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ESTIMATES OF GENETIC PARAMETERS IN DANISH WHITE RABBITS USING AN ANIMAL MODEL : I. GROWTH AND CARCASS TRAITS

SU G.[1], KJAER J.B.[2], BRENØE U.T.[3], SØRENSEN P.[1]

[1] Danish Institute of Agricultural Science, Dept. of Animal Breeding and Genetics, DK-8830 TJELE
[2] Danish Institute of Agricultural Science, Dept. of Animal Health and Welfare, DK-8830 TJELE
[3] Norwegian Agricultural University, Dept. of Animal Science, N-1432 ÅS

ABSTRACT : Growth data from 2033 individuals and carcass data from 1386 individuals representing 3 Danish rabbit lines were analysed to draw inferences on genetic parameters, using restricted maximum likelihood (REML) procedures based on animal models. In the models, birth year, season, line, parity, sex, litter size at weaning and slaughter age were treated as fixed effects, individual additive genetic and litter were taken as random effects. Litter effects in proportion of phenotypic variance were 0.60, 0.32 and 0.19 for daily gain during pre-weaning (DG_{1-35}), daily gain during the period from weaning to 90 days (DG_{36-90}), and daily gain during the whole period from birth to 90 days (DG_{1-90}), respectively, and ranged from 0.08 to 0.17 for carcass traits. Heritability estimates were 0.16, 0.17, 0.31 for DG_{1-35}, DG_{36-90}, and DG_{1-90}, respectively; and 0.17, 0.26, 0.10, 0.10 and 0.09 for carcass yield, carcass length, back score, thigh score and fat score, respectively. Genetic correlations between daily gains were positive and strong, and genetic correlations between daily gains and carcass traits (except for carcass yield) were favourable. Based on these estimates, selection for DG_{1-90} would effectively improve not only growth rates during both pre-weaning and during post-weaning periods but also carcass quality.

RESUME : Estimation des paramètres génétiques en utilisant le modèle animal chez le lapin Danois Blanc : 1- croissance et caractéristiques de la carcasse.
Les données concernant la croissance de 2033 lapins et les caractéristiques de 1386 carcasses, représentant 3 lignées de lapins Danois Blanc, ont été analysés pour mettre en évidence les paramètres génétiques, en utilisant la procédure du maximum de vraisemblance restreint (REML) basée sur le modèle animal. Dans les modèles utilisés, l'année de naissance, la saison, la lignée, le numéro de portée, le sexe, la taille de la portée au sevrage et l'âge à l'abattage ont été traités comme effets fixes. L'effet génétique individuel additif et celui de la portée ont été considérés comme effets aléatoires. Les effets dus à la portée, rapportés à la variance phénotypique, sont de 0,60 - 0,32 et 0,19 pour le gain de poids journalier avant le sevrage (DG_{1-35}), pendant la période allant du sevrage à 90 jours (DG_{36-90}) et pendant la période allant de la naissance à 90 jours (DG_{1-90}) respectivement. Ils vont de 0,08 à 0,17 pour les caractéristiques de carcasse. Les estimations de l'héritabilité sont de 0,16 - 0,17 et 0,31 pour DG_{1-35}, DG_{36-90}, et DG_{1-90} respectivement. Elles sont respectivement de 0,17 - 0,26 - 0,10 - 0,10 et 0,09 pour le rendement et la longueur de la carcasse, ainsi que pour les notes (de 1 à 5) correspondant la proportion de râble ou de cuisse et pour la note d'adiposité (de 1 à 3). Les corrélations génétiques entre les différentes vitesses de croissance sont positives et fortes (0,90 à 0,99). Les corrélations génétiques entre les gains journaliers et les caractéristiques de la carcasse (excepté pour le rendement à l'abattage) sont favorables. Compte tenu de ces résultats, la sélection sur le gain de poids DG_{1-90} pourrait améliorer non seulement la vitesse de croissance avant et après sevrage mais aussi la qualité de la carcasse.

INTRODUCTION

Like other meat animals, high juvenile growth rate and carcass traits are often taken into consideration in a selection program. Compared with most farm animals, information about genetic parameters in rabbits is limited, especially those for carcass traits and their relationship with growth traits.

