

## ESTIMATES OF (CO)VARIANCE COMPONENTS AND GENETIC PARAMETERS FOR BODY WEIGHTS AND GROWTH EFFICIENCY TRAITS IN THE NEW ZEALAND WHITE RABBIT

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**Abstract:** The genetic parameters of growth traits in the New Zealand White rabbits kept at Sheep Breeding and Research Station, Sandynallah, The Nilgiris, India were estimated by partitioning the variance and covariance components. The (co)variance components of body weights at weaning (W42), post-weaning (W70) and marketing (W135) age and growth efficiency traits viz., average daily gain (ADG), relative growth rate (RGR) and Kleiber ratio (KR) estimated on a daily basis at different age intervals (42 to 70 d; 70 to 135 d and 42 to 135 d) from weaning to marketing were estimated by restricted maximum likelihood, fitting 6 animal models with various combinations of direct and maternal effects. Data were collected over a period of 15 yr (1998 to 2012). A log-likelihood ratio test was used to select the most appropriate univariate model for each trait, which was subsequently used in bivariate analysis. Heritability estimates for W42, W70 and W135 were  $0.42 \pm 0.07$ ,  $0.40 \pm 0.08$  and  $0.27 \pm 0.07$ , respectively. Heritability estimates of growth efficiency traits were moderate to high (0.18 to 0.42). Of the total phenotypic variation, maternal genetic effect contributed 14 to 32% for early body weight traits (W42 and W70) and ADG1. The contribution of maternal permanent environmental effect varied from 6 to 18% for W42 and for all the growth efficiency traits except for KR2. Maternal permanent environmental effect on most of the growth efficiency traits was a carryover effect of maternal care during weaning. Direct maternal genetic correlations, for the traits in which maternal genetic effect was significant, were moderate to high in magnitude and negative in direction. Maternal effect declined as the age of the animal increased. The estimates of total heritability and maternal across year repeatability for growth traits were moderate and an optimum rate of genetic progress seems possible in the herd by mass selection. The genetic and phenotypic correlations among body weights and between growth efficiency traits were also estimated. Moderate to high heritability and higher genetic correlation in body weight traits promise good scope for genetic improvement provided measures are taken to keep the inbreeding at the lowest level.

**Key Words:** genetic parameters, maternal effects, genetic correlations, growth traits, rabbit genetics.

## INTRODUCTION

Rabbits are becoming increasingly popular as an additional source of animal protein to meet the increasing demand from the ever-growing human population. Rabbit rearing gained momentum in the recent past owing to their high prolificacy, early maturity, shorter generation interval and efficiency in feed utilisation. In developing countries, it has been realised that domestic rabbit is an important livestock species which has immense potential to improve the socio-economic status of the rural poor (Risam *et al.*, 2005). Therefore, genetic improvement of domestic rabbits is sorely needed to increase their contribution to the animal protein much needed in developing countries (Okoro *et al.*, 2010). Genetic improvement for economic traits is possible if the estimates of variance-covariance components

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and genetic parameters of those traits are accurate. Studies on (co)variance components of growth in various rabbit breeds have shown that the body weight and growth rate are considerably affected by maternal as well as direct genetic effects (Niranjan *et al.*, 2010; Nagy *et al.*, 2011; Dige *et al.*, 2012; Nagy *et al.*, 2013). Compared to most farm animals, the information on (co)variance components and genetic parameters of growth traits in farm-reared rabbits is available for only a few populations. The New Zealand White is one of the most commonly used rabbit breeds for meat production and is available in almost all parts of the world irrespective of geographical location. Therefore, studying the genetic parameters for growth in this breed of rabbit would set a model to carry out similar studies in developing countries. In the present study, the genetic parameters of growth traits in the New Zealand White rabbits were estimated by partitioning the variance and covariance components due to additive and maternal effects.

