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Determination of the best non-linear function and genetic parameter estimates of early growth in Romane lambs

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Abstract The objectives of this study were a) to compare growth functions for describing the early growth curve of Romane sheep based on weighing records, b) to estimate the heritability of the growth curve parameters, and c) to estimate genetic parameters for 90-days-old bodyweight utilizing the data of earlier age. The raw data included 662 lambs (316 males and 346 females) bred at the Romane Sheep Research Center, INRAE, France. The studied trait was the bodyweight of lambs at birth, 15, 21, 35, 60, and 90 days of age. The number of measurements was approximately six for each animal. Dataset after mining consisted of 3261 weight records of 574 lambs. We applied four non-linear growth functions, including Gompertz, Brody, Logistic, and Richards. The goodness of fit for each equation was compared using the Akaike information criterion (AIC), coefficient of determination (R^2) and residual mean square (MSE). Predicting abilities of the included models were evaluated by comparing the predicted and observed phenotypes until 90 days of age. Genetic parameters of the non-linear functions were obtained using a specific two steps approach; in first step, the parameters of the different functions were estimated, and in the second, the parameters were considered as observations and we analyzed them using a multiple trait animal models. Residual mean square and R^2 for the models of Brody, Gompertz, Logistic and Richards were 106.71 and 0.37, 4.79 and 0.94, 7.41 and 0.88, and 9.04 and 0.88, respectively. The Logistic function had the smallest AIC and MSE values, and also had the highest R^2 value, indicating the best fit. The estimated heritability of the parameters in the logistic function were low (ranging from 0.007 to 0.017). In our study, the correlation between BV90 and BV35 was 0.54 with a confidence interval of 0.47-0.61. Since BV90 and BV35 have a positive genetic correlation, BV35 could be used to select the lambs for best growth until the slaughter age of Romane using the Logistic model.

Keywords: genetic parameter, growth curves, meat sheep, non-linear model, selection

Introduction

Growth, defined as an increase in live weight per unit of time (Lonergan et al., 2019), is an important trait in meat sheep production. The lifetime weight–age relationship is of great interest for animal breeders and producers (Kopuzlu et al., 2014). Mature weight, maturing rate, growth rate and related characteristics are economically valuable traits (Bangar et al., 2021). Early estimation of slaughter weight can be helpful for selection programs, given their relationship with other traits and the production economy (Beltran et al., 1992).

Analysis of the lifetime growth performance can be helpful in establishing proper feeding strategies and determining profitable slaughtering weight (Kenyon et al., 2014). Different approaches have been proposed to analyze the genetic aspects of growth performances in livestock. The study of growth in specific periods of growth from birth to mature age is one of these approaches (Hanset and Michaux, 1987). Among them, the most frequently used are: 1) analyzing one specific or several bodyweights at fixed ages (birth-, weaning-, slaughter-, and yearling-weight) using single or multiple trait model (Riggio et al., 2008; Splan et al., 2008), 2) analyzing the growth through the average daily gain (ADG) calculated over relevant economically- important ages (Chen et al., 2008), and 3) evaluation of bodyweight changes during animal growth with different non-linear models in a simulation study (Jaffrézic et al., 2006) or with actual data e.g., lamb (Lambe et al., 2006) and cattle (Forni et al., 2009). The use of mathematical growth functions provides the right way of condensing the information contained in such data series into a few parameters with biological meaning to facilitate both the expression and the understanding of the phenomenon (Fitzhugh, 1976). A wide range of non-linear growth functions has been proposed in the literature, e.g., Brody (Brody, 1945), Logistic (Cramer, 2002), Gompertz (Gompertz, 1825), Von Bertalanffy (Bertalanffy, 1957) and Richards (Richards, 1959). The most appropriate function is the one that can predict the overall shape of the growth curve fully with more flexibility and accuracy (Moore-Ede, 1986). However, there is not a consensus on the best growth function. The most suitable function depends on the species, breed or the population under study (Forni et al., 2009). Bahreini Behzadi et al. (2014) showed in sheep, Gompertz and Logistic models were the best predictors of the overall growth curves. Brunner and Kühleitner (2020) analyzed the data in 122 studies and found the Brody model as the best one. Zakizadeh (2020) introduced artificial neural networks and Brody models as the best growth models in Kurdish sheep from birth to yearling age. The fit of a growth model depends on the number of records and time of record measurements. However, growth curves are likely to be more suitable than linear regression on BW to describe early growth, partly because of their flexibility (Lambe et al., 2006). Our aims in this study were: a) to compare four non-linear growth models to describe early growth (from birth to slaughter age) in Romane lambs by few observations per subject, b) to estimate the corresponding genetic parameters with selected model, and c) to predict genetic parameters of body weight at 90 days of age with employing the data at days 0 to 35.

