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ESTIMATES OF GENETIC PARAMETERS IN DANISH WHITE RABBITS USING AN ANIMAL MODEL : II. LITTER TRAITS

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ABSTRACT : Data from about 1000 litters were analysed to draw inferences of genetic parameters for doe litter traits, using restricted maximum likelihood (REML) procedures based on a doe repeatability model. The traits under analyses were litter size at parturition (LSB = 9.53 on average), litter size at weaning (LSW = 7.63), mortality during pre-weaning (Mort =18,02%), average offspring body weight at weaning (ABW = 740 g), and total litter weight at weaning (LTW = 5557 g). The statistical model contained a permanent environmental effect and that was significant for only LSW (0.106). The estimates of heritabilities were 0.188, 0.081, 0.113, 0.196 and 0.194 for LSB, LSW, Mort, ABW and LTW, respectively. Repeatability estimates for these traits were 0.188, 0.187, 0.145, 0.196 and 0.214, respectively. Genetic correlations between these traits were consistent with environmental and phenotypic correlations. The correlation between LSB and LSW was strongly positive. ABW was negatively correlated with mortality, LSB and LSW. Mortality was strongly and positively correlated with LSB, but negatively with LSW. The correlations of LTW with other traits were favourable, especially strong with LSW and ABW. Thus, selection for LTW would result in an effective overall improvement on litter traits.

RESUME : **Estimation des paramètres génétiques des lapins de race Blanc Danois : II. caractéristiques de la portée.** Les données provenant d'environ 1000 portées ont été analysées pour estimer les paramètres génétiques des caractéristiques de portée en utilisant la méthode du maximum de vraisemblance restreint (REML) basée sur un modèle utilisant la répétabilité intra-mère. Les caractéristiques analysées ont été la taille portée à la naissance (LSB = 9,53 en moyenne), puis au sevrage (LSW = 7,63), la mortalité naissance-sevrage (Mort = 18,02%), le poids moyen individuel au sevrage (ABW = 740 g) et le poids moyen de portée au sevrage (LTW = 5557 g). Le modèle statistique utilisé incluait un effet fixe de l'environnement qui n'a été significatif que pour LSW (expliquant 10,6% de la variance phénotypique). Les héritabilités estimées ont été de 0,188 - 0,081 - 0,113 - 0,196 et 0,194 pour LSB, LSW, Mort, ABW et LTW respectivement. Pour les mêmes caractères, les répétabilités ont été estimées à 0,188 - 0,187 - 0,145 - 0,196 et 0,214 dans le même ordre. Les corrélations génétiques entre ces caractères sont cohérentes avec les corrélations environnementales et phénotypiques observées. Les corrélations entre les tailles de portée à la naissance et au sevrage sont fortes et positives. La mortalité naissance-sevrage est fortement et positivement corrélée avec la taille de la portée à la naissance, mais négativement avec celle mesurée au sevrage. Le poids total de portée au sevrage est fortement corrélé avec les autres paramètres, dans un sens favorable. Il est en particulier fortement corrélé avec les autres caractères mesurés au sevrage (LSW et ABW). Par voie de conséquence, une sélection basée uniquement sur le poids de portée au sevrage devrait se traduire par une amélioration de l'ensemble des caractéristiques des portées.

INTRODUCTION

Reproductive capacity of does is one of most important economic traits in meat production of rabbits. As in other multiparous species, litter size at parturition is a criterion of reproductive ability that is determined by number of eggs ovulated and prenatal survival of embryos. BLASCO *et al.* (1993) found in their review that doe genotype seems much more important for the prenatal survival than the genotype of the embryos/foetus. Litter weight at weaning and mortality during pre-weaning reflect milking and nursing ability of doe. FERRAZ and ELER (1994) showed that heritability of individual body weight at weaning in Californian and New Zealand White breeds was 0.12 to 0.14 for maternal effects and almost negligible for direct effects. HANSEN and BERG (1997) found similar results in mink with the highest proportion of maternal to direct heritability at 4 weeks of age. Thus, growth in the pre-weaning period seems to a great extent to be determined by the milking and nursing ability of the doe. Therefore, genetic improvement in litter traits has to be initiated with the does as the important part.