## MATERIALS AND METHODS

### Data

Data were collected from the breeding flock of New Zealand White rabbits maintained at the Sheep Breeding and Research Station (SBRS), Sandynallah, The Nilgiris, Ooty, India (11°25' N latitude and 76°46' E longitude), at an altitude of 2200 m above mean sea level. Different growth traits studied were body weights at weaning (W42), post-weaning (W70) and marketing (W135) and growth efficiency traits *viz.*, average daily gains (ADG1, ADG2 & ADG3), relative growth rates (RGR1, RGR2 & RGR3) and Kleiber ratios (KR1, KR2 & KR3) on a daily basis at different age intervals (1=42 to 70 d; 2=70 to 135 d and 3=42 to 135 d) from weaning to marketing. The average daily gain (ADG) is the change in size over time and was calculated by the formula  $(y_{t_2} - y_{t_1}) / (t_2 - t_1)$ , where  $y_{t_1}$  and  $y_{t_2}$  refer to body weights in grams at  $t_1$  and  $t_2$  ages in days, respectively (Fitzhugh and Taylor, 1971). The relative growth rate (RGR) is the growth rate relative to current size and indicates the per cent increase in body weight per day. It was calculated using the formula  $(\ln y_{t_2} - \ln y_{t_1}) / (t_2 - t_1)$ , where 'ln' denotes the natural logarithm and  $y_{t_1}$  and  $y_{t_2}$  the weights in grams at time 1 ( $t_1$ ) and time 2 ( $t_2$ ) respectively (Fitzhugh and Taylor, 1971). The Kleiber ratio (KR) is the proportion of ADG to the metabolic body weight and was calculated using the formula  $ADG/W^{0.75}$  where,  $W^{0.75}$  denotes the metabolic body weight at the older age of the period for which KR is calculated (Prakash *et al.*, 2012). The number of sires and dams, least squares means, standard deviations and coefficients of variation for the respective traits are summarised in Table 1. Data were obtained over a period of 15 yr from 1998 to 2012, which were divided into 5 periods of 3 yr each. According to the agro-climatic condition prevailing in the study area, the year was divided into 4 seasons, namely winter (December to February), summer (March to May), south-west monsoon (June to August) and north-east monsoon (September to November). Kit gender, season and period of birth of the individual were the various non-genetic sources of variation studied. Records were available from a total of 2445 animals descended from 130 sires and 154 dams. The herd was a closed type where 40 to 60 breeding females were maintained every year with a male to female ratio of 1:5. Animals after weaning at 42 d of age were kept individually in wire cages of standard dimensions (61×46×46 cm) under

**Table 1:** Characteristics of data structure for growth traits of the New Zealand White rabbit.

Trait	W42	W70	W135	ADG1	ADG2	ADG3	RGR1	RGR2	RGR3	KR1	KR2	KR3
Number of records	2445	1834	900	1834	900	900	1834	900	900	1834	900	900
Number of sires with progeny	130	125	118	125	118	118	125	118	118	125	118	118
Number of dams with progeny	154	147	143	147	143	143	147	143	143	147	143	143
Least squares mean (g)	706.47	1260.18	2144.96	19.76	13.48	15.49	20.71	7.99	11.78	16.32	7.41	8.57
SEM	3.62	5.87	10.29	0.16	0.15	0.11	0.16	0.09	0.09	0.10	0.07	0.04
SD	179.13	251.20	308.78	6.59	4.49	3.23	6.75	2.82	2.64	4.11	2.13	1.22
CV (%)	25.35	19.90	14.45	33.77	34.03	21.28	32.65	35.48	22.52	25.31	29.03	14.37

W42: weaning weight; W70: post weaning weight; W135: marketing weight; ADG: average daily gain; RGR: relative growth rate; KR: Kleiber ratio; SEM: standard error of the mean; SD: standard deviation; CV: coefficient of variation.

similar housing and management conditions. Animals were fed concentrate (16% crude protein; 2500 kcal digestible energy) in graded quantity from 75 to 200 g (according to age, body weight and lactation), and seasonal grasses (*Pennisetum clandestinum* and *Phalaris aquatica*), tree Lucerne and carrots *ad libitum*. Animals were weighed exactly on the target ages. The bucks start breeding at 5 mo of age and the does at 6 mo of age. Mating of close relatives was avoided as far as possible to keep the inbreeding at its lowest level. Selection pressure applied was 2 to 5 per cent and 10 to 20 per cent for males and females, respectively. The bucks were culled after 2 yr and the does after 3 yr of age. Standard prophylactic schedule besides symptomatic treatment was adopted in disease management.

### Statistical Methods

The (co)variance components were estimated by restricted maximum likelihood (REML) using derivative-free algorithm fitting an animal model (Meyer, 2007). Data were first analysed by least squares analysis of variance (SPSS, 2005) to identify the fixed effects to be included in the model. Statistical model for least squares analyses included effects of sex of the kit (2 levels), season of birth (4 levels) and period of birth (5 levels) as fixed effects. All the body weight traits were significantly ( $P<0.01$ ) influenced by season and period of birth but not by sex of the kit. On the growth efficiency traits, these fixed effects had influence with varying levels of significance. Only significant effects ( $P<0.05$ ) were included in the models that were subsequently used for the genetic analysis. The convergence criterion for REML iterations were based on change in log likelihood ( $<5 \times 10^{-4}$ ), change in vector of parameters ( $<10^{-6}$ ) and norm of gradient vectors ( $<10^{-3}$ ), the details of which are provided by Meyer (2007). To ensure that a global maximum was reached, analyses were restarted. When estimates did not change, convergence was confirmed. Six different single trait linear models as described by Meyer (1992), which accounts for the direct and maternal effects, allowing for and ignoring genetic covariances between direct and maternal effects were fitted initially.

