 3. From the joint analysis of Tables 2 and 3, it can clearly be seen that maternal effect is more important in New Zealand White rabbits than in Californian ones, at least in the sample analyzed. This can be a nice indicator for further studies, carried out with other populations, other breeds in different environment.

Model 1, that considers only the direct effect of animal should not be used in any trait, because permanent effects of does were very important for all of them, or because a statistical difference was detected by the likelihood ratio test or because the differences in heritabilities was considered important. Model 2, that takes into account the direct genetic effect of the animal plus the common effects of litter is the model of choice of the majority of traits for Californian rabbits, and that shows that maternal effects are not very important for animals of that breed, except for growth traits. However, for New Zealand White rabbits, Models 3 and 4 seem to be the most adequate for almost all traits, except for the majority of reproductive traits.

When comparing the models of choice in relation to the type of trait, it can be seem that the majority of reproductive traits are not affected by maternal effects, but were affected by permanent environmental effects and Model 2 can be used. For all growth and slaughter traits, permanent environmental effects are very important for both breeds and, depending on the breed and the importance of maternal effects, Models 2, 3 or even 4 should be used. The complete model, Model 4 was not statistically different from Model 3 and should be used only if the correlation between direct and maternal effects are supposed to be important, as CPU time increases with this choice. That was true for several traits in New Zealand White rabbits. There is a variation in total heritability values from Model 3 to Model 4, but they are not very large. If CPU time is not a problem, Model 4 is preferable to Model 3, as it's results are slightly closer to « real » parameters, as it's likelihood function value is higher, even though not statistically different.

In conclusion, this paper points out not only the models of choice to be used in analysis of reproductive, growth and slaughter traits of Californian and New Zealand White rabbits, but also showed the influence of permanent environmental and maternal effects on the estimation of (co)variance components of rabbits. Values of total heritabilities for the traits are shown and their variation among models were important to define the most adequate animal models. The results here shown have to be verified in other populations of rabbits of same breeds, raised in other environments.

Table 3 : Total heritabilities for 23 reproductive, growth and slaughter traits of Californian and New Zealand White rabbits, estimated by four different animal models

	Californian Models				New Zealand White Models			
Trait	1	2	3	4	1	2	3	4
LSB	.222	.077	.098	.072	.240	.083	.027	.033
LSBA	.303	.110	.120	.094	.207	.098	.036	.052
LS21	.148	.000	.000	.013	.197	.119	.118	.115
LSW	.146	.000	.002	.023	.226	.100	.100	.095
LWB	.124	.057	.058	.059	.129	.000	.010	.002
LW21	.311	.130	.082	.095	.167	.080	.079	.082
LWW	.103	.083	.079	.048	.293	.126	.126	.145
MORT	.181	.000	.014	.000	.190	.001	.000	.039
WW	.608	.030	.093	.136	.554	.117	.109	.116
W5	.583	.090	.110	.155	.532	.076	.068	.090
W6	.324	.000	.033	.045	.516	.170	.134	.158
W7	.558	.209	.209	.249	.533	.170	.137	.153
W8	.554	.194	.187	.212	.434	.133	.116	.170
W9	.467	.187	.186	.203	.516	.203	.164	.184
W10	.398	.241	.236	.244	.516	.309	.220	.243
W11	.412	.264	.264	.275	.541	.261	.212	.245
ADG	.439	.358	.357	.365	.573	.346	.312	.316
WS	.723	.177	.181	.129	.817	.215	.092	.141
CW	.712	.178	.177	.129	.761	.152	.049	.096
VW	.240	.033	.035	.029	.459	.111	.044	.096
HEAD	.473	.159	.159	.148	.568	.225	.225	.270
SKIN	.770	.309	.311	.321	.747	.088	.036	.075
CY	.344	.152	.055	.050	.118	.000	.014	.000

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