MISZTAL (1990) pointed out that the accuracy of estimates of variance components is dependent on the choice of data, methods, and models. Estimates of heritability and repeatability for litter traits have a broad range among reports, as reviewed by KHALIL *et al.* (1986) and ROCHAMBEAU (1988). The dissimilarity of the estimates could reflect real differences among populations and environmental conditions, but it could be partly due to different methods and models used. BLASCO (1996) claimed that according to the literature there is a strong consensus for the reported low values of heritability for litter size, generally under 0.10, and maternal effects appear to be small. In recent years, statistical methods used to estimate variance components have been greatly improved, for example, animal repeatability models have been extensively used to estimate variance components for reproductive traits in various farm animals.

The objectives of the present study are to estimate variance components and heritabilities, as well as genetic and environmental correlations for litter traits in rabbits using an animal model based procedure.

MATERIALS AND METHODS

The data were collected from the Skovvang rabbitry at the Danish Institute of Agricultural Sciences (DIAS), located approximately 56° N and 10° E and 60 m above sea level, where temperatures ranged from 10° C during winter to 24° C in summer. The population was comprised of three lines. Lines 2 and 3 originated from a common gene pool of Danish White rabbits since 1977, and has been maintained without migration. These two lines have followed almost the same breeding procedure, involving selection of males for average daily gain from weaning to slaughter age, and females were recruited mainly from large litters. But during 5 years, one of the lines was fed the diet with ammonia treated straw, while the other line during the same years was fed a normal diet. The third line (Line 1) was established in 1990 by crossing line 2 with an imported batch of males of the Hungarian White breed. All three lines have been kept and used as a potential gene pool for the Danish rabbit breeders to replenish their own stock.

Rearing system and measurement of traits

On the day after kindling, litters were examined and the number of young were counted. The doe and her young were kept in a cage system where the nest box design limited the access of the doe to her young. From the age of 14 days and onwards, the opening to the nest box was closed with a net, which was removed once a day to allow does to enter the nest for suckling. The young started to eat solid feed 14 days after birth.

The compound feed used during the pre-weaning period was produced at the feed mill at DIAS and pelleted into 2 mm pellets. In a digestibility experiment (BØRSTING *et al.*, 1995), the compound was found to contain 11.1 MJ digestible energy per kg feed and 18.6% protein. The age at weaning was approximately 35 days during 1993-1996 and 28 days during 1996-1998 with a 5 days difference between the eldest and the youngest within year. At weaning, young were earmarked, individually weighed and transferred to the rearing house. Thus, the traits involved were litter size at parturition (LSB), litter size at weaning (LSW), mortality during pre-weaning (Mort), average offspring weight at weaning (ABW) and total litter weight at weaning (LTW).

In general, about 15 bucks and 30 does currently breed in each line. Mating was usually allowed after weaning by choosing randomly a buck from the panel of selected breeding males, and placed with the doe; thus, a doe was mated with different bucks in different parities. The length of gestation ranged from 28 to 36 days with an average of 31.2 days. Data for litter traits were collected from 1993 to 1998. The data structure is shown in Table 1. Due to missing records in different traits, the numbers of sires, dams and does were different among the traits.

Statistical methods

Data from each line was not large enough to provide good estimates of genetic parameters. Lines which originated from the same base population were therefore pooled to estimate variance components across the three lines, under the assumption that the variance components were the same among the three lines. Variance components for each trait were estimated using a single-trait doe repeatability model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Wc} + \mathbf{Za} + \mathbf{e} \quad (1)$$

and covariance components between the traits were estimated using a two-trait model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e} \quad (2)$$

where **y** is the vector of observations on the individual does for a particular litter; **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 permanent environmental effects; **a** is the vector of additive genetic effects, and **e** is the vector of random residuals. The distribution of the random effects were assumed as

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

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

Fixed effects included year, season at parturition, line, and parity for the analyses on litter sizes and mortality, and with age of offspring at weaning as a covariable for the analyses on litter weight and average weight at weaning. Season at parturition was defined as four periods, starting with January, February and March as winter, etc. Parity was divided into two groups,

Table 1 : Data structure, means and standard deviations for reproductive traits.

