World Rabbit Science

World Rabbit Sci. 2024, 32: 161-174
https://doi.org/10.4995/wrs.2024.18562
WRSA, UPV, 2003

EVALUATING ANIMAL MODELS COMPRISING ADDITIVE GENETIC AND MATERNAL EFFECTS ON GROWTH TRAITS IN GERMAN ANGORA RABBIT

Abdul Rahim*, K. Sri Rajaravindra†, Rajni Chaudhary*, Om Hari Chaturvedi*, Gopal R. Gowane‡

*North Temperate Regional Station, ICAR-Central Sheep and Wool Research Institute, Garsa, Kullu (H.P.) 135141, India.
†ICAR-Directorate of Poultry Research (DPR), Rajendranagar, Hyderabad 500030, Telangana, India.
‡Division of Animal Genetics and Breeding, ICAR-National Dairy Research Institute, Karnal, India.

Abstract: This investigation was carried out to estimate the genetic parameters for German Angora rabbits using most appropriate animal model comprising additive and maternal effects. The pedigree information and data on growth traits were collected from 5221 rabbits, which descended from 699 does and 294 bucks over a period of 21 yr (2001–2021) kept at Northern Temperate Regional Station, Garsa, Kullu (Himachal Pradesh), India. The average daily gain (ADG) and Kleiber ratio (KR) were calculated at different age intervals. Analyses were carried out by restricted maximum likelihood procedure fitting six animal models with various combinations of direct and maternal effects. The best model was evaluated on the basis of a likelihood ratio test. Analysis revealed that the model including both direct and maternal genetic effects along with permanent effect of the dam was most suitable for all traits except for body weight (BW) at 6th wk of age, ADG from 6th to 12th wk of age and KR associated to ADG from 12th to 18th wk of age. The direct heritability estimates from the best model were ranged from, 0.34±0.05 to 0.49±0.05 for BW; 0.19±0.04, to 0.46±0.06 for ADG and 0.21±0.04 to 0.41±0.05 for KR, respectively. Direct heritability estimates were overestimated when maternal effects were ignored. Maternal effects on BW declined from 0.49±0.04 at weaning to 0.06±0.03 at 12th wk of age and 0.09±0.04 at 18th wk of age. Correlations between direct and maternal effects ranged from –0.44±0.15 to–0.52±0.14 for body weights, indicating biological antagonism between these effects. Genetic correlations among various growth traits were positive and high, indicating scope for correlated response in later expressed traits. Analysis revealed that maternal additive influences were only important until weaning, whereas permanent environmental maternal influences were present in all growth traits considered in this study. The moderate estimates of heritability for growth traits and Kleiber ratio of rabbit in this study indicate that rates of genetic progress may be possible for these traits by selection under the standard management system.

Key Words: direct heritability, German Angora rabbit, genetic correlation, growth traits, maternal effects.

INTRODUCTION

Angora rabbit farming is a profitable self-employment enterprise for small and marginal rural farmers. The profitability of Angora farming largely depends on fibre production and its production potential is much higher and priced 10 to 30 times more than that of sheep (Ossard *et al.*, 1995). Angora fibre is one of the finest speciality animal fibres, with its well-known reputation for fineness, lightness, softness and thermal insulation properties (Pokharna *et al.*, 2004). Rabbit meat is healthier than other meats due to its high protein content and low fat and cholesterol contents (Nistor *et al.*, 2013). German Angora is one of the heaviest varieties of Angora rabbit breed, with high prolificacy and a faster

Correspondence: A. Rahim, *choudhary633@gmail.com*. Received *October 2022 - July 2024.*
https://doi.org/10.4995/wrs.2024.18562

Cite as: Rahim A., Rajaravindra K.S., Chaudhary R., Chaturvedi O.M., Gowane G.R. 2024. Evaluating animal models comprising additive genetic and maternal effects on growth traits in German Angora rabbit. *World Rabbit Sci., 32: 161-174. https://doi.org/10.4995/wrs.2024.18562*

growth rate capability (Sarma *et al.*, 2020). Due to the shorter gestation period, genetic progress is expected to be achieved within a short time and selection of superior lines can be possible based on the sizeable number of progeny performances. Kit body weight (BW) is an economically important trait in rabbit production, as it is directly related to kit survivability and growth rate (Agea *et al.*, 2019 and Belabbas *et al.*, 2023). Measuring BW of rabbit at different intervals is important to assess the growth trajectory and health status of the herd. A strong positive correlation between the BW and wool yield dictates growth as a desirable trait for early selection in Angora rabbits in order to increase wool production (Singh *et al.*, 2008; Niranjan *et al.*, 2010; Rahim *et al.*, 2022). The cost of rabbit rearing can be reduced by enhancing growth rate during the early period, which directly enhances farmer's economy. Kleiber ratio (KR) is an important indicator of growth efficiency and can be expressed as the ratio of average daily gain (ADG) to metabolic BW. KR is a moderately heritable trait, has a strong correlation with growth traits and can be used to improve growth efficiency (Sakthivel *et al.*, 2017).

Growth traits are influenced by both direct and maternal components, which affect the phenotypic expression of the kit. To maximise accuracy of response to selection, it is necessary to estimate the unbiased genetic parameters, as bias of any kind will give unrealistic estimates. Likewise, accurate estimates of genetic parameters such as additive and residual variances are essential for prediction of breeding values using Best Linear Unbiased Prediction (BLUP). Biased genetic parameters also result in biased estimates of breeding values. Therefore, it is essential to evaluate different animal models to identify the most appropriate genetic model for evaluating the targeted traits (McGlothlin and Galloway, 2013). However, only a few studies have attempted to estimate genetic parameters accounting for direct and maternal effects on growth and wool traits in rabbits (Krogmeier *et al.*, 1994; Allain *et al.*, 1999; Niranjan *et al.*, 2010; Niranjan *et al.*, 2011; Sakthivel *et al.*, 2017). For genetic evaluation, unbiased estimates of the direct additive genetic, maternal genetic and maternal permanent (common) environmental components are very important for breed improvement programmes (Hanford *et al.*, 2006; Zhang *et al.*, 2008). Several reports have shown inflated direct heritability estimates when maternal effects were not included in the model (Mandal *et al.*, 2008; Sakthivel *et al.*, 2017; Magotra *et al.*, 2021). Thus, accurate estimation of (co)variance components is a prerequisite for designing any breed improvement programme and genetic evaluation system. There is no report related to genetic parameter estimates for KR and ADG gain in Angora rabbit. Therefore, the aim of the present study was to estimate the genetic parameters for BW, ADG and KR, as well as to obtain genetic and phenotypic correlations between these traits to formulate future selection plans for obtaining the desired response to selection in growth traits of German Angora rabbit.

MATERIALS AND METHODS

Ethical approval

The present study was conducted using phenotypic records maintained at Angora Rabbit Unit (ARU), North Temperate Regional Station, ICAR-Central Sheep and Wool Research Institute, Garsa, Kullu (Himachal Pradesh) India. There were no elements of intervention that caused any kind of stress during the non-invasive, non-interactive study. So, the research did not require any ethical approval.