The reliability and accuracy of estimates of genetic parameters depend not only on number of animals and family structure but also on statistical methods and models used. Estimates based on dam components or the regression of offspring on dam could be biased due to common environmental and maternal effects. Even estimates based on sire components may be biased when some factors such as non-random mating and selection are involved. Restricted maximum likelihood (REML) (PATTERSON and THOMPSON, 1971) fitting an animal model (Henderson, 1984) has been widely used in estimation of (co)variance components. An animal model incorporates all known relationship for the individuals in data. Under certain conditions, the REML estimate of additive genetic variance is free from selection bias (HENDERSON, 1988).

The objectives of the present study are to provide information about (co)variance components and resulting heritabilities as well as genetic and environmental correlations for growth and carcass traits in rabbits, using animal model based procedures.

MATERIALS AND METHODS

Rearing system and measurement of traits

Data were collected from the Skovvang rabbitry at the Danish Institute of Agricultural Science (DIAS) during 1995-1997. The population studied was comprised of three lines. Two lines originated from a mutual gene pool of the Danish White breed in 1977 and has been maintained without migration. The two lines have followed almost the same breeding procedure, involving selection of males for average daily gain from weaning to slaughter age, but during 5 years was kept in an environment with ammonia treated straw as litter while the other line during the same years was kept in an environment with untreated straw. The third line was established in 1990 by crossing line 2 with an imported batch of males from the Hungarian White breed. These lines have been used by Danish rabbit breeders to improve their own stock.

Table 1 : Data structure, means and standard deviations for daily gains and carcass traits

Traits	Number of sires	Number of dams	Number of litters	Number of indiv.	Mean	Std
Daily gain						
$DG_{1\text{-}35}$ (g)	34	95	272	2033	19.76	4.49
$DG_{36\text{-}90}$ (g)	34	95	268	1762	35.98	4.26
$DG_{1\text{-}90}$ (g)	34	95	268	1767	29.83	2.89
Carcass						
Yield (%)	34	95	252	1386	57.95	2.46
Length (cm)	34	95	252	1386	36.56	1.23
Back (score)	34	95	252	1386	3.25	0.77
Thigh (score)	34	95	252	1386	3.41	0.76
Fat (score)	34	95	252	1386	2.01	0.64

[a] $DG_{1\text{-}35}$, $DG_{36\text{-}90}$ and $DG_{1\text{-}90}$: daily gain during the period from birth to 35 days, from 36 to 90 days and from birth to 90 days, respectively.

On the day after kindling, litters were examined and the number of the young were counted. The nest box was placed beside the mother's cage. The does entered the nest box through a circular opening and the young had no access to their mother's cage. On the 14th day after kindling, the circular opening was closed with a net, which was removed once a day when the does entered the nest for suckling. The young gained access to solid feed 14 days after birth.

At weaning, young were earmarked, weighed and transferred to the rearing house and placed in cages (450 cm^2) made of electroplated welded wire net containing up to 5 young rabbits each, which meant that a litter was put into two cages. The compound feed used was produced at the feed mill at DIAS and pelleted into 2 or 3 mm sized pellets. The 2 mm pellet was used until weaning and the 3 mm pellets after weaning. In a balance experiment (BØRSTING *et al.*, 1995), the compound was found to contain 11.1 MJ of digestible energy per kg feed and 18.6% crude protein.

Body weight was measured individually at weaning and at the day when rabbits left for slaughter. The age at weaning was approximately 35 days with 5 days difference between the oldest and the youngest within year, and the age when rabbits left for slaughter was about 90 days with a range from 73 to 107 days, dependent on the size of the rabbits and the facilities of the rearing unit. Thus, daily gains during the pre-weaning period ($DG_{1\text{-}35}$), and from weaning to about 90 days ($DG_{36\text{-}90}$), and during the whole period from birth to about 90 days ($DG_{1\text{-}90}$) were calculated by the total gain divided by the length (days) of the period. The average birth weight (60 g) was taken into calculation of daily gains. At slaughter, carcass yield was measured as carcass weight including head divided by live weight (dressing percentage); carcass length was measured as the distance from *atlas vertebra* to the 7th *lumbar vertebra*. The conformation and fleshiness of carcass was subjectively evaluated by giving a score (1-5) for the back and thigh cuts where a score of 5 was the best rating. The degree of fatness was evaluated into three groups with score 3 for too much fat, score 2 for moderate amount of fat and score 1 for low amount of fat. Data for individual growth traits and carcass traits were collected from 1995 to 1997. The data structure is shown in Table 1.