$$\text{Model 1: } y = X\beta + Z_a a + \varepsilon$$

$$\text{Model 2: } y = X\beta + Z_a a + Z_m m + \varepsilon \text{ with Cov}(a_m, m_o) = 0$$

$$\text{Model 3: } y = X\beta + Z_a a + Z_m m + \varepsilon \text{ with Cov}(a_m, m_o) = A\sigma_{am}$$

$$\text{Model 4: } y = X\beta + Z_a a + Z_c c + \varepsilon$$

$$\text{Model 5: } y = X\beta + Z_a a + Z_m m + Z_c c + \varepsilon \text{ with Cov}(a_m, m_o) = 0$$

$$\text{Model 6: } y = X\beta + Z_a a + Z_m m + Z_c c + \varepsilon \text{ with Cov}(a_m, m_o) = A\sigma_{am},$$

where  $y$  is the vector of records;  $\beta$ ,  $a$ ,  $m$ ,  $c$  and  $\varepsilon$  are vectors of fixed, additive direct genetic, maternal additive genetic, permanent environmental effects of the dam and residual effects, respectively;  $X$ ,  $Z_a$ ,  $Z_m$  and  $Z_c$  are incidence matrices that relate these effects to the records;  $A$  is the numerator relationship matrix between animals; and  $\sigma_{am}$  is the covariance between additive direct and maternal genetic effects. Assumptions for variance ( $V$ ) and covariance ( $Cov$ ) matrices involving random effects were

$$V(a) = A\sigma_a^2, V(m) = A\sigma_m^2, V(c) = I\sigma_c^2, V(e) = I\sigma_e^2, \text{ and } Cov(a, m) = A\sigma_{am},$$

where  $I$  is an identity matrix and  $\sigma_a^2$ ,  $\sigma_m^2$ ,  $\sigma_c^2$  and  $\sigma_e^2$  are additive direct, additive maternal, maternal permanent environmental and residual variances, respectively. The direct-maternal correlation ( $r_{am}$ ) was obtained for all the traits under analyses. Maternal across year repeatability for ewe performance ( $t_m = (1/4)h^2 + m^2 + c^2 + mr_{am}h$ ) was calculated. The total heritability ( $h_t^2$ ), was calculated using the formula  $h_t^2 = (\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am})/\sigma_p^2$  (Willham, 1972).

Log-likelihood ratio tests (LRT) were used to choose the most appropriate model for each trait (Meyer, 1992). An effect was considered to have significant influence when its inclusion caused a significant increase in log likelihood, compared with the model in which it was ignored. Significance was tested at  $P<0.05$ , by comparing differences in log-likelihoods to values for a  $\chi^2$  distribution with degrees of freedom equal to the difference in the number of (co) variance components fitted for the 2 models. The most appropriate model for each trait as per LRT was subsequently used in the bivariate analyses for estimation of genetic, phenotypic and residual correlations between the traits with starting values derived from single trait analyses.

## RESULTS

Least squares mean (LSM) along with the standard deviation and per cent coefficient of variation for the traits under study are given in Table 1. The (co)variance components and genetic parameters estimated by the most appropriate model in univariate analysis for various traits of the New Zealand White rabbits are presented in Table 2. As per LRT, the best model for W42 was Model 6, the most complete model, which includes direct genetic, maternal genetic and maternal permanent environmental variation as random effects including non-zero direct maternal genetic covariance. The apt model for W70 was Model 3, which includes direct genetic and maternal genetic as random effects, including non-zero direct maternal genetic covariance. For W135, Model 1, the simple animal model was the best that included only direct additive effect. Among the growth efficiency traits, Model 1 was apt for ADG2, ADG3 and KR2, whereas Model 3 was the best for ADG1. All the other traits were best represented by Model 4, which includes direct additive and maternal permanent environmental effects. The estimates of (co)variance components for the calculation of correlations were obtained through bivariate analyses. The non-genetic factors and inbreeding classes, significant for each trait, were included to adjust for the same. The correlation estimates of the traits under study are given in Table 3.

**Body weight traits**

The direct heritability estimates of body weight traits from the best models were  $0.42 \pm 0.07$ ,  $0.40 \pm 0.08$  and  $0.27 \pm 0.07$  for W42, W70 and W135, respectively. For W42, the addition of maternal genetic ( $m^2$ ) and maternal permanent environmental effect ( $c^2$ ) to the direct genetic effect increased the likelihood in model 6 (best model), in which 22 and 18% of the phenotypic variance were attributed to maternal genetic and maternal permanent environmental effect, respectively. For W70, the addition of maternal genetic effect ( $m^2$ ) alone increased the likelihood in model 3 (the best model), in which 32% of the phenotypic variance was attributed to maternal genetic effect. For W135, the maximum likelihood was given by the simplest model (Model 1). Significantly high and negative correlation between animal and maternal genetic effects was observed for W42 ( $-0.96$ ) and W70 ( $-0.57$ ). The estimates from the best models for W42, W70 and W135, respectively, of total heritability values ( $h_t^2$ ) were 0.09, 0.25 and 0.27 and of repeatability of doe performance ( $t_m$ ) were 0.21, 0.21 and 0.07.