Data description

The information utilised in the study was collected from the database of 5221 Angora rabbits maintained at the Angora Rabbit Unit (ARU) during the period from 2001 to 2021. The ARU is located at an altitude of 1400-2100 m above mean sea level at 31.28° North latitude and 77.20° east longitude. The climate is sub-temperate, with temperatures ranging from –4°C to 35°C and average annual rainfall is about 840 mm, mainly during the monsoon season.

Management practices

The flock was kept with optimum inputs under a conventional intensive rearing system in all-wire cages with provision of fresh drinking water and *ad libitum* feeding in the morning and evening. Animals were fed seasonal grasses *ad libitum* and concentrate (15 to 20% crude protein) in graded quantity from 90 to 220 g according to age, BW and lactation. Approximately 40 to 60 breeding females were kept each year, with a male to female ratio of 1:5. Each doe was brought for mating to the assigned breeding buck cage. Mating of closely related individuals was avoided as far as possible to keep inbreeding at the lowest level. Pregnant does were shifted to kindling cages 2-3 days before expected date of kindling and clean dry jute wool was provided for nesting. After kindling, the does were allowed to nurse their kits in the morning. Twenty days after birth, they were offered mashed concentrate diet until weaning. The lactating doe and kits were kept together in kindling nest box until weaning (42 d). Sexing was done at the time of weaning and ear tagging performed accordingly. Kits were properly identified by ear tagging and then gradually separated into individual wire cages of standard dimensions under similar housing and management practices (Rahim *et al.*, 2023). A standard prophylactic schedule and symptomatic treatment was adopted in disease management.

Recording of growth traits

The BW records of German Angora rabbit at weaning (BW6: 6^{th} wk of age) and post-weaning BW12, BW18, BW24 (12^{th}, 18^{th} and 24^{th} wk of age) were obtained for the period 2001 to 2021. The growth efficiency traits studied were ADG in grams ADG1 (from weaning to 12^{th} wk), ADG2 (from 12^{th} to 18^{th} wk), ADG3 (from 18^{th} to 24^{th} wk age), ADGT (from weaning to 24^{th} wk), and KR. The KR is the proportion of ADG to the metabolic BW and was calculated using the formula $ADG/BW^{0.75}$, where $BW^{0.75}$ denotes the metabolic BW at the older age of the period for which KR is calculated (Kleiber, 1947). KR traits used for genetic evaluation were: KR1 from weaning to 12^{th} wk ($ADG1/(BW12)^{0.75}$), KR2 from 12^{th} to 18^{th} wk ($ADG2/(BW18)^{0.75}$), KR3 from 18^{th} mo to 24^{th} wk ($ADG3/(BW24)^{0.75}$) and KRT from weaning to 24^{th} wk ($ADGT/(BW24)^{0.75}$).

Statistical analysis

Initially, the data were subjected to least squares analysis of variance using the general linear model in SPSS version 25.0 (IBM Corporation, 2019) to identify the major significant effects. These fixed effects were separated into seven periods of kindling, each lasting for three years [P1 (2001–2003), P2 (2004–2006), P3 (2007–2009), P4 (2010–2012), P5 (2013–2015), P6 (2016–2018), P7 (2019–2021)], kindling season (4 levels: January-March, April-June, July-September, October-December), sex of kit (2 levels: Male, female) and litter size at kindling (3 levels, *i.e.* up to 5, 6–8 and above 8). Only effects significantly affecting traits (P<0.05) were included in six different animal models to derive genetic parameter estimates using the Restricted Maximum Likelihood (REML) approach. WOMBAT was used to undertake univariate analyses for each of the twelve traits under consideration to select the best model (Meyer, 2007). The models used for estimating genetic parameters were as follows:

$$y=X\beta+Z_a a+e \quad (1)$$

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

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

$$y=X\beta+Z_a a+Z_c c+e \quad (4)$$

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

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

where y is the phenotypic record's vector; β, a, m, c and e are vectors for fixed, direct additive, maternal additive, maternal permanent environmental and residual effects, respectively. X, Z_a, Z_m and Z_c were their corresponding incidence matrices. A is the numerator relationship matrix and σ_{am} is the covariance between direct and maternal genetic effects. Assumptions for variance (V) and covariance (Cov) matrices involving random effects were $V(a) = A\sigma^2_a$, $V(m) = A\sigma^2_m$, $V(c) = I\sigma^2_c$, $V(e) = I\sigma^2_e$, and $Cov(a,m) = A\sigma_{am}$, where I is an identity matrix and σ^2_a, σ^2_m, σ^2_c and σ^2_e are direct additive, maternal additive, maternal permanent environmental and residual variances, respectively. The correlation between direct and maternal genetic effects (r_{am}) was estimated as $\sigma_{am}/(\sigma_a\times\sigma_m)$. Total heritability ($h^2_t$) was calculated by accounting for the maternal effects as $h_t^2=(\sigma_a^2+0.5\sigma_m^2+1.5\sigma_{am})/\sigma_p^2$ described by Willham (1972). The maternal repeatability across the year for doe performance (t_m) was calculated as $t_m=(1/4)h^2+m^2+c^2+mr_{am}h$ (Niranjan *et al.*, 2010). To select the best univariate model, we employed Likelihood Ratio Tests (LRT) 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-square distribution with degrees of freedom equal to the difference in the number of (co)variance components fitted for the two models. Subsequently, a series of bivariate analyses from the best model were carried out using WOMBAT to estimate genetic and phenotypic correlations among the studied traits.

RESULTS

The data structure and number of records in pedigree and summary statistics pertaining to various body weights, ADG and KR obtained in this study in German Angora rabbit are presented in Table 1. The coefficients of variations ranged from 12.27 to 25.28 % for body weights, 14.49 to 42.12% for ADGs and 8.47 to 40.14% for KRs. The coefficients of variation indicate that these traits are moderately to highly variables. Least square means and standard errors of various growth traits are presented in Table 2. The means (±standard deviation) for BW6, BW12, BW18, BW24, ADG1, ADG2, ADG3, ADGT, KR1, KR2, KR3 and KRT were 669±3.33 g, 1451±5.51 g, 2036±5.70 g, 2438±6.03 g, 18.41±0.09 g, 14.01±0.09 g, 9.43±0.09 g, 13.99±0.04 g, 13.82±0.05, 8.22±0.05, 4.82±0.04 and 7.16±0.01, respectively. Least squares analysis of variance revealed significant ($P<0.05$) influence of kindling period, kindling season, sex of kit and litter size at birth on several growth traits (Table 2). Kindling period had a significant effect ($P<0.01$) on all the studied traits. Kits born during the spring season had higher body weights recorded from weaning up to 24th wk of age followed by winter season and lowest during summer season. The male kits showed significantly higher growth at BW12, BW18, ADG1 and KR1 than their females. The litter size at birth significantly ($P<0.01$) affected the body weights at all ages (Table 2) and growth traits except ADGT. The body weight of kits gradually declined as the litter size at birth increased due to negative correlation between both traits.

(Co) variance components and genetic parameters estimated by different models for BW traits are presented in Table 3. The inclusive animal model-6 was most appropriate model for BW at different weeks of age except weaning weight as per the Likelihood ratio test (LRT) that included direct genetic, maternal genetic and maternal permanent environmental variation as random effects, including non-zero direct maternal genetic covariance.