Statistic methods

The basic model used to describe the component effects of an individual observation was

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Wc} + \mathbf{Za} + \mathbf{e}$$

where **y** is the vector of observations; **X**, **W** and **Z** are the design matrices for **b**, **c** and **a**, respectively; **b** is the vector of fixed effects; **c** is the vector of litter effects; **a** is the vector of additive genetic effects; and **e** is the vector of random residuals. The distributions of the random effects were assumed as

$$\mathbf{a} \sim \mathrm{N}\,(\mathbf{0}, \mathbf{A}\sigma_a^2),\quad \mathbf{c} \sim \mathrm{N}\,(\mathbf{0}, \mathbf{I}_c\sigma_c^2) \text{ and } \mathbf{e} \sim \mathrm{N}\,(\mathbf{0}, \mathbf{I}_e\sigma_e^2)$$

respectively, where σ_a^2, σ_c^2 and σ_e^2 are variance components (scalars), and **A** is the numerator of Wright's relationship matrix, and **I** is an identity matrix. The **a**, **c** and **e** were assumed to be independent from each other.

For the analyses on growth traits, fixed effects in the model comprised year, season at birth, line, sex and parity as class variables with litter size at weaning as a covariable. For carcass traits, fixed effects included year, season at slaughter, line, sex and parity as class variables with slaughter age and litter size at weaning as covariables. Parities were grouped into three classes, *i.e.*, parity 1, parity 2, and parity 3 or over parity 3. Seasons were consistent with the four seasons of year.

Table 2 : Estimates of additive genetic variance (σ_a^2), litter variance (σ_c^2), residual variance (σ_e^2), phenotypic variance (σ_p^2), the ratio of litter variance to phenotypic variance (c^2) and heritability (h^2) for daily gains and carcass traits

Traits	σ_a^2	σ_c^2	σ_e^2	σ_p^2	c^2	h^2
Daily gains						
DG_{1-35}	2.783	10.650	4.312	17.75	0.600**	0.157 *
DG_{36-90}	2.816	5.376	8.743	16.93	0.318**	0.166**
DG_{1-90}	2.442	1.485	3.997	7.924	0.187**	0.308**
Carcass						
Yield	0.633	0.978	4.002	5.613	0.113**	0.174**
Length	0.268	0.400	0.872	1.540	0.174**	0.260**
Back	0.042	0.053	0.449	0.543	0.077**	0.098**
Thigh	0.055	0.054	0.457	0.566	0.098**	0.095**
Fat	0.034	0.036	0.342	0.412	0.083**	0.086**

* $P<0.05$, ** $P<0.01$.

Variance and covariance components were analysed using bivariate (two traits) animal models. The final estimates of variance components were calculated as the average of the estimates over the three pairs of combination for daily gains and over the ten pairs of combinations for carcass traits. The analyses were carried out using a restricted maximum likelihood algorithm (REML) applying the package DMU (JENSEN and MADSEN, 1993).

RESULTS

Means and standard deviations for each trait are shown in Table 1. The daily gain during the period from weaning to 90 days was almost twice the daily gain during the pre-weaning period. However, when calculated as relative growth rate $\left(\frac{Daily\,gain_{t1-t2}}{(BW_{t1}+BW_{t2})/2}\right)$, the relative growth rate during pre-weaning was 2.36 times as high as that during post-weaning. As a whole, growth was high during both periods. Consequently, average body weight was 752 g at weaning and 2745 g at 90 days of age. Standard deviations for each trait were calculated on the basis of the observations adjusted for year, line and sex. As can be read from the table, the phenotypic variation for most of the traits was moderate or high. Thus, the coefficients of variation were less than 5% for carcass yield and length, were 12% for DG_{36-90} and 10% for DG_{1-90}, and ranged from 22% to 32% for the subjectively scored carcass traits and DG_{1-35}.

The effects of year, season and line on daily gains were significant. It was also found that males had higher values in DG_{36-90} and DG_{1-90} than females but not in DG_{1-35}. On the other hand, parity had a significant effect only on DG_{1-35}, i.e., the rabbits from first parity grew slower than those from later parities during pre-weaning. There was a significant negative regression of DG_{1-35} and DG_{1-90} on litter size at weaning but not on DG_{36-90}. All these factors accounted for 15% - 28% of overall variation. The effects of year, season, line, sex, parity, litter size on the carcass traits were small though some of them were statistically significant on some traits. On the other hand, slaughter age has a large and positive effect on the carcass traits except for yield. All these factors resulted in a reduction of overall variation by 3% - 16%.