**Table 2:** (Co)variance components and genetic parameter estimates for the growth traits fitting the most appropriate model in the New Zealand White rabbit.

Trait	Model						$h^2 \pm \text{SEM}$	$c^2 \pm \text{SEM}$	$h_t^2$	$t_m$
	fitted	$\sigma_a^2$	$\sigma_m^2$	$\sigma_c^2$	$\sigma_e^2$	$\sigma_p^2$				
W42	6	0.01	0.01	0.01	0.02	0.03	$0.42 \pm 0.07$	$0.18 \pm 0.04$	0.09	0.21
W70	3	0.03	0.02	-	0.03	0.07	$0.40 \pm 0.08$	-	0.25	0.22
W135	1	0.02	-	-	0.06	0.08	$0.27 \pm 0.07$	-	0.27	0.07
ADG1	3	18.96	6.30	-	27.44	45.26	$0.42 \pm 0.09$	-	0.24	0.08
ADG2	1	3.41	-	-	12.90	16.31	$0.21 \pm 0.07$	-	0.21	0.05
ADG3	1	1.77	-	-	6.60	8.38	$0.21 \pm 0.07$	-	0.21	0.05
RGR1	4	9.31	-	3.69	33.07	46.06	$0.20 \pm 0.05$	$0.08 \pm 0.02$	0.20	0.13
RGR2	4	1.44	-	0.54	4.60	6.58	$0.22 \pm 0.07$	$0.08 \pm 0.03$	0.22	0.14
RGR3	4	1.25	-	0.81	4.04	6.10	$0.21 \pm 0.07$	$0.13 \pm 0.04$	0.21	0.18
KR1	4	3.52	-	1.01	12.80	17.33	$0.20 \pm 0.05$	$0.06 \pm 0.02$	0.20	0.11
KR2	1	0.80	-	-	2.84	3.64	$0.22 \pm 0.07$	-	0.22	0.06
KR3	4	0.22	-	0.13	0.87	1.22	$0.18 \pm 0.07$	$0.11 \pm 0.03$	0.18	0.15

W42: weaning weight; W70: post weaning weight; W135: marketing weight; ADG: average daily gain; RGR: relative growth rate; KR: Kleiber ratio; SEM: standard error of mean.

$\sigma_a^2$ ,  $\sigma_m^2$ ,  $\sigma_c^2$ ,  $\sigma_e^2$  and  $\sigma_p^2$  are additive direct, maternal direct genetic, maternal permanent environmental, residual variance and phenotypic variance, respectively;  $h^2$  is heritability;  $m^2$  is  $\sigma_m^2/\sigma_p^2$ ;  $c^2$  is  $\sigma_c^2/\sigma_p^2$ ;  $t_m$  is maternal across year repeatability for doe performance;  $h_t^2$  is total heritability.

### Growth efficiency traits

**Average daily gain:** The direct heritability estimates of the average daily gains from the best models were  $0.42 \pm 0.09$ ,  $0.21 \pm 0.07$  and  $0.21 \pm 0.07$  for ADG1, ADG2 and ADG3, respectively. For ADG1, the likelihood was maximum (Model 3) with the addition of only maternal genetic ( $m^2$ ) effect to the direct genetic effect. In this model, 14% of the phenotypic variance was attributed to maternal genetic effect. For ADG2 and ADG3, the maximum likelihood was given by the simplest model (Model 1). Significant negative correlation ( $-0.68$ ) between animal and maternal genetic effects was observed in ADG1. For the respective ADGs, the estimates of total heritability values ( $h_t^2$ ) were 0.24, 0.21 and 0.21 and of repeatability of doe performance ( $t_m$ ) were 0.08, 0.05 and 0.05 from the best models.

**Relative growth rate:** The direct heritability estimates of relative growth rates from the best model (Model 4) were 0.20, 0.22 and 0.21 for RGR1, RGR2 and RGR3, respectively. Addition of maternal permanent environmental effect alone to the direct genetic effect resulted in maximum likelihood value. Estimates of permanent environmental effect ( $c^2$ ) for the respective RGRs were 0.08, 0.08 and 0.13. The maternal genetic variance seemed unimportant for any of the relative growth rates. The  $c^2$  estimates were lower than  $h^2$  values for these traits ( $c^2 < h^2$ ). The correlations between animal and maternal genetic effects (ram) for these traits were found to be non-significant. The estimates of  $h_t^2$  and  $t_m$  for the respective RGRs were 0.20, 0.22 and 0.21 and 0.13, 0.14 and 0.18, respectively.

**Kleiber ratio:** The direct heritability estimates of Kleiber ratios from the best models were 0.20, 0.22 and 0.18 for KR1, KR2 and KR3, respectively. Maximum likelihood estimates for KR1 and KR3 were obtained with inclusion of maternal permanent environmental effect (Model 4) in which 6 to 11% of total phenotypic variance could be attributed to maternal permanent environmental effect. The simplest model (Model 1) had the maximum likelihood value and was sufficient to explain the variation for KR2. The maternal genetic variance was not important for any of the ratios. The estimates of  $h_t^2$  and  $t_m$  for the respective KRs were 0.20, 0.22 and 0.18 and 0.11, 0.06 and 0.15, respectively.