Weaning weight at six weeks of age (BW6)

Results revealed that model 3 (including maternal genetic effect (m^2) in addition to direct additive variance for weaning weight) was the most appropriate model to analyse BW6. The likelihood was maximum for Model 3 due to addition of maternal genetic effect and because the covariance between direct and maternal genetic effects was not ignored. The direct heritability (h^2) estimates were 0.35±0.04 and corresponding maternal heritability was 0.49±0.04. The direct h^2 estimates ranged from 0.26±0.03 to 0.43±0.03 over different animal models for BW6. The overestimation of direct h^2(0.43±0.04) was due to ignorance of maternal effects in model 1. Reduction of direct h^2 in model 2 to 0.26±0.03 was due to further partition of genetic variance into maternal genetic variance component (0.37±0.02). The more comprehensive Model 5 gave estimates of h^2, m^2 and c^2 as 0.31±0.04, 0.05±0.03 and 0.22±0.03,

Table 1: Characteristics of data structure for growth traits in German Angora rabbit.

Traits	BW6	BW12	BW18	BW24	ADG1	ADG2	ADG3	ADGT	KR1	KR2	KR3	KRT
Number of records	5221	4876	4542	4237	4876	4542	4237	4237	4876	4542	4237	4237
Number of sires with progeny	294	294	288	282	294	288	282	282	294	288	282	282
Number of dams with progeny	629	623	613	602	623	613	602	602	623	613	602	602
Mean	679 g	1468 g	2042 g	2479 g	18.58 g	13.40 g	9.98 g	14.16 g	13.84	7.85	5.03	7.16
Standard error of the mean	2.37	4.11	4.43	4.67	0.07	0.06	0.06	0.03	0.03	0.03	0.03	0.01
Standard Deviation	171.53	286.93	298.27	304.09	4.66	4.18	4.20	2.05	2.25	2.32	2.02	0.61
Coefficient of variation (%)	25.28	19.55	14.61	12.27	25.07	31.20	42.12	14.49	16.22	29.54	40.14	8.47

BW6, body weight at 6th wk; BW12, body weight at 12th wk; BW18, body weight 18th wk and BW24, body weight at 24th wk; ADG1, average daily gain from 6th to 12th wk of age; ADG2, average daily gain from 12th to 18th wk of age; ADG3, average daily gain from 18th to 24th wk of age; ADGT, average daily gain from 6th to 24th wk of age; KR1, Kleiber ratio associated with ADG1; KR2, Kleiber ratio associated with ADG2; KR3, Kleiber ratio associated with ADG3; KRT, Kleiber ratio associated with ADGT.

Table 2: The least squares means±standard errors of various growth traits in German Angora rabbit.

Factors	N	BW6 (g)	BW12(g)	BW18(g)	BW24(g)	ADG1(g)	ADG2(g)	ADG3(g)	ADGT(g)	KR1	KR2	KR3	KRT
Overall	5521	669±3.33	1451±5.51	2036±5.70	2438±6.03	18.41±0.09	14.01±0.09	9.43±0.09	13.99±0.04	13.82±0.05	8.22±0.05	4.82±0.04	7.16±0.01
Kindling period		**	**	**	**	**	**	**	**	**	**	**	**
2001-2003	907	687^{b}±6.31	1534^{b}±10.34	2103^{c}±10.47	2496^{c}±11.04	20.00^{b}±0.17	13.76^{b}±0.16	9.40^{c}±0.17	14.38^{b}±0.08	14.42^{a}±0.09	7.89^{c}±0.09	4.73^{b}±0.08	7.23^{b}±0.02
2004-2006	1011	701^{b}±6.20	1560^{b}±10.17	2199^{b}±10.31	2626^{a}±10.94	20.26^{ab}±0.17	15.35^{a}±0.16	10.15^{ab}±0.17	15.28^{a}±0.08	14.43^{a}±0.08	8.54^{b}±0.09	4.91^{b}±0.08	7.40^{a}±0.02
2007-2009	904	675^{b}±5.96	1457^{c}±9.94	2108^{c}±10.34	2539^{b}±11.05	18.29^{c}±0.16	15.01^{a}±0.16	9.74^{c}±0.17	14.57^{b}±0.08	13.69^{b}±0.08	8.58^{b}±0.09	4.79^{b}±0.08	7.23^{b}±0.02
2010-2012	1190	600^{c}±5.36	1296^{e}±9.26	1833^{e}±9.74	2325^{d}±11.24	16.34^{d}±0.15	12.50^{b}±0.15	10.91^{a}±0.17	13.46^{c}±0.08	13.34^{c}±0.08	7.88^{c}±0.08	5.70^{a}±0.08	7.13^{b}±0.03
2013-2015	571	683^{b}±7.39	1365^{d}±12.20	1838^{e}±13.81	2228^{e}±15.03	16.01^{d}±0.20	12.34^{c}±0.21	9.72^{c}±0.23	12.52^{d}±0.11	12.65^{d}±0.10	7.80^{c}±0.12	5.31^{a}±0.11	6.85^{c}±0.03
2016-2018	171	765^{a}±12.51	1656^{a}±20.15	2266^{a}±20.08	2595^{b}±20.76	21.20^{a}±0.33	14.47^{a}±0.31	7.85^{d}±0.32	14.51^{b}±0.15	14.53^{a}±0.17	7.85^{c}±0.17	3.79^{d}±0.15	7.10^{b}±0.05
2019-2021	467	574^{d}±7.69	1288^{e}±12.73	1906^{d}±12.82	2256^{e}±13.42	16.74^{d}±0.21	14.65^{a}±0.20	8.26^{d}±0.21	13.25^{c}±0.09	13.69^{b}±0.10	9.01^{a}±0.11	4.47^{c}±0.10	7.18^{b}±0.03
Kindling season		**	**	**	**	**	**	NS	*	**	**	*	**
Winter	898	693^{a}±6.33	1470^{b}±10.42	2078^{ab}±10.62	2447^{a}±11.41	18.49^{c}±0.17	14.73^{a}±0.16	8.99±0.18	14.03^{bc}±0.08	13.73^{b}±0.09	8.57^{a}±0.09	4.60^{c}±0.08	7.16^{b}±0.03
Spring	3056	689^{a}±3.94	1496^{a}±6.46	2049^{a}±6.64	2457^{a}±7.28	19.09^{a}±0.11	12.93^{b}±0.10	9.51±0.11	13.93^{ac}±0.05	14.04^{a}±0.05	7.56^{c}±0.06	4.80^{b}±0.05	7.09^{b}±0.02
Summer	600	627^{c}±6.79	1377^{c}±11.07	1955^{c}±12.07	2363^{c}±12.66	17.79^{b}±0.18	14.20^{a}±0.19	9.58±0.20	13.87^{a}±0.09	13.92^{a}±0.09	8.53^{a}±0.11	4.98^{a}±0.09	7.25^{a}±0.03
Autumn	667	668^{b}±6.65	1460^{b}±11.87	2062^{a}±12.26	2484^{b}±13.10	18.24^{bc}±0.19	14.19^{a}±0.19	9.64±0.20	14.15^{b}±0.09	13.60^{b}±0.10	8.23^{b}±0.11	4.88^{a}±0.10	7.14^{b}±0.03
Sex of kits		NS	**	**	NS	**	NS	NS	NS	*	NS	NS	NS
Males	2696	672±4.02	1462^{a}±6.68	2046^{a}±6.88	2442±7.34	18.59^{a}±0.11	13.99±0.11	9.35±0.11	14.01±0.05	13.89^{a}±0.06	8.18±0.06	4.78±0.05	7.16±0.02
Females	2525	667±4.01	1440^{b}±6.62	2026^{b}±6.87	2434±7.27	18.22^{b}±0.11	14.04±0.11	9.52±0.11	13.98±0.05	13.76^{b}±0.05	8.27±0.06	4.85±0.05	7.16±0.02
Litter size group		**	**	**	**	**	**	**	NS	**	**	**	**
Up to 5	1963	715^{a}±4.28	1481^{a}±7.09	2058^{a}±7.37	2474^{a}±7.81	18.07^{b}±0.12	13.86^{b}±0.11	9.79^{a}±0.12	13.94±0.06	13.38^{b}±0.06	8.06^{b}±0.06	4.95^{a}±0.06	7.06^{b}±0.02
5-8	2689	660^{b}±3.93	1446^{ab}±6.50	2024^{b}±6.80	2443^{a}±7.17	18.50^{a}±0.11	13.76^{b}±0.11	9.77^{a}±0.11	14.07±0.05	13.93^{a}±0.05	8.11^{b}±0.06	5.00^{a}±0.05	7.19^{a}±0.02
Above 8	589	634^{c}±6.94	1425^{b}±11.51	2026^{b}±11.77	2396^{b}±12.70	18.65^{a}±0.19	14.42^{a}±0.18	8.73^{b}±0.20	13.97±0.09	14.15^{a}±0.09	8.50^{a}±0.10	4.49^{b}±0.09	7.23^{a}±0.03