Traits	No. of sires	No. of dams	No. of does	No. of litters	Mean	SD
LSB	45	56	259	808	9.53	2.18
LSW	52	70	291	1021	7.63	1.50
Mort (%)	45	53	250	785	18.02	15.39
ABW (g)	52	70	291	1014	739.5	115.6
LTW (g)	52	70	291	1014	5557	1162

one for the first parity and the other for the second and later parities. The analyses were carried out using a restricted maximum likelihood algorithm (REML) with the package DMU (JENSEN and MADSEN, 1993).

In addition, least squares means for fixed effects were estimated using a mixed model including the fixed effects as described in the above animal model, but only including doe as a random variable and without combining pedigree information. The estimation was conducted using the MIXED procedure (REML) of SAS (SAS INSTITUTE, 1992). If genetic change over generations differed among the three lines, the least squares means of lines reflected the average performance over generations, instead of the average performance in the base generation as given by the animal model.

Table 2 : Least squares means by lines, seasons and parities.

Fix effect	LSB	LSW	Mort	ABW	LTW
Line:					
L1	9.31^a	7.45^a	17.69^a	724.5^b	5388^b
L2	9.28^a	7.58^a	18.26^a	761.4^a	5678^a
L3	9.56^a	7.62^a	19.07^a	731.9^b	5515^{ab}
Season:					
Winter	9.62^{ab}	7.68^a	19.02^a	752.8^a	5712^a
Spring	9.73^a	7.70^a	19.06^a	730.4^b	5595^{ab}
Summer	9.24^{bc}	7.41^b	19.36^a	734.1^{ab}	5304^c
Autumn	8.94^c	7.41^b	15.92^b	739.9^{ab}	5496^{bc}
Parity:					
1	8.46^b	7.01^b	16.27^a	705.5^b	4830^b
2 and later	9.51^a	7.61^a	18.61^a	743.3^a	5608^a

a-c : Least squares means in each block without a common superscript differed significantly (P<0.05).

RESULTS

The mean and standard deviation for each trait are shown in Table 1. Litter size at parturition and at weaning, average offspring weight and total litter weight at weaning were high in the present population. However, mortality during pre-weaning was also high. The standard deviation for each trait was calculated based on adjustment for effects of year, season, line, and parity. For ABW and LTW, the standard deviation was further adjusted for age at weaning. As shown in the table, phenotypic variation for all traits were either moderate or high. The coefficients of variation ranged from 15% to 23% for the traits, except for mortality which was 85%.

Table 2 shows the least squares mean for each trait in relation to line, season and parity. No significant difference was found in litter size and mortality between lines, except for weight at weaning. Season had a significant influence on all traits. Litter size in winter and spring was higher than in summer and autumn. The lowest mortality was in autumn and the lowest litter weight at weaning in summer. The highest average offspring weight at weaning was found in spring. The performances of the traits in the latter parities were significantly better than in the first parity, except for mortality.

The estimates of variance components and their ratios to phenotypic variance were obtained according to model (1) and the results are shown in Table 3. No permanent environmental effects could be found for litter size at parturition and average offspring weight. Permanent environmental effects were small and not significantly different from zero for mortality and total litter weight, but was considerable for litter size at weaning. Heritabilities for litter size at parturition, average offspring weight and total litter weight were near 0.2, while heritabilities for litter size at weaning and mortality were low (0.081 and 0.113, respectively). Consequently, repeatabilities (the sum of heritability and the ratio of permanent environmental variance to phenotypic variance) ranged from 0.145 to 0.214.