### Correlation estimates

The estimates of genetic and phenotypic correlations among the body weight traits were high and positive (Table 3). Phenotypic correlations were observed to be lower than the genetic correlations. The estimates of genetic and phenotypic correlations among ADGs were low to high in magnitude. The correlation estimates were positive among ADGs, except between ADG1 and ADG2. Barring the negligible correlation between RGR1 and RGR2, other traits showed a medium to high correlation among relative growth rates. The Kleiber ratio also showed similar trend of correlations like ADGs. Among various growth efficiency traits, barring the negative and low correlation between ADG1 vs. KR2, RGR1 vs. ADG2 and KR2 and KR1 vs. ADG3 and RGR2, almost all the other correlation values were positive and medium to high in magnitude. The estimates of correlation coefficients of body weights with growth efficiency parameters were mostly negative in direction and varied from very low to high in magnitude. The weaning weight had negative direction with all the growth efficiency parameters for both genetic and phenotypic correlations. The coefficients of W70 and W135 had varying degrees of positive and negative correlations with other growth efficiency parameters. Compared to ADG, RGR and KR had lower genetic as well as phenotypic correlations with later stage body weight traits.

## DISCUSSION

### Body weight traits

The direct heritability ( $h^2$ ) estimates of body weight traits were moderate to high in the present study on New Zealand White rabbits. Earlier studies on heritability of weaning weights reported a range between 0.1 and 0.61. The heritability estimate obtained for W42 (0.42) was lower than that found in German Angora (Singh *et al.*, 2008), crossbred involving White Giant, Soviet Chinchilla and Grey Giant (Rojan *et al.*, 2009) and New Zealand White (Choudhury and Goswami, 2012) and higher than those found in New Zealand White (Bhushan and Ahlawat, 1999; Farghaly and El-Mahdy, 1999) and Danish White (Sorensen *et al.*, 2001) breeds of rabbit. The estimated heritability for weight at marketing (W135) in the present study was 0.27, which is similar to that reported by Bhushan and Ahlawat (1999), lower than Choudhury and Goswami (2012) (0.75) and higher than the report of Dige *et al.* (2012) (0.13).

**Table 3:** Estimates (mean±SEM) of genetic ( $r_g$ ), environmental ( $r_e$ ) and phenotypic ( $r_p$ ) correlations among body weights, average daily gains, relative growth rates and Kleiber ratios in the New Zealand White rabbit