BW6, body weight at 6th wk; BW12, body weight at 12th wk; BW18, body weight 18th wk and BW24, body weight at 24th wk; ADG1, average daily gain from 6th to 12th wk of age; ADG2, average daily gain from 12th to 18th wk of age; ADG3, average daily gain from 18th to 24th wk of age; ADGT, total average daily gain from 6th to 24th wk of age; KR1, Kleiber ratio associated with ADG1; KR2, Kleiber ratio associated with ADG2; KR3, Kleiber ratio associated with ADG3; KRT, Kleiber ratio associated with ADGT; NS, non-significant (P>0.05); Means bearing different superscripts in each subclass within a column differ significantly from another; *P<0.05; **P<0.01.

Table 3: (Co)variance components and genetic parameter estimates of growth traits in German Angora rabbit.

Traits	Model	σ^2_a	σ^2_m	σ_{am}	σ^2_c	σ^2_e	σ^2_p	h^2_d±SE	m^2±SE	c^2±SE	r_{am}	h^2_t	t_m	Log L
BW6	1	12 288.20				15 985.80	28 274.00	0.43±0.03				0.43	0.11	−28 883.88
	2	9314.43	13 217.60			13 324.80	35 856.80	0.26±0.03	0.37±0.02			0.44	0.43	−28 689.89
	3	11 955.00	16 748.00	−6670.40		12 037.00	34 069.20	0.35±0.04	0.49±0.04		−0.47±0.07	0.30	0.38	−28 677.06
	4	9826.70			7816.60	12 975.00	30 618.30	0.32±0.04		0.26±0.02		0.32	0.34	−28 661.30
	5	9614.07	1504.99		6756.36	13 049.00	30 924.40	0.31±0.04	0.05±0.03	0.22±0.03		0.34	0.34	−28 659.45
	6	12 416.00	4500.70	−5585.20	6846.41	11 646.60	82 883.80	0.42±0.05	0.15±0.04	0.23±0.03	−0.75±0.09	0.22	0.30	−28 645.88
BW12	1	28 780.50				43 485.40	72 265.90	0.40±0.03				0.40	0.10	−29 305.74
	2	20 611.70	23 696.30			39 296.70	83 604.70	0.25±0.04	0.28±0.24			0.39	0.34	−29 188.16
	3	23 755.00	26 524.00	−5654.50		37 759.80	82 384.90	0.29±0.05	0.32±0.03		−0.23±0.11	0.45	0.33	−29 186.74
	4	21 693.40			14 854.40	38 333.20	74 880.90	0.29±0.04		0.20±0.02		0.29	0.27	−29 162.54
	5	21 192.00	1893.19		13 544.30	38 541.00	75 170.50	0.28±0.04	0.03±0.03	0.18±0.03		0.29	0.28	−29 161.91
	6	25 119.00	4336.80	−5214.200	13 726.10	36 573.00	74 540.40	0.34±0.05	0.06±0.03	0.18±0.03	−0.50±0.18	0.26	0.26	−29 159.96
BW18	1	33 151.10				39 619.70	72 770.80	0.46±0.03				0.46	0.11	−27 244.97
	2	26 803.40	22 058.80			35 062.10	83 924.30	0.32±0.04	0.26±0.02			0.45	0.34	−27 147.61
	3	31 692.00	26 470.00	−8208.80		32 593.90	82 547.60	0.38±0.05	0.32±0.04		−0.28±0.10	0.40	0.32	−27 145.00
	4	27 992.50			13 956.80	34 264.50	76 213.80	0.37±0.04		0.18±0.02		0.37	0.27	−27 134.44
	5	27 367.80	3878.03		11 355.60	34 463.50	77 064.90	0.35±0.04	0.05±0.03	0.15±0.03		0.38	0.29	−27 132.83
	6	31 889.00	7166.20	−6604.40	11 569.70	32 168.10	76 188.80	0.42±0.06	0.09±0.04	0.15±0.03	−0.44±0.15	0.34	0.26	−27 130.61
BW24	1	39 942.60				38 452.00	78 394.60	0.51±0.03				0.51	0.13	−25 514.86
	2	35 490.20	27 711.60			31 412.40	94 614.10	0.38±0.04	0.29±0.03			0.52	0.39	−25 410.77
	3	40 586.00	32 404.00	−10 387.00		28 933.30	91 535.80	0.44±0.05	0.35±0.04		−0.29±0.09	0.45	0.35	−25 406.92
	4	35 808.00			17 156.30	31 154.70	84 119.00	0.43±0.04		0.20±0.02		0.43	0.31	−25 397.43
	5	35 705.40	3930.58		14 485.50	31 095.60	85 217.00	0.42±0.04	0.05±0.04	0.17±0.03		0.44	0.32	−25 396.50
	6	40 783.00	7918.60	−9268.90	14 852.50	28 598.30	82 883.80	0.49±0.05	0.10±0.04	0.18±0.03	−0.52±0.04	0.37	0.29	−25 392.73

BW6, body weight at 6th wk or weaning; BW12, body weight at 12th wk; BW18, body weight 18th wk; BW24, body weight at 24th wk; σ^2_a, Direct additive genetic variance; σ^2_m, Maternal additive genetic variance; σ_{am}, Direct maternal covariance; σ^2_c, Maternal common (permanent) environmental variance; σ^2_e, Residual variance; σ^2_p, Phenotypic variance; h^2_d, direct heritability; SE, Standard error; m^2, Maternal heritability (σ^2_m / σ^2_p); c^2, ratio of maternal permanent effects to phenotypic variance (σ^2_c / σ^2_p); r_{am}, correlation between direct and maternal genetics variance; h^2_t, total heritability; t_m, repeatability of doe performance; Log L, Log likelihood value; Bold rows represent the estimates from best model as per LRT.

respectively. However, these models were not superior to Model 3, as there was no increment in log likelihood value. The likelihood ratio test did not show difference between Models 4, 5 and 6. The estimates of repeatability of doe performance (t_m) for weaning weight were moderate (from 0.11 to 0.43). The total heritability (h_t^2) ranged from 0.22 to 0.44 over different models for weaning weight.