The estimates of variance components and their ratios to phenotypic variance are shown in Table 2. Litter effects (including maternal and common environmental effects as well as part of non-additive genetic effects in the present study) were rather high for all the three daily gains with the highest for DG_{1-35}, reflecting large maternal and/or common environmental effects due to individuals in the same litter being nursed by the same dam and reared in the same cage. Litter effect for DG_{36-90} was about half that for DG_{1-35}, reflecting a rapid reduction of maternal and/or common environmental effects. In contrast to litter effects, heritabilities for daily gain were low or moderate, i.e., 0.16, 0.17 and 0.31 for DG_{1-35}, DG_{36-90} and DG_{1-90}, respectively. The heritabilities for carcass traits were also low or moderate with the highest (0.26) for carcass length and lowest (0.09) for fat score. The ratios of litter effects were a little lower than heritabilities except for thigh score in which the ratio of the litter effect was a little higher than heritability.

Correlations between daily gains at different periods are shown in Table 3. The genetic correlation between DG_{1-35} and DG_{36-90} was very strong, while environmental correlations were weak, consequently causing a weak phenotypic correlation. The weak environmental correlations could be explained by individuals receiving temporary environmental effects randomly from time to time whereas the environmental effect common to the members of a litter was different in different periods. It is also implied that permanent environmental effects could be small. Daily gain from birth to 90 days was a function of DG_{1-35} and DG_{36-90}. Therefore, as expected, various correlations for DG_{1-90} with DG_{1-35} and DG_{36-90} were very strong, especially genetic correlations.

Correlations between carcass traits are shown in Table 4. The genetic correlations between carcass yield,

Table 3 : Phenotypic, genetic, litter and environmental correlations between daily gain traits

Traits	DG$_{1-35}$	DG$_{36-90}$	DG$_{1-90}$
DG$_{1-35}$		0.069* 0.895**	0.510** 0.969**
DG$_{36-90}$	-0.156** 0.070		0.846** 0.987**
DG$_{1-90}$	0.452** 0.457**	0.698** 0.895**	

Phenotypic and genetic correlations in the upper and lower rows above diagonal, litter and environmental correlations in the upper and lower rows below diagonal.
** P<0.01.

carcass length, back score and thigh score were not significantly different from zero, except for the correlations between back and length and between back and thigh which were strong and positive. The correlations for fat score with carcass length, back score and thigh score were not consistent, with negative genetic correlations but positive environmental correlations. The great discrepancy between genetic and environmental correlations usually reflects that genetic and environmental sources of variation affect the traits through different physiological mechanisms (FALCONER, 1989).

Table 5 shows correlations between daily gains and carcass traits. The correlations between daily gains and carcass yield were not significant. All the correlations between carcass length, back score, thigh score and daily gains were positive, and the genetic correlations were much higher than environmental correlations. Correlations between fat score and daily gains were not consistent with negative genetic correlations and positive environmental correlations.

Table 4 : Phenotypic, genetic, litter and environmental correlations between carcass traits

Traits	Yield	Length	Back	Thigh	Fat
Yield		-0.045 -0.224	0.293** 0.156	0.284** 0.173	0.218** 0.136
Length	-0.076 0.066		0.272** 0.561**	0.238** 0.027	0.031 -0.906**
Back	0.487** 0.287**	0.109 0.275**		0.734** 0.821**	0.180** -0.772**
Thigh	0.592** 0.257**	0.248* 0.317**	0.884** 0.704**		0.281** -0.453*
Fat	0.410** 0.204**	0.476** 0.188**	0.148 0.320**	0.335** 0.381**	

Phenotypic and genetic correlations in the upper and lower rows above diagonal, litter and environmental correlations in the upper and lower rows below diagonal.
* P<0.05, ** P<0.01.

DISCUSSION

Litter effects for daily gains were very large especially during the pre-weaning period, indicating large maternal effects and/or common environmental effects, which is quite agreeable with previous studies (MGHENI *et al.*, 1982; KHALIL *et al.*, 1987; FERRAZ *et al.*, 1991; FERRAZ *et al.*, 1992; MCNITT and LUKEFAHR, 1993). In the present study, litter size was taken as a covariable in the model. Thus, the presented estimates of litter effects included the various maternal effects such as common uterine environment, nursing behaviour, milk yield and ability to teach the young to eat solid feed, but omitting litter size. The regression of litter size was found to be significantly negative for DG$_{1-35}$ and DG$_{1-90}$ but was not significant for DG$_{36-90}$, indicating that litter size has an unfavourable influence on daily gain during pre-weaning but not on daily gain during post-weaning. Therefore, litter effects are expected to become larger for DG$_{1-35}$ and DG$_{1-90}$ but not for DG$_{36-90}$ when a model excluding litter size is used.