Materials and methods

Animals

The raw data included the measurement on 662 lambs (316 males and 346 females) which were born from 2009 to 2011 at the Romane Sheep Research Center, INRAE, France. The mating procedure is described in detail by David et al. (2013). Briefly, dams and sires were selected based on their genetic effects on the average daily gain from 0 to 45 days of age. Three groups of dams (low, medium and high maternal genetic effects) and two groups of sires (low and high direct genetic effects) were identified. The lambs were randomly selected and removed from their dams 24 hours after lambing and reared artificially. The lambs were weighed at birth, 15, 21, 35, 60 and 90 (slaughter) days after lambing. Animals with less than four records were eliminated from the genetic analysis. The final dataset consisted of 3261 BW of 574 lambs. The number of records and average body weights at different ages are given in Figure 1. Romane, also known as INRA 401, was bred by breeding Romanov (due to fertility characteristics) with Berrichon du Cher (for carcass production quality) sheep.

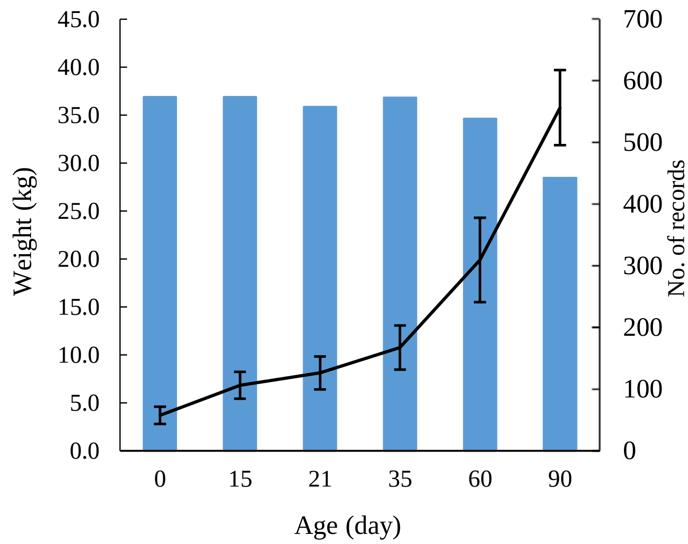

Figure 1. The number of records and mean weights (±standard deviation) among age intervals.

Statistical analysis and model selection

Piecewise regression has been used to find the breakpoint of growth. Four modified non-linear growth functions were fitted to the data using the NLMIXED procedure of SAS. Also, a simple linear regression was applied to the data. The functions used and their characteristics are shown in Table S1. Each lamb in the data set had four to six BW records. Parameters of the growth functions are discussed in detail by France et al. (1996). The Logistic, Gompertz, and Brody models have three parameters (*A*, *B, k*), and Richards has one more parameter (*M*). When all the parameters were considered at the same time, the equations did not converge. Therefore, in the estimation of parameters for each animal, one parameter was fixed to obtain a reasonable estimate of the two other parameters according to the method of Lehodey and Leroy (1999).
For each studied growth model, the individual R^2 and Akaike's information criterion (AIC) were calculated, and the goodness of fit was evaluated by the following criteria: average R^2, calculated AIC, and the absolute m-

ean residual deviation (MAD) calculated according to Sarmento et al. (2006), using the following formula:

$$MAD = \frac{\sum_{i=1}^{n} |y_{i-}\hat{y}_i|}{N}$$

in which, y_i is the observed value, $\hat{y_i}$ is the predicted value, and n is the sample size. A smaller value of AIC and MAD and a higher value of R^2 indicates a better fit for the data.

We evaluated the predictive ability of the models. For evaluation of models, we removed BW at 90_d of age, and then re-estimated it for each model and animal. The BW at 90_d using these estimations was predicted. We evaluated the predictive ability using the Residual Mean Square (MSE) for each model as:

$$MSE = \frac{\sum_{i=1}^{N}(y_i - GIND90)^2}{N}$$

in which, y_i and $GIND90$ were the observed and predicted weight at day 90, respectively, and N was the sample size. The lower MSE values showed the better predictive ability of the model. We selected the data set of 0-35 to determine the best model. The animals having less than four records were excluded from genetic analysis. From the studied non-linear models, the logistic model was selected as the best model. Then we calculated A and B by logistic model.