Because permanent effects were zero or small, except for litter size at weaning, genetic and environmental correlations between the litter traits were estimated using model (2) that excluded permanent

Table 3 : Estimates of permanent environmental variance (σ_c^2), additive genetic variance (σ_a^2), residual variance (σ_e^2), phenotypic variance (σ_p^2), and the ratio of permanent variance (c^2) to phenotypic variance, heritability and its standard error ($h^2 \pm$ SE), and repeatability (R), based on model (1).

Traits	σ_c^2	σ_a^2	σ_e^2	σ_p^2	c^2	$h^2 \pm$ SE	R
LSB	0.000	0.904	3.901	4.806	0.000	0.188 ± 0.053**	0.188**
LSW	0.252	0.192	1.934	2.378	0.106*	0.081 ± 0.041*	0.187**
Mort.	7.5	27.0	204.2	238.7	0.031	0.113 ± 0.043**	0.145**
ABW	0.2	2660.7	10921.0	13581.9	0.000	0.196 ± 0.051**	0.196**
LTW	27505	269840	1093550	1390895	0.020	0.194 ± 0.058**	0.214**

* P<0.05; **P<0.01.

Table 4 : Phenotypic, genetic and environmental correlations between reproductive traits [a].

Traits	LSB	LSW	Mortality	ABW	LTW
LSB		0.728** ± 0.068	0.818** ± 0.065	- 0.307** ± 0.116	0.276* ± 0.115
LSW	0.579** 0.543**		- 0.048 ± 0.151	- 0.130 ± 0.118	0.686** ± 0.064
Mortality	0.653** 0.623**	- 0.262** - 0.303**		- 0.346** ± 0.136	- 0.237* ± 0.121
ABW	- 0.275** - 0.267**	- 0.282** - 0.317**	- 0.125** - 0.083**		0.599** ± 0.080
LTW	0.232** 0.222**	0.651** 0.642**	- 0.338** - 0.361**	0.466** 0.431**	

[a] Genetic correlations and their standard errors in the upper and lower rows above diagonal, Phenotypic and environmental correlations in the upper and lower rows below diagonal.

* P<0.05; ** P<0.01.

effects. As shown in Table 4, litter size at parturition has a significant and favourable genetic correlation with litter size at weaning and total litter weight, while being unfavourable with mortality and average offspring weight. Genetic correlations for total litter weight with all the other traits are significantly favourable. Significant and favourable genetic correlations were also found between mortality and average offspring weight. The environmental and phenotypic correlations for each pair of litter traits were consistent with corresponding genetic correlations.

DISCUSSION

Seasonal effect

In the present study, season of parturition was found to have a significant influence on litter size at parturition, and consequently litter size and total litter weight at weaning. The performances of these traits were better in winter and spring than in summer and autumn. Poor performance of litter size in summer has been previously reported (KHALIL *et al.*, 1988; MCNITT and MOODY, 1990; WU *et al.*, 1998). AYYAT *et al.* (1995) showed that the milk production of does in Egypt during the summer was reduced by 15-20% causing a reduction of litter size at weaning by 15% compared to the rest of the year. The effect of the summer season in subtropical areas seems to overrule the effect we have seen in the temperate zone with more modest temperatures.

Parity effects

The results from the present study showed that the performances of litter traits were better in later parities than in the first parity, except for mortality. Previous studies have shown that the relationship between litter traits and parity was curvilinear (*i.e.*, the performance increased with advancing parity up to a specific parity then decreased gradually thereafter) (LANGE and SCHLOLAUT, 1988; FERRAZ *et al.*, 1991b; KHALIL and KHALIL, 1991; KHALIL, 1993; DAVOUST *et al.*, 1995; CHANG *et al.*, 1998). Mortality during pre-weaning is expected to decrease with advancing parity because doe's nursing ability may increase with experience and/or maturity. However, the present study showed that the mortality in the first parity was lower than the later parities though not significant. This may be due to a correlation between mortality and litter size at parturition.