Litter effects on carcass traits were found to be almost as high as heritability estimates. FERRAZ *et al.* (1992) and LUKEFAHR *et al.* (1993) reported that maternal or litter influences may be more important than additive genetic effects for several carcass traits. Considerable litter effects even for post-weaning growth and carcass traits could be due to rabbits from the same litter after weaning being reared in the same cage, and also due to the remaining effects from the pre-weaning period, the post-weaning period being just 60% longer than the pre-weaning period.

Heritability estimates for growth reported in previous studies varied over a wide range, in general, were low or moderate. The presented estimate of 0.16 for DG$_{1-35}$ was agreeable with those reported by ESTANY *et al.* (1992). The estimate for DG$_{36-90}$ and DG$_{1-90}$ was consistent with the reports by BLASCO *et al.* (1987), ESTANY *et al.* (1992), POLASTRE *et al.* (1992) and LUKEFAHR *et al.* (1996). There were very few previous reports on heritabilities for carcass traits. The heritability (0.17) for carcass yield estimated by the present study was higher than the estimate of 0.07 documented by AYYAT *et al.* (1994) but lower than the estimate of 0.37 obtained by LUKEFAHR *et al.* (1996).

The heritability estimate for DG$_{1-35}$ and for DG$_{36-90}$ was low. On the other hand, DG$_{1-90}$ had a moderate heritability. Further, similar to the report by LUKEFAHR *et al.* (1996), genetic correlations for DG$_{1-90}$ with DG$_{1-35}$ and DG$_{36-90}$ were very strong. Based on the estimates of the parameters in the present

Table 5 : Phenotypic (r_p), genetic (r_a), litter (r_c) and environmental (r_e) correlations between carcass traits and daily gains

Traits		Yield	Length	Back	Thigh	Fat
DG_{1-35}	R_p	0.052	0.256**	0.261**	0.254**	0.173**
	R_a	0.168	0.653**	0.807**	0.693**	-0.061
	R_c	-0.030	0.197**	0.331**	0.202*	0.150
	R_e	0.077	0.128*	0.227**	0.268**	0.241**
DG_{36-90}	R_p	-0.087	0.345**	0.354**	0.355**	0.155**
	R_a	-0.226	0.884**	0.867**	0.828**	-0.297
	R_c	-0.157	0.202*	0.092	0.240**	0.056
	R_e	0.002	0.188**	0.351**	0.380**	0.300**
DG_{1-90}	R_p	-0.027	0.506**	0.523**	0.500**	0.264**
	R_a	-0.153	0.811**	0.968**	0.765**	-0.272
	R_c	0.017	0.448**	0.418**	0.474**	0.363**
	R_e	0.032	0.271**	0.462**	0.504**	0.425**

* $P<0.05$, ** $P<0.01$.

study, given the same selection intensity and selection on the basis of individual performance, the correlated responses of DG1-35 and DG36-90 by selection for DG1-90 are expected to be larger than direct selection for these two traits themselves. Clearly, selection for average daily gain from birth to market age or for body weight at market age would effectively improve growth rate during both pre-weaning and post-weaning periods.

Carcass length is not an important trait. The measurement and analysis of this trait was to detect if it is genetically related to some economically important traits so that an indirect selection approach could be useful. It was found that the genetic correlations for carcass length with back score, fat score, and daily gains were significant. Because of a moderate heritability for carcass length, a low heritability for fat score and a strong negative genetic correlation between the two traits, selection for carcass length would be expected to improve fat score effectively. On the other hand, some retail dealers may not prefer a long rabbit carcass. In this case, culling of rabbits with lengthy body could be practised.

Carcass yield is an important trait because an improvement on this trait could increase net profits. However, direct selection for this trait would result in a small response due to a low or moderate heritability (0.17) with a small phenotypic variation. In addition, genetic correlations for carcass yield with other traits in the present study were not significant. The possibilities of genetic improvement on carcass yield needs to be further studied.

Back, thigh and fat scores influence carcass quality. These traits are difficult to measure on live rabbits. Further, these traits were found to have low heritabilities. On the other hand, these traits have favourable genetic correlations with daily gain. Therefore, it is suggested that direct selection for these carcass traits is not necessary at present and that selection for growth rate could result in a favourable correlated response for these traits.

In conclusion, selection for average daily gain from birth to market age or selection for body weight at market age is expected to improve all of the traits involved in the present study except for carcass yield.

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