Trait	$r_g$	$r_e$	$r_p$	Trait	$r_g$	$r_e$	$r_p$
W42-W70	0.76±0.05	0.59±0.04	0.66±0.02	ADG1-RGR2	-0.61±0.13	-0.50±0.04	-0.52±0.03
W42-W135	0.76±0.05	0.59±0.03	0.66±0.02	ADG1-RGR3	0.37±0.17	0.29±0.05	0.31±0.04
W42-ADG1	0.05±0.12	-0.13±0.04	-0.07±0.03	ADG1-KR1	-1.00*	0.16±0.10	0.12±0.08
W42-ADG2	-0.19±0.15	-0.06±0.05	-0.10±0.04	ADG1-KR2	-0.12±0.96	-0.11±0.05	-0.11±0.05
W42-ADG3	-0.17±0.15	-0.22±0.05	-0.20±0.04	ADG1-KR3	0.04±0.33	0.02±0.06	0.02±0.05
W42-RGR1	-0.73±0.06	-0.62±0.02	-0.65±0.02	ADG2-ADG3	0.66±0.12	0.77±0.02	0.75±0.02
W42-RGR2	-0.52±0.11	-0.29±0.05	-0.37±0.03	ADG2-RGR1	-0.26±0.18	-0.18±0.05	-0.20±0.04
W42-RGR3	-0.90±0.04	-0.80±0.02	-0.83±0.01	ADG2-RGR2	0.88±0.05	0.91±0.01	0.90±0.01
W42-KR1	-0.51±0.10	-0.48±0.03	-0.48±0.02	ADG2-RGR3	0.33±0.21	0.53±0.04	0.49±0.03
W42-KR2	-0.45±0.12	-0.21±0.05	-0.29±0.04	ADG2-KR1	0.50*	0.01±0.07	0.03±0.06
W42-KR3	-0.75±0.08	-0.60±0.03	-0.65±0.02	ADG2-KR2	0.42±0.80	0.05±0.15	0.07±0.08
W70-W135	0.62±0.11	0.49±0.04	0.53±0.03	ADG2-KR3	-1.00*	0.01±0.11	-0.02±0.09
W70-ADG1	0.68±0.07	0.72±0.02	0.71±0.02	ADG3-RGR1	0.24±0.18	0.40±0.04	0.36±0.03
W70-ADG2	-0.40±0.15	-0.33±0.05	-0.34±0.04	ADG3-RGR2	0.31±0.20	0.56±0.04	0.50±0.03
W70-ADG3	0.27±0.17	0.14±0.05	0.17±0.04	ADG3-RGR3	0.52±0.16	0.73±0.03	0.68±0.02
W70-RGR1	-0.09±0.14	0.23±0.04	0.13±0.03	ADG3-KR1	-0.24±0.48	0.16±0.08	0.11±0.06
W70-RGR2	-0.77±0.07	-0.67±0.03	-0.70±0.02	ADG3-KR2	0.04±0.94	0.03±0.13	0.02±0.08
W70-RGR3	-0.44±0.14	-0.36±0.05	-0.38±0.03	ADG3-KR3	0.78±0.09	0.90±0.01	0.87±0.01
W70-KR1	0.19±0.13	0.40±0.03	-0.34±0.03	RGR1-RGR2	-0.09±0.18	-0.22±0.05	-0.18±0.04
W70-KR2	-0.69±0.10	-0.56±0.04	-0.60±0.03	RGR1-RGR3	0.77±0.08	0.68±0.03	0.70±0.02
W70-KR3	-0.20±0.18	-0.16±0.05	-0.17±0.04	RGR1-KR1	0.96±0.01	0.97±0.00	1.00±0.00
W135-ADG1	0.17±0.17	0.26±0.05	0.24±0.04	RGR1-KR2	-0.14±0.19	-0.21±0.05	-0.19±0.04
W135-ADG2	0.58±0.13	0.68±0.03	0.65±0.02	RGR1-KR3	0.68±0.11	0.61±0.03	0.62±0.02
W135-ADG3	0.83±0.07	0.82±0.02	0.82±0.01	RGR2-RGR3	0.56±0.18	0.59±0.04	0.56±0.03
W135-RGR1	-0.35±0.16	0.02±0.05	-0.08±0.04	RGR2-KR1	-0.30±0.18	-0.31±0.04	-0.31±0.03
W135-RGR2	0.11±0.21	0.33±0.05	0.27±0.04	RGR2-KR2	1.00±0.01	0.98±0.00	0.98±0.00
W135-RGR3	-0.04±0.23	0.22±0.05	0.15±0.04	RGR2-KR3	0.42±0.20	0.60±0.03	0.56±0.03
W135-KR1	-0.40±0.40	0.03±0.09	-0.03±0.60	RGR3-KR1	0.65±0.11	0.57±0.03	0.59±0.02
W135-KR2	0.16*	-0.12±0.10	-0.10±0.08	RGR3-KR2	0.44±0.19	0.57±0.04	0.54±0.03
W135-KR3	-0.99±0.63	0.09±0.12	-0.06±0.09	RGR3-KR3	0.92±0.04	0.95±0.01	0.94±0.01
ADG1-ADG2	-0.39±0.17	-0.31±0.04	-0.33±0.03	KR1-KR2	-0.32±0.18	-0.28±0.04	-0.29±0.03
ADG1-ADG3	0.39±0.17	0.37±0.04	0.37±0.03	KR1-KR3	0.61±0.13	0.55±0.03	0.56±0.03
ADG1-RGR1	0.66±0.08	0.82±0.01	0.78±0.01	KR2-KR3	0.45±0.19	0.64±0.03	0.60±0.03

W42: weaning weight; W70: post weaning weight; W135: marketing weight; ADG: average daily gain; RGR: relative growth rate; KR: Kleiber ratio; SEM: standard error of the mean.

\*Indicates that the approximation used to define standard errors of parameter estimates failed.

The estimation method in most of the earlier studies was paternal half-sib correlation, while the maternal genetic and maternal permanent environmental effects were not accounted for. However, Lukefahr *et al.* (1992) reported moderate heritability for 90 d body weight in domestic rabbit breeds using an animal model by REML method. There was an overall decrease in heritability estimates as the age advanced, indicating declination in genetic variability as revealed by the low coefficient of variation in body weights as animals grew older. Moreover, these traits are subject to high environmental variation due to the seasons, which play a major role in the body weights of animals through availability of seasonal grasses. In addition, being a closed population, inbreeding was on the rise in the present study and in general inbreeding leads to reduction in additive genetic variance and heritability (Falconer and Mackay, 1996; Kristensen and Sorensen, 2005).