Post-weaning growth traits for BW (BW12, BW18 and BW24)

Analysis for the (co)variance components along with log likelihood estimates for post-weaning weights (BW12, BW18 and BW24) for all models are presented in Table 3. The present results indicate that, Model-6 yielded better estimates for all post-weaning weights, which includes all the effects (direct, maternal genetic and permanent environmental components) along with the covariance between the direct and maternal genetic effects to explain the variability. Direct heritability estimates from the best Model were 0.34±0.05, 0.42±0.06 and 0.49±0.05 and their corresponding maternal heritabilities were 0.06±0.03, 0.09±0.04 and 0.10±0.04 at 12, 18 and 24 wk of age, respectively. Maternal permanent environment (c^2) estimates ranged from 0.15 to 0.18 across the age. Maternal genetic effect was most evident during weaning stage. Estimates of h^2, m^2 and c^2 for post-weaning weights from the inclusive model-6 were 0.34±0.05, 0.06±0.03 and 0.18±0.03, respectively, for BW12; 0.42±0.06, 0.09±0.04 and 0.15±0.03, respectively for BW18 and 0.49±0.05, 0.10±0.04 and 0.18±0.03, respectively for BW24. Negative and high correlation between direct and maternal genetic effects was observed for post-weaning weights from best models that included σ_{am}. The total heritabilities for BW12, BW18 and BW24 were 0.26, 0.34 and 0.37, respectively. Moderate repeatability of doe performance was 0.26, 0.26 and 0.29 for BW12, BW18 and BW24.

ADG and KR

The estimates of variance components and heritability for ADG and KR are shown in Table 4. Based on the logarithm of the likelihood function, Model-4 was best for ADG1 and KR2, whereas Model-6 was the best for ADG2, ADG3, ADGT, KR1, KR3 and KRT. The direct heritability estimates of the ADG from the best models were 0.19±0.04, 0.30±0.05, 0.38±0.06 and 0.46±0.06 for ADG1, ADG2, ADG3 and ADGT, respectively and direct heritabilities estimates of KR1, KR2, KR3 and KRT were 0.23±0.05, 0.21±0.04, 0.37±0.06 and 0.41±0.05, respectively. Maximum likelihood values for ADG1 and KR2 were obtained due to addition of maternal permanent environmental effect to direct genetic effect (Model 4), which contributed 13% and 12% of total phenotypic variance. The direct h^2 estimates were similar to the total h^2 estimates and slightly higher than c^2 values for these traits. The comprehensive animal model (Model 6) with inclusion of all the effects along with covariance between the direct and maternal genetic effects had the maximum likelihood value to explain the variation for all traits except ADG1 and KR2. Estimates of correlation between direct and maternal genetic effects were negative for all the traits studied except ADG1. The estimates of h_t^2 ranged from 0.19 to 0.74 for ADGs, 0.16 to 0.47 for KRs and t_m for the respective traits ranged from 0.14 to 0.25 and 0.15 to 0.27, respectively.

Genetic and phenotypic correlations

Estimates of genetic and phenotypic correlations among various growth traits are presented in Table 5. Genetic and phenotypic correlations between BW traits were positive and high in magnitude associated with low standard errors. Genetic correlations were larger than the majority of corresponding phenotypic correlations. The largest relationship was found between chronologically adjacent body weights. Genetic correlations between body weights under consideration ranged from 0.48±0.06 (BW6-BW12) to 0.88±0.02 (BW18-BW24) and phenotypic correlations ranged from 0.51±0.02 (BW6-BW12) to 0.85±0.01 (BW12-BW18), respectively. ADG1 had negative genetic and phenotypic correlations with ADG2 and ADG3. However, the genetic correlation between ADG1 and ADG3 estimates was close to zero. Genetic correlation estimates among KR traits studied were positive and low (0.08±0.07) to high (0.72±0.07) magnitude except KR1-KR2. The phenotypic correlations between KR1-KR2 and KR1-KR3 were found to be negatively correlated. However, other traits showed positive correlation with each other, with values ranging from as low as 0.02±0.02 to as high as 0.64±0.07. BW6 was negatively correlated with post-weaning ADG and KR except ADG1 and KR1, whereas BW24 was positively correlated with ADG and KR for both genetic and phenotypic correlations. BW18 was positively correlated with ADG and KR except ADG3 and KR3.

Table 4: (Co)variance components and genetic parameter estimates of growth rate and Kleiber ratio in German Angora rabbit.