Genetic parameters

Once the parameters were obtained for each model within an animal, the genetic parameters were estimated that best fit the data using a multiple trait animal model. The tested fixed effects included sex of the lambs, litter size at birth in 4 levels (single, double, triple, quadruple), age of the dam in 5 levels, year of birth in 3 levels, month of birth in two levels, and rearing type (artificial or maternal). The random effects to be included in the final model were selected by comparing the likelihood ratio test (LRT) of the nested models. The variance component of the genetic models was obtained using the REMLF90 software. Finally, genetic parameters were calculated using six models.

Six tested models were as followings:

Equation		Model
$\boldsymbol{y = Xb + Z_a a + e}$		**1**
$\boldsymbol{y = Xb + Z_a a + Z_c c + e}$		**2**
$\boldsymbol{y = Xb + Z_a a + Z_m m + e}$	Cov (a, m) = 0	**3**
$\boldsymbol{y = Xb + Z_a a + Z_m m + e}$	Cov (a, m) ≠ 0	**4**
$\boldsymbol{y = Xb + Z_a a + Z_m m + Z_c c + e}$	Cov (a, m) = 0	**5**
$\boldsymbol{y = Xb + Z_a a + Z_m m + Z_c c + e}$	Cov (a, m) ≠ 0	**6**

in which, $\boldsymbol{y}$ is the vector of parameter estimates obtained with the NLIN procedure; b is the vector of fixed effects;-

a is the direct genetic effects; m the maternal genetic effects; c the maternal permanent environmental effect; e the residual effects; **X**, $\boldsymbol{Z_a}$ $\boldsymbol{Z_m}$, and $\boldsymbol{Z_c}$ are the corresponding incidence matrices linking the effects to the observations. Random effects were assumed as normally distributed as:

$$\begin{bmatrix} a \\ m \\ c \\ e \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} A\sigma_a^2 & & & \\ A\sigma_{am} & A\sigma_m^2 & symm & \\ 0 & 0 & I_d\sigma_c^2 & \\ 0 & 0 & 0 & I_n\sigma_e^2 \end{bmatrix}\right)$$

A is the additive numerator relationship matrix, I_d and I_n are identity matrices of appropriate size, and σ_{am} is the covariance between direct and maternal additive genetic effects.

Genetic parameters were estimated using a multiple trait animal model. The total heritability was estimated according to:

$$h_t^2 = \frac{(\sigma_a^2 + 1.5\sigma_{am} + 0.5\sigma_m^2)}{\sigma_p^2}$$

Of the six mentioned models, the fifth model was selected as the most appropriate one. Correlation between BV at days 35 and 90 was estimated using the fifth model. The pedigree structure is presented in Table S2.

Results and discussion

Fixed effects

Table 1 presents the least-square means of fixed effects. The effects of sex, rearing type (maternal or artificial), litter size, and age of dam were significant. The live weight of male lambs was higher than females. Artificial breeding of lambs also reduces the live weight of lambs. In the Poll Dorset sheep breed, mean growth rates of artificially reared lambs were lower than those of day-suckling lambs (Knight et al.,1993). Natural suckling lambs of Chios breed grew faster before weaning (318 g/day) than artificially reared lambs (275 g/day) and were heavier at weaning (15.6 *vs.* 13.9 kg) (Koumas and Papachristoforou, 2008). González-García and Hazard (2016) concluded that parity and litter size affect the growth rate of the ewe lambs in the Romane breed. Similar to our results, some studies showed significant differences in growth performance depending on litter size, lamb's sex (Ptacek et al., 2015), and age of ewe (Aktaş et al., 2015). Moreira et al. (2016) reported that BW of Ile de France sheep breed at 0, 30, 60, and 90 days of age, were 4.58, 13.58, 19.58, and 27.99, respectively.

Table 1. The least square means and standard error of fixed effects on live weight (grams)

Effect	Level	LSmeans	SEM
Sex	Male	14751[a]	110.33
	Female	13633[b]	105.52
Rearing type	Maternal	14647[a]	102.84
	Artificial	13736[b]	126.76
Litter size	1	17238[a]	380.00
	2	14029[b]	92.00
	3	14046[b]	80.00
	4	13098[c]	131.00
	5	12546[d]	182.00
Mother age	2	14973[a]	158.00
	3	14528[b]	103.00
	4	13796[c]	109.00
	5	13469[d]	158.00

a,b: for each effect, LSmeans with common superscript do not differ (P>0.05)

Comparison of different growth models

Piecewise regression showed different slopes for three age periods (Table S3). Figure S1 shows the raw data trajectories for 20 lambs selected randomly from all data. Some of these lamb trajectories were non-linear; therefore, we evaluated the non-linear forms. A negative value at zero time (intercept) shows that the model is not flattened (SAS, 2012).