Environmental effects

Estimates of permanent environmental effects were low and negligible for all litter traits except for litter size at weaning. As the doe is moved to a new parturition barn for each new litter, the permanent effect is hardly related to the surrounding but only to the animal herself. Among the non-genetic effects of the doe that could be considered as responsible for litter size at weaning is the nursing behaviour and the milking ability of the does. This effect is due to the doe during the growing period of her young and remains permanently expressed throughout all her litters. An additional analysis based on model (2) that did not include the permanent effect showed that the estimate of heritability (not presented) was, as expected, equal to the estimate of repeatability using model (1) except for litter size at weaning. In agreement, LUKEFAHR and HAMILTON (1997) did not observe significant permanent environmental effects on litter traits. Similarly, AYYAT *et al.* (1995) showed that the differences between heritability and repeatability estimates were very small, reflecting very small permanent environmental effects.

Heritabilities

Heritability estimates for litter traits reported in previous studies vary considerably. As a whole, the heritabilities were low to moderate. Present estimates of heritability for litter traits ranged from 0.081 to 0.196. Similar estimates have been found in previous reports, for example, litter size at parturition and at weaning (AYYAT *et al.*, 1995; LUKEFAHR and HAMILTON, 1997), average offspring weight at weaning (KHALIL *et al.*, 1987), litter weight at weaning (FERRAZ *et al.*, 1991a; MOURA *et al.*, 1991), and pre-weaning mortality (ROLLINS and CASADY, 1967; ERJAVEC *et al.*, 1990).

Due to low heritability and small permanent environmental effects, the estimates of repeatability were also low for litter traits. KHALIL *et al.* (1986) stated that most results in the literature showed litter traits of does to be low to moderately repeatable. It indicates that doe productivity is mainly determined by temporary environmental conditions that are different from parity to parity. Therefore, culling of does due to poor reproductive capacity should be based on records from several parities.

Based on records from the same population and approximately the same span of time, SU *et al.* (1999) estimated the heritability for pre-weaning daily gain of individual to be 0.16. In the present study, the heritability for average offspring weight at weaning, which is an indicator of additive genetic effects on milking and nursing ability of the doe, termed the maternal effect, was found to be 0.20. Low heritability estimates (0.04 to 0.08) for individual body weight at weaning have been reported by POLASTRE *et al.* (1992), ROCHAMBEAU *et al.* (1994) and LUKEFAHR *et al.* (1996). FERRAZ and ELER (1994), analysing the effects of direct and maternal genotypes on weight at weaning, found a heritability of 0.05 for direct and 0.12 for maternal genotypes. Our results, as well as the literature, shows that maternal additive genetic effects are important for growth rate of the young during the pre-weaning period and even more important than the direct effect of their own genotype.

Genetic correlations

The trend of the present estimates of genetic correlations is agreeable with previous reports (GARCIA *et al.*, 1980; LAHIRI and MAHAJAN, 1982; KHALIL *et al.*, 1987a, 1988). Litter size is an important criterion of doe productivity. But a high genetic correlation between litter size at birth and pre-weaning mortality, while the correlation is almost zero between mortality and litter size at weaning, indicates that litter size at weaning (rather than litter size at parturition) should be used in breeding programmes. Further, the most interesting observation is that genetic correlations involving total litter weight at weaning with other litter traits were all favourable and significant. Moreover, litter weight at weaning had a moderate heritability of 0.194 ± 0.058 and a large phenotypic variation (coefficient of variation = 21%). These results suggest that selection for litter weight at weaning would be effective and also result in an overall improvement in other litter traits.

Breeding strategy

SU *et al.* (1999) reported that selection for average daily gain from birth to market age or selection for body weight at market age would be expected to effectively improve growth rate. Based on present results and the results of SU *et al.* (1999), a breeding program using a selection index combining total litter weight at weaning and average daily gain from birth to market age would be expected to optimise the overall improvement realized in litter traits and growth rate.

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