Traits	Model	σ_a^2	σ_m^2	σ_{am}	σ_c^2	σ_e^2	σ_p^2	h_d^2±SE	m^2±SE	c^2±SE	r_{am}	h_t^2	t_m	Log L
ADG1	1	6.57	-		-	12.79	19.37	0.34± 0.03	-	-		0.34	-	–9381.37
	2	3.84	3.37		-	12.95	20.15	0.19± 0.04	0.17 ± 0.02	-		0.27	0.21	–9334.70
	3	3.66	3.2	0.33	-	13.03	20.22	0.18±0.04	0.16±0.03	-	0.10±0.18	0.28	0.16	–9334.59
	4	3.68	-		2.48	12.88	19.04	0.19±0.04	-	0.13±0.02		0.19	0.18	–9320.20
	5	3.66	0.06		2.44	12.89	19.05	0.19±0.04	0.003±0.02	0.13±0.02		0.19	0.18	–9320.19
	6	3.58	0.02	0. 01	2.41	12.93	19.06	0.19±0.04	0.001±0.02	0.13±0.02	0.41*	0.29	0.18	–9320.17
ADG2	1	5.56	-		-	11.45	17.02	0.33±0.03	-	-		0.33	-	–8460.94
	2	4.17	2.19		-	11.34	17.69	0.24±0.04	0.12±0.02	-		0.20	0.18	–8440.09
	3	4.96	2.94	–1.24	-	10.92	17.58	0.28±0.05	0.17±0.03	-	–0.32±0.13	0.50	0.17	–8438.40
	4	3.85	-		1.8	11.3	16.94	0.23±0.04	-	0.11±0.02		0.23	0.16	–8423.16
	5	3.85	0.001		1.81	11.3	16.95	0.23±0.04	0.00±0.02	0.11±0.02		0.23	0.16	–8423.16
	6	5.1	0.38	–1.38	2.1	10.65	16.85	0.30±0.05	0.02±0.02	0.12±0.02	–0.99±0.39	0.30	0.14	–8419.59
ADG3	1	5.74	-		-	12.21	17.95	0.32±0.03	-	-		0.37	-	–8021.91
	2	4.57	5.06		-	10.8	20.43	0.22± 0.04	0.25± 0.03	-		0.35	0.30	–7938.89
	3	6.91	7.3	–3.97	-	9.6	19.85	0.35±0.05	0.37±0.04	-	–0.56±0.08	0.23	0.25	–7926.14
	4	4.6	-		3.33	10.73	18.66	0.25±0.04	-	0.18±0.02		0.25	0.24	–7926.06
	5	4.55	0.92		2.72	10.71	18.9	0.24±0.04	0.05±0.03	0.14±0.03		0.27	0.25	–7924.82
	6	7.14	2.83	–3.58	2.86	9.37	18.62	0.38±0.06	0.15±0.05	0.15±0.03	–0.80 ±0.09	0.34	0.21	–7911.73
ADGT	1	1.68	-		-	2.1	3.78	0.44± 0.03	-	-		0.44	-	–4586.72
	2	1.4	1.23		-	1.81	4.45	0.32± 0.04	0.28± 0.03	-		0.45	0.36	–4498.81
	3	1.8	1.61	–0.72	-	1.62	4.3	0.42±0.05	0.37±0.04	-	–0.42±0.08	0.35	0.31	–4490.3
	4	1.49	-		0.78	1.75	4.02	0.37±0.04	-	0.19±0.02		0.37	0.29	–4476.26
	5	1.49	0.001		0.78	1.75	4.02	0.37± 0.04	0.000±0.03	0.19±0.03		0.37	0.29	–4476.26
	6	1.8	0.19	–0.48	0.81	1.6	3.92	0.46±0.06	0.05±0.04	0.21±0.03	–0.81±0.23	0.74	0.25	–4470.88

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KR1	1	1.7	-		-	3.23	4.94	0.35± 0.03	-	-		0.35	-	–6051.56
	2	1.03	0.81		-	3.28	5.13	0.20± 0.04	0.16± 0.02	-		0.28	0.21	–6011.33
	3	1.22	1.07	–0.42	-	3.19	5.06	0.24±0.05	0.21±0.03	-	–0.37±0.13	0.22	0.19	–6009.21
	4	0.87	-		0.62	3.33	4.82	0.18±0.04	-	0.13±0.02		0.18	0.17	–5997.34
	5	0.72	0.001		0.61	3.19	4.52	0.16±0.04	0.000±0.02	0.14±0.03		0.18	0.17	–5997.34
	6	1.11	0.21	–0.48	2.29	3.2	4.76	0.23±0.05	0.05±0.03	0.15±0.02	–0.99±0.18	0.16	0.15	–5993.19
KR2	1	1.76	-		-	3.6	5.36	0.33± 0.03	-	-		0.33	-	–5845.27
	2	1.21	0.83		-	3.57	5.61	0.22± 0.04	0.15± 0.02	-		0.33	0.29	–5815.65
	3	1.36	0.99	–0.29	-	3.49	5.56	0.25±0.05	0.18±0.03	-	–0.25±0.14	0.26	0.19	–5814.69
	4	1.12	-		0.66	3.55	5.34	0.21±0.04	-	0.12±0.02		0.21	0.18	–5797.48
	5	1.13	0.001		0.69	3.57	5.39	0.21±0.04	0.000±0.03	13±0.02		0.21	0.18	–5797.48
	6	1.41	0.08	–0.33	0.73	3.4	5.3	0.27±0.05	0.02±0.02	0.14±0.02	–0.96±0.53	0.28	0.04	–5795.16
KR3	1	1.27	-		-	2.82	4.08	0.31±0.02	-	-		0.31	-	–4902.87
	2	0.97	1.11		-	2.52	4.6	0.55±0.03	0.21±0.02	-		0.29	0.38	–4822.91
	3	1.50	1.64	–0.90	-	2.25	4.49	0.34±0.06	0.36±0.04	-	–0.57±0.08	0.22	0.25	–4811.09
	4	0.99	-		0.73	2.50	4.22	0.24±0.04	-	0.17±0.02		0.23	0.23	–4809.38
	5	0.97	0.19		0.61	2.50	4.27	0.23±0.04	0.05±0.03	0.14±0.03		0.25	0.24	–4808.15
	6	1.56	0.64	–0.79	0.63	2.19	4.22	0.37±0.06	0.15±0.05	0.15±0.03	–0.79±0.09	0.32	0.20	–4796.34
KRT	1	0.14	-		-	0.22	0.36	0.38± 0.03	-	-		0.31	-	292.001
	2	0.11	0.15		-	0.22	0.45	0.24±0.03	0.34± 0.03	-		0.41	0.40	415.357
	3	0.16	0.2	–0.95	-	0.16	0.42	0.37±0.05	0.47±0.04	-	–0.54±0.07	0.27	0.34	431.076
	4	0.12	-		0.09	0.18	0.39	0.30±0.04	-	0.24±0.02		0.30	0.41	450.714
	5	0.12	0.001		0.09	0.18	0.4	0.29±0.03	0.003± 0.03	0.25±0.03		0.30	0.32	439.428
	6	0.15	0.03	–0.06	0.09	0.16	0.38	0.41±0.05	0.08±0.04	0.25±0.03	–0.92±0.14	0.47	0.27	462.387

ADG1, average daily gain from 6th to 12th wk of age; ADG2, average daily gain from 12th to 18th wk of age; ADG3, average daily gain from 18th to 24th wk of age; ADGT, total average daily gain from 6th to 24th wk of age; KR1, Kleiber ratio associated with ADG1; KR2, Kleiber ratio associated with ADG2; KR3, Kleiber ratio associated with ADG3; KRT, Kleiber ratio associated with ADGT; σ^2_a, Direct additive genetic variance; σ^2_m, Maternal additive genetic variance; σ_{am}, Direct maternal covariance; σ^2_c, Maternal common (permanent) environmental variance; σ^2_e, Residual variance; σ^2_p, Phenotypic variance; h^2_d, direct heritability; S.E., Standard error; m^2, Maternal heritability (σ^2_m / σ^2_p); c^2, ratio of maternal permanent effects to phenotypic variance (σ^2_c / σ^2_p); r_{am}, correlation between direct and maternal genetics variance; h^2_t, total heritability; t_m, repeatability of doe performance; Log L, Log likelihood value; Bold rows represent the estimates from best model as per LR; *Indicates that the approximation used to define standard errors of parameter estimates failed.

Table 5: Estimates of heritability (at diagonal) and genetics (above diagonal) and phenotypic (below diagonal) correlation±standard error among various traits in German Angora rabbit from bivariate analysis.