The appropriate models for different body weight traits show that maternal genetic and maternal permanent environmental influence were important for weaning weight. The proportion of maternal genetic variance was large for weaning (W42) and post-weaning (W70) weights. The maternal heritability ( $m^2$ ) for different body weight traits showed a decreasing trend with the advance of age. Gowane *et al.* (2010) also reported that the maternal genetic effects expressed during gestation and lactation are expected to have a diminishing influence on weight as the kits grow. Higher importance of maternal effect over additive genetic effect on the post weaning growth traits in rabbits had been reported earlier (Ferraz *et al.*, 1992; Lukefahr *et al.*, 1993). The  $m^2$  estimates were lower than  $h^2$  values of these traits. Similar result of  $m^2 < h^2$  was reported by Niranjana *et al.* (2010) in the Angora rabbit and Dige *et al.* (2012) in the New Zealand White rabbit. The maternal permanent environmental variance was also found to influence the early stage body weight traits (W42 and W70) more than the marketing weight. The moderate  $c^2$  estimate for weaning weight indicates the importance of maternal permanent environment and maternal care during the period from birth to weaning, as kits remained with their dams longer. The  $c^2$  estimates for these body weight traits also showed a decreasing trend with the advance of age. This was expected, as weaners became more independent of the doe with as they grew older. These observations were consistent with the higher maternal permanent environmental effect for growth traits at the initial stage which decreased in later stages (Ferrez *et al.*, 1992). Dige *et al.* (2012) also found that the maternal genetic and maternal permanent environmental effects were important for weight at 15, 30, 90 and 180 d in a laboratory-reared New Zealand White rabbit population. Similar findings were also reported by Abdel-Kafy *et al.* (2012) in Baladi Black rabbit. Contrary to the present study, several authors have reported that the direct genetic effect along with permanent environmental influence alone was important for body weight traits in different breeds of rabbits (Sorensen *et al.*, 2001 in Danish White; Piles *et al.*, 2004 in Spanish lines C & R; Iraqi, 2008 in Gabali and Bolet *et al.*, 2012 in Algerian synthetic rabbits). Results suggest that the maternal effects were maximum at weaning stage and accounted for a significant portion of the total genetic variance and then declined as the animal became independent of the mother, but contributed towards the variation for post-weaning and marketing weights.

The estimates of correlation between direct and maternal genetic effects ( $r_{am}$ ) were moderate to very high and negative for all body weight traits. In model 3, inflated  $h^2$  estimates were observed for all the traits, probably due to a very high negative covariance between direct and maternal effect. The high negative correlation between direct and maternal genetic effects is an indication of how difficult it is to simultaneously improve both these traits in a selection programme (Prakash *et al.*, 2012). This antagonism between the effects of an individual's genes for growth and those of its dam for a maternal contribution may arise from genes having antagonistic pleiotropic effects on maternal performance and offspring trait. Thus, by limiting an evolutionary response, it may act to maintain genetic variance after natural selection for an intermediate optimum (Wilson and Reale, 2006). The simple model overestimated additive genetic variation and potential for response to selection primarily by ignoring the negative correlation between direct and maternal genetic effects. Results suggest that due importance should be given to maternal effects in the selection programme, due to antagonism between direct and maternal genes. The direct maternal genetic correlation ( $r_{am}$ ) was significant and resulted in maximum likelihood for weaning as well as immediate post-weaning weights in the present study. Similar patterns of correlation among direct and maternal genetic effects were reported by Niranjana *et al.* (2010) in the Angora rabbit and Dige *et al.* (2012) in the New Zealand White rabbit.

The total heritability described by Willham (1972), which is calculated from the values of  $h^2$ ,  $m^2$  and  $r_{am}$  can be used to predict responses (Snyman *et al.*, 1995). For traits where maternal  $r_{am}$  effects are absent, direct heritability and total heritability will be the same. Estimates of  $h^2$  and  $t_m$  are sensitive to the model fitted. The low  $h^2$  of W42 can be attributed to high influence of maternal genetic and maternal permanent environmental effects on this trait. Moderate  $h^2$  and  $t_m$  of W70 indicates that the expected response to phenotypic selection would be moderate for this trait. Estimates of  $t_m$  were almost similar for all the models, suggesting consistent repeatability of doe performance across different models which included maternal effects. The moderate repeatability estimates reflect the consistency of the maternal performance and indicate that selection for marketing weight is possible only by culling of less productive dams. Slightly higher values of  $h^2$  and  $t_m$  for body weight traits were reported by Niranjana *et al.* (2010) and Dige *et al.* (2012). Similarly, another option to expect faster response would be to use both maternal and direct genetic breeding values for selection of animals in the traits where maternal influence is more evident.