The MSE, R^2, MAD, and AIC values for each model are presented in Table 2. The model showing the highest R^2 and the lowest MSE, MAD, and AIC was the logistic model with a fixed k parameter. In different sheep breeds, for prediction of slaughter weight of lamb, the logistic model presented the lowest RMSE and AIC values (Van der Merwe et al., 2019). Figure 2 shows the observed average weight change accompanied by the mean estimated weight obtained with different models for birth weight, and weights at 15,21,35,60, and 90 days of age. Except for the Gompertz function for the 0-21d period and Richards function for the 60-90 period, all models tended to overestimated the average BW. For the initial weight period (birth to 21 days), the Gompertz model provided the closest match to the observation, but overestimated the body weight at later ages. The Richards function underestimated the average body weight during the 60-90 period.

Lewis et al. (2002), Sarmento et al. (2006) and Lambe et al. (2006) showed that the Gompertz is the best model to describe growth in sheep. Brody (1945) presented his modeling of growth at the mature weight. The Brody model was not suitable for use in our data on young sheep, which is the preferred model for adult weights. Van der Merwe et al. (2019) introduced the logistics model as the best one for prediction of growth in sheep.

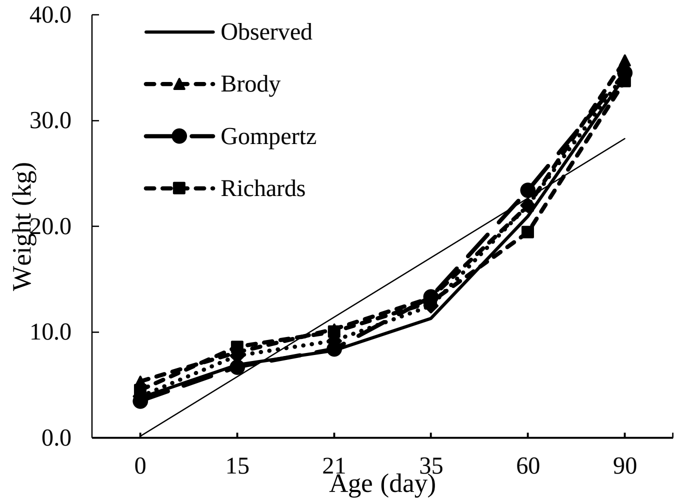

Figure 2. The observed and predicted weight change from birth to 90-d weight by five different models. Linear model: y=1.51+0.3436x

Table 2. The mean residual deviation ***(****MAD)*, coefficient of determination (R^2), Akaike's information criterion (AIC) values and residual mean square (MSE) of the different growth models in Romane sheep

When the growth parameter *A* was fixed				
Model	MSE	R^2	MAD	AIC
Brody	106.71	0.37	9.92	21910
Gompertz	4.79	0.94	2.005	17431
Logistic	7.41	0. 88	1.251	14799
Richards	9.04	0.89	2.83	16342
When the growth parameter *B* was fixed				
Model	MSE	R^2	MAD	AIC
Brody	107.34	0.37	23.78	23945
Gompertz	13.91	0.92	3.628	16544
Logistic	1.33	0.97	0.877	14815
Richards	23.78	0.82	4.719	17518
When the growth parameter *K* was fixed				
Model	MSE	R^2	MAD	AIC
Brody	147.43	0.37	23.84	30739
Gompertz	10.43	0.92	3.078	17851
Logistic	0.48	0.97	0.549	14787
Richards	32.04	0.81	4.417	18233

The values of parameters (*A, B, K,* and *M*) for the four different models (*K* fixed) are given in Table 3. The parameter *A* represents an estimate of the asymptotic weight, interpreted as the weight at maturity. This value does not represent the maximum animal weight (Fitzhugh et al., 1976). The definition of an optimum adult weight is controversial since it depends on the species, breed, selection method, management system and environmental conditions. The estimated values of parameters for the best non-linear model, i.e., Logistic when the *K* parameter was fixed to 0.03 were 90.34 and 23.9 for *A* and *B,* respectively.