Traits	BW6	BW12	BW18	BW24	ADG1	ADG2	ADG3	ADGT	KR1	KR2	KR3	KRT
BW6	0.32 ±0.03	0.87 ±0.03	0.71 ±0.04	0.48 ±0.06	0. 51 ±0.09	–0.02 ±0.09	–0.29 ±0.07	–0.03 ±0.07	0.34 ±0.08	–0.37 ±0.06	–0.36 ±0.07	–0.60 ±0.04
BW12	0.77 ±0.01	0.28 ±0.03	0.85 ±0.03	0.71 ±0.05	0.77 ±0.03	–0.19 ±0.07	–0.16 ±0.07	0.33 ±0.06	0.30 ±0.07	–0.51 ±0.05	–0.29 ±0.07	–0.23 ±0.07
BW18	0.67 ±0.01	0.85 ±0.01	0.34 ±0.04	0.88 ±0.02	0.61 ±0.05	0.45 ±0.05	–0.09 ±0.07	0.57 ±0.04	0.19 ±0.07	0.04 ±0.07	–0.31 ±0.06	0.06 ±0.07
BW24	0.51 ±0.02	0.63 ±0.01	0.80 ±0.01	0.40 ±0.04	0.54 ±0.05	0.42 ±0.06	0.49 ±0.06	0.81 ±0.02	0.15 ±0.07	0.09 ±0.07	0.24 ±0.07	0.36 ±0.06
ADG1	0.23 ±0.02	0.82 ±0.01	0.57 ±0.01	0.44 ±0.02	0.19 ±0.03	–0.14 ±0.08	–0.04 ±0.14	0.44± 0.10	0.75 ±0.05	–0.32 ±0.11	–0.14 ±0.13	0.26 ±0.08
ADG2	–0.12 ±0.02	–0.27 ±0.02	0.39 ±0.02	0.32 ±0.02	–0.30 ±0.02	0.25 ±0.04	0.20 ±0.12	0.59 ±0.08	0.03 ±0.12	0.91 ±0.02	0.05 ±0.12	0.49 ±0.07
ADG3	–0.20 ±0.02	–0.21 ±0.02	–0.27 ±0.02	0.44 ±0.02	–0.12 ±0.02	–0.05 ±0.02	0.24 ±0.04	0.75 ±0.06	0.20 ±0.14	0.20 ±0.12	0.96 ±0.08	0.65 ±0.06
ADGT	–0.14 ±0.18	0. 25 ±0.02	0.43 ±0.03	0.80 ±0.01	0.41 ±0.02	0.42 ±0.02	0.60 ±0.01	0.37 ±0.04	0.41 ±0.06	0.30 ±0.07	0.47 ±0.06	0.61 ±0.08
KR1	–0.37 ±0.03	0.36 ±0.02	0.23 ±0.02	0.20 ±0.02	0.83 ±0.01	–0.21 ±0.02	–0.01 ±0.02	0.43 ±0.02	0.22 ±0.04	–0.22 ±0.08	0.08 ±0.07	0.61 ±0.50
KR2	–0.36 ±0.03	–0.61 ±0.02	0.04 ±0.02	0.03 ±0.02	–0.53 ±0.01	0.90 ±0.01	–0.03 ±0.02	0.23 ±0.02	–0.30 ±0.02	0.24 ±0.04	0.13 ±0.08	0.50 ±0.09
KR3	–0.32 ±0.02	–0.06 ±0.02	–0.41 ±0.02	0.24 ±0.02	–0.23 ±0.02	–0.12 ±0.02	0.98 ±0.01	0.45 ±0.02	–0.04 ±0.02	0.02 ±0.02	0.23 ±0.04	0.72 ±0.07
KRT	–0.64 ±0.02	–0.27 ±0.03	0.02 ±0.02	0.33 ±0.02	0.23 ±0.02	0.39 ±0.02	0.51 ±0.02	0.82 ±0.07	0.57 ±0.02	0.64 ±0.07	0.53 ±0.01	0.30 ±0.04

BW6, body weight at 6^{th} wk; BW12, body weight at 12^{th} wk; BW18, body weight 18^{th} wk and BW24, body weight at 24^{th} wk; ADG1, average daily gain from 6^{th} to 12^{th} wk of age; ADG2, average daily gain from 12^{th} to 18^{th} wk of age; ADG3, average daily gain from 18^{th} to 24^{th} wk of age; ADGT, average daily gain from 6^{th} to 24^{th} wk of age; KR1, Kleiber ratio associated with ADG1; KR2, Kleiber ratio associated with ADG2; KR3, Kleiber ratio associated with ADG3; KRT, Kleiber ratio associated with ADGT.

DISCUSSION

The overall least squares means obtained in the present study were comparable with earlier reports for weaning and post-weaning weights at different weeks of age (Singh *et al.*, 2004; Niranjan *et al.*, 2010; David *et al.*, 2015; Assad *et al.*, 2017), ADG gain (Xian-bo *et al.*, 2014; Sakthivel *et al.*, 2017) and KR (Sakthivel *et al.*, 2017). Least square means of body weights increased with age, while growth rates (ADGs and KRs) at different weeks of ages decreased with age. This may be due to the rapid growth of kits at young ages. The coefficient of variation ranged from 8.47 (KRT) to 42.12% (ADG3) and similar results were reported by Niranjan *et al.*, 2010 and Sakthivel *et al.*, 2017 in rabbits. Least squares analysis of variance revealed that all the fixed effects were found to be significant on different traits studied, with few exceptions. Present estimates agree with those obtained in different breeds of rabbits (Belhadi *et al.*, 2002; Gupta *et al.*, 2002; Ghosh *et al.,*2008; Niranjan *et al.*, 2010; Sivakumar *et al.*, 2012; Dige *et al.*,2012; Rojan *et al.*, 2017; Sakthivel *et al.*, 2017; Rahim *et al.*, 2022). The differences could be attributed to the variation in environmental conditions such as temperature, humidity, rainfall, disease outbreaks, change in feeding practices and breeding strategies that prevailed over the years. The lower performance of kits born in larger sized litters could be due to competition of foetuses for nutrients and space during the pregnancy and lactation period (Gupta *et al.*, 2002).

The traits in this study were moderately heritable in nature. This augurs that there is scope for selection of the traits. The direct heritability estimates were in accordance with previous reports in German Angora and New Zealand White rabbit (Singh *et al.*, 2008; Niranjan *et al.*, 2010; Niranjan *et al.*, 2011; David *et al.*, 2015; Sakthivel *et al.*, 2017). The direct heritability and corresponding maternal heritability estimates were a little inflated due to negative estimate of covariance between animal and maternal genetic effects. Similarly, a moderate to high estimate of c^2 indicated the importance of maternal care during lactation age, as kits remain with their dams for longer and this corroborates earlier findings (Iraqi, 2008; Niranjan *et al.*, 2010; Sakthivel *et al.*, 2017). In the current study, maternal influences on weaning weight comprised both maternal genetic effects and maternal common environmental effects (c^2). We found that m^2 for BW6 explained 49% of the overall phenotypic variance. The m^2 component represents the genetic component of the mother that is passed down to the kit and expressed when the kit becomes a dam. The maternal permanent environment and maternal genetics define the competition among the individual foetuses in the uterus, the limited capacity of a doe to provide nutrients and space to a large number of kits in her womb during pregnancy and the lack of sufficient milk during lactation stage, all of which have a significant impact on the kit's overall development. The moderate estimate of total heritability and repeatability of doe performance in this study was comparable with the results of New Zealand white rabbit (Sakthivel *et al.*, 2017; Dige *et al.*, 2012). The covariance between direct and maternal effect has biological antagonism, which was also revealed in our findings. This was in accordance with the estimate obtained by Niranjan *et al.*, 2010, although in contrast to Sakthivel *et al.*, 2017.