### Growth efficiency traits

From the estimates, it seems that growth efficiency in terms of daily weight gain, relative growth rate and Kleiber ratio is moderately heritable and could be applied in selection for increasing growth efficiency. Earlier studies on heritability of post-weaning absolute growth rate or average daily gain reported a range between 0.16 and 0.64. The estimate of heritability obtained for ADG1 in the present study was higher than those found in New Zealand White, California synthetic, Spanish lines, Sinai Gabali, Algeria synthetic and Pannon White terminal line (Ayyat *et al.*, 1995; Piles and Blasco, 2003; Piles *et al.*, 2004; Iraqi, 2008; Bolet *et al.*, 2012; Gyovai *et al.*, 2012, respectively). The proportion of maternal genetic variance ( $m^2$ ) was comparatively smaller for ADG1 and the estimate was lower than the  $h^2$  value of the trait ( $m^2 < h^2$ ). Moderate  $h^2$  of ADGs indicated that the expected response to phenotypic selection would be moderate for these traits. The low  $t_m$  of ADGs can be attributed to high influence of maternal genetic effects on these traits. Moderate  $h^2$  and low  $t_m$  of RGRs and KRs suggested that the expected response to phenotypic selection would be moderate for these traits. The low  $t_m$  of RGRs and KRs can be attributed to strong influence of maternal permanent environmental effects on these traits. Selection for Kleiber ratio will improve the feed efficiency traits through its correlated improvement in average daily gain, with little effect on feed intake and live weight (Arthur *et al.*, 2001). Therefore, Kleiber ratio can be effectively used as a selection criterion in multi-trait selection programmes that will lead to an improved biological efficiency of a population.

### Correlation estimates

Precise estimates of genetic correlations are important to identify early available traits that could bring about change in desired traits through indirect selection and could provide scope for better selection intensity by selection in both the sexes. In the present study, strong positive correlations of weaning weight were found with weights at subsequent stages. The weaning weight also had a high heritability, so selection for the trait could bring about a good weight response when marketing. Selection can be done based on early traits (W42 or W70) to improve the later traits (W70 or W135), as the genetic and phenotypic correlations are high among these traits. The genetic correlations of weaning weight with subsequent post-weaning weights were generally reported as positive and medium to high in magnitude for New Zealand White breed (Bhushan *et al.*, 1998; Bhushan and Ahlawat, 1999) and crossbred involving White Giant, Soviet Chinchilla and Grey Giant breeds of rabbits (Rojan *et al.*, 2009). The magnitude of phenotypic correlations was lesser than for genetic correlations in the present study. Relevant literature on other breeds of rabbit also showed that the genetic correlations in general were higher than the phenotypic correlations for most of the growth traits.

Among the growth efficiency traits, selection can be practised based on early stage traits (RGR1 and KR1) to achieve improvement in later stage traits (RGR3 and KR3). The negative estimates among certain parameters could be due to the distinct seasonal fluctuations with respect to climate and nutrition prevailing in the study area. The negative phenotypic correlation could be due to possible genotype $\times$ environment interaction, where the animals with superior body weight during favourable nutrition could become inferior during harsh conditions. Among the body weights and growth efficiency traits, the positive correlations existing between the post-weaning body weights and average daily gains could be used for indirect selection on the early trait to achieve higher body weights at later ages which are economically important. Negative correlation among body weight traits and growth efficiency traits implies that different mechanisms are involved in expression of these traits at different stages of growth (Prakash *et al.*, 2012). Overall, high genetic correlation between W42-W70 (0.76), W42-W135 (0.76), W70-W135 (0.62), RGR1-RGR3 (0.77), RGR1-KR3 (0.68), RGR3-KR1 (0.65) and KR1-KR3 (0.61) clearly shows that performance of the kit at weaning and post-weaning can be considered a suitable indicator of growth and feed conversion efficiency at marketing age, hence either of the first 2 growth stage performances can be used for selection.

Overall from the results, the moderate to high estimates of direct heritability for body weights and growth efficiency traits suggest that the population of the New Zealand White rabbits can be improved through selection for economic meat production. Models which included maternal genetic and permanent environmental components with and without interaction revealed that maternal heritability was a major component responsible for maternal effect in body weight traits and maternal environment was a major component responsible for maternal effect in growth efficiency traits. Maternal heritability was evident for W42, W70 and ADG1, and hence the matter of concern for

genetic evaluation of weaning and post-weaning weights as well as post-weaning daily gain. Maternal permanent environmental effects were significant for most of the growth efficiency traits due to carryover effect of maternal care during weaning. Thus, inclusion of these effects for genetic evaluation is desirable, as ignorance of these effects leads to an inflated heritability estimate. Positive and high genetic correlations among the body weight traits show the scope of multi-trait selection for efficient meat production. The negative relationship among certain growth efficiency traits needs to be considered when planning a breeding strategy. Moreover, as the growth efficiency traits are derived traits, there will be no additional cost of indicating them in the selection index along with the body weights.

## CONCLUSIONS

In this study, genetic parameters for different growth traits were estimated for a closed population of New Zealand White rabbits. High genetic correlations between weaning weight and post-weaning weights suggest that the selection of animals at weaning can be a suitable criterion for the selection of the New Zealand White rabbits under sub-temperate conditions. Moderate heritability of growth traits indicates further scope for genetic improvement. Moderate repeatability reflects the consistency of maternal performance and indicates that selection for growth is possible only by culling the less productive dams. Inbreeding was on the rise, which might lead to reduction in additive genetic variance and heritability. Opening the herd with new animals would help to increase the genetic variability. This study can help in carrying out similar studies to meet the demand for animal protein in developing countries.

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