In case of post-weaning body weights, the estimated heritabilities were moderate to high in the present study, which was similar to the earlier estimates reported by Xian-bo *et al.* (2014) for New Zealand White rabbits and Dutch breeds of rabbits (Akanno and Ibe, 2005). However, Niranjan *et al.*, 2010 reported lower estimates at 6 (0.25±0.05), 12 (0.17±0.05), 18 (0.21±0.06) and 24 (0.12±0.05) weeks BW than the present study in German Angora rabbit. Lower estimates for BW12 than in the present study were also reported by Khalil *et al.*, (2000) for New Zealand white rabbit and Californian rabbits and Iraqi *et al.* (2002) for purebred and crossbred rabbits. Analysis revealed that direct heritability at weaning (0.35 from Model 3) was similar to the value of 0.34 obtained at BW12, but that the heritability subsequently increased to 0.42 at BW18 and 0.49 at BW24 indicating the importance of direct additive effects on BW with advancement of age. Other studies (Dige *et al.*, 2012; Xian-bo *et al.*, 2014; Farouk *et al.*, 2022) also confirmed that overall heritability estimate increased as the age advanced. Moderate to high h^2 estimates for weaning and post-weaning body weights revealed the presence of sizable additive genetic variance, implying the possibility of selection in these traits for further genetic improvement. Maternal heritability estimates ranged from high (0.49) at weaning to low at post-weaning body weights (0.06, 0.09 and 0.10), highlighting the importance of maternal influences on animal growth. Maternal influence was found to be maximum at weaning stage and its contribution considerably dropped after weaning. Similar trends were reported by Niranjan *et al.*, 2010; Dige *et al.*, 2012; Sakthivel *et al.*, 2017 and Abdel-Kafy *et al.*, 2021.

The m^2 values were lower than the estimates of h^2 for post-weaning body weights and are consistent with previous reports of Niranjan *et al.* (2010) in this breed and Dige *et al.* (2012) in the New Zealand White rabbit. This was anticipated when weaners grew older and were less dependent on does. Several authors reported a higher maternal genetic heritability and permanent environment effect for growth traits at the initial stage, which significantly decreased in the magnitude of the maternal genetic influence in latter stages (Ferraz *et al.*, 1992; Niranjan *et al.*, 2010; Dige *et al.*, 2012; Sakthivel *et al.*, 2017; Abdel-Kafy *et al.*, 2021 and Farouk *et al.*, 2022). All the body weights had high and negative r_{am} and revealed an unfavourable association for the direct and maternal direct effects (–0.23 to –0.52) and were similar to growth and wool traits in German Angora (Niranjan *et al.*, 2010; Niranjan *et al.*, 2011). Genes with antagonistic pleiotropic effects on maternal performance and the growth traits could cause negative r_{am} (Wilson and Reale, 2006). Post-weaning weights in this breed had moderate to high total heritability, ranging from 0.26 to 0.38.

The direct heritability estimates of ADG and KR were moderate to high in the present study. The present findings of direct h^2 estimated were in accordance with estimates in New Zealand white rabbits using REML method (Iraqi, 2008; Xian-bo *et al.*, 2014; Sakthivel *et al.*, 2017). Most of the reported heritabilities for weaning and post-weaning body weights and other growth-related traits of this breed were estimated mainly by paternal half-sib method based on ratios of variance components without taking into consideration the maternal effects. With the advancement of age, the constraints faced at weaning age do not exist at post-weaning weight and impacts of permanent environmental maternal influences existed at all growth traits considered in present study.

In the current study, weaning weight had strong and positive additive genetic as well as phenotypic correlations with different post-weaning weights indicating the usefulness of early BW as selection criterion for genetic improvement of BW at later ages. Similar results for positive and medium to high correlation were also reported by Bhushan *et al.*, 1998; Bhushan and Ahlawat,1999; Rojan *et al.*, 2009; Xian-bo *et al.*, 2014; Sakthivel *et al.*, 2017 in different rabbit breeds. A high genetic correlation between weaning weight and wool yields was reported by Niranjan *et al.*, 2011;

Singh *et al.*, 2006 and Qinyu, 1992 in German Angora rabbit, indicating that individuals with weaning weight above mean would often indicate superior genetic merit for wool production (Niranjan *et al.*, 2011). Weaning weight had a low to moderate negative correlation with ADG and KR except ADG1 and was consistent with the findings of Sakthivel *et al.*, 2017 in New Zealand white rabbit. However, BW24 had a positive correlation with all these traits. Sakthivel *et al.*, 2017 reported positive genetic correlation ADGs with BW at 35 wk of age and negative with KRs in New Zealand white rabbit. Genetic and phenotypic correlations among ADGs were positive except ADG1-ADG2, ADG1-ADG3 and ADG2-ADG3 and ranged from low to high in magnitude. Negative correlation was found among ADGs, indicating that these traits tend to compensate for high or low gain in corresponding traits. In the present research, additive genetic correlations were higher in magnitude than the phenotypic correlations and similar trends were also reported in various breeds of rabbit for growth traits (Xian-bo *et al.*, 2014; Sakthivel *et al.*, 2017; Rahim *et al.*, 2022). Positive genetic correlation among various growth traits indicated that traits are under the control of some common genes. Therefore, early selection at weaning age in the Angora rabbit could be advantageous, since selection for any one trait would lead to the overall genetic improvement of other correlated traits. In addition, this will also help in culling of surplus animals and less productive animals to increase the selection intensity and accuracy of selection for profitable rabbit farming.

CONCLUSION

The results of the present study demonstrated that environmental factors played a significant role in BW, ADG and KR of German Angora rabbits from weaning to adult age. The maternal genetic effect was only important for weaning weight, but maternal effects declined as the age of the rabbits increased. The permanent environmental maternal influences were present in all growth traits in our study. The high and positive correlation of weaning weight with post-weaning traits indicates that selection based on weaning weight of kits would be more effective as a basis for selection to improve body weights at later ages. The moderate estimates of heritability for growth traits and Kleiber ratio of rabbit in this study indicate that modest rates of genetic progress may be possible for these traits from selection under the standard management system.

Acknowledgement: Authors gratefully acknowledge the contribution of all the former managers associated with the German Angora Rabbit projects and the technical staff for data management and recording. The support provided by Director, ICAR-CSWRI, Avikanagar, in providing the necessary facilities and funds for execution of the project is also gratefully acknowledged.

Authors contribution: Rahim A.: writing – original draft, formal analysis, supervision and writing – review & editing. Rajaravindra K.S.: conceptualization and writing – original draft. Chaudhary R.: writing – review & editing. Chaturvedi O.M.: writing – review & editing. Gowane G.R.: conceptualization and writing – review & editing.

Data availability statement: Data available on request due to privacy/ethical restrictions.

Conflict of interest: We certify that none of the authors of this manuscript have any conflict of interest for this research work.

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