Table 3. Estimates of the parameters *A*, B, K and M (± standard deviation) for each function

Function	*A*	B	k	M
Brody	16.44 (0.164)	0.145 (0.003)	0.01	-
Gompertz	31.72 (0.32)	6.09 (0.21)	0.05	-
Logistic	90.34 (1.03)	23.9 (0.59)	0.03	-
Richards	30.63 (0.28)	0.02 (0.0006)	0.01	35.01 (0.009)

According to the criteria in Table 2, the logistic model was chosen as the most appropriate function to model early growth in Romane lambs. Malhado et al. (2009) evaluating the growth curves in crossbred Santa Inês and Texel lambs based on Gompertz function, estimated a mean value of 30.6 for the *A* parameter. In a study on Segureña sheep breed at the same age as our research, the parameters of *A*, B and *K* for the logistic model were reported as 34.99, 3.20 and 0.026, respectively (Lupi et al., 2016). In the bibliography, different models of growth have been identified as the best model for lamb growth.- The age of puberty is considered different in various sheep breeds. For example, in the Baluchi sheep breed, the puberty age was 360 d, and the Brody function was presented as the best model (Bahreini Behzadi et al., 2014).

Least squares means of the fixed effect in logistic growth curve

The least square means of the fixed effects related to growth curve parameters of the logistic model are presented in Table 4. The fixed effect of the year and the mother's age at lamb birth were significantly associated with the growth curve parameters. Type of birth is one of the most critical factors influencing the growth curve. We observed that the asymptotic BW decreased with increasing litter size. Fetal growth is affected by the quality of feedstuff during pregnancy. In this study, the ewes were kept outdoors during gestation, but were housed indoors after parturition, and thereafter, their nutrition status was not changed.

Table 4. The least squares means (± standard error of the mean) of the logistic growth curve variables in Romane lambs

Fixed effect	Level	No. of records	*A*	*B*
Sex				
	Male	257	77.09±2.18	9.45±0.82
	Female	241	74.72±2.14	9.34±0.81
Birth year				
	2009	121	75.44±2.78	7.64±1.05[a*]
	2010	291	76.95±1.73	8.46±0.65[a]
	2011	86	75.33±2.83	12.09±1.07[b]
Month of birth				
	9	323	70.55±1.76[a]	10.41±0.66
	10	175	81.27±3.21[b]	8.38±1.22
Litter size				
	Single	8	96.27±5.59[a]	8.38±2.12
	2	235	74.93±1.88[b]	9.23±0.71
	3	191	69.97±1.74[c]	9.47±0.66
	4	64	62.46±2.43[d]	10.50±0.92
Mother age				
	2	59	78.82±2.61	10.74±0.99
	3	217	76.55±1.72	9.79±0.65
	4	172	74.22±2.53	9.25±0.96
	5	50	74.05±3.91	7.81±1.48
Rearing type				
	Artificial	79	72.35±2.48 [a]	9.21±0.94
	Maternal	419	79.47±2.06 [b]	9.58±0.78

a,b: for each effect, means with common superscript do not differ (P>0.05).

Estimation of genetic parameters of the Logistic function

The AIC and LRT values for different genetic models are presented in Table 5. The genetic model that best fitted the data contained the same random effects for *A* and B: direct additive genetic, maternal additive genetic and maternal permanent environmental, ignoring the covariance between the direct additive and maternal additive genetic effects. The asymptotic BW (*A*) was highest in model 2 and lowest in model 5.

Table 5. The Akaike's information criterion (AIC) and likelihood ratio test (LRT) values for the studied traits under different models with the best model shown in bold face

	Parameter			Model			
		Model 1	Model 2	Model 3	Model 4	**Model 5**	Model 6
AIC	*A*	4314.56	4316.56	3376.47	3378.45	**3070.38**	3380.46
	B	3418.84	3420.88	2489.22	2491.22	**2163.65**	2493.265
LRT	*A*	0	0.09	940.09	940.11	**1248.18**	940.1
	B	0	0.04	931.66	931.46	**1259.23**	931.615

Choosing the best model based on either BIC, MSE or AIC alone is questionable. The logistic function is the best considering AIC, but other parameters must be considered in selecting the best model. The Gompertz model is the best if the environmental factors are not limiting (Lewis et al., 2002).

The corresponding genetic parameter in Model 5 is presented in Table 6. The estimated direct heritability values for *A* and *B* were 0.017 and 0.007, respectively, being lower than those reported in previous studies: 0.30 in Chios sheep (Mavrogenis and Papachristoforou, 1990), 0.29 in Hero sheep (Lewis et al., 2002), 0.36 (Lambe et al., 2006) and 0.36 in Suffolk sheep (Abegaz et al., 2005). An explanation for higher h^2 in these studies is the omission of the maternal effects. Consequently, a part of which is included in the direct genetic effect. In the animal models in which the maternal effects had been ignored, the direct heritability was overestimated (Waldron et al., 1993). These results showed that maternal genetic effects influenced on the growth variables in Romane sheep. The total heritability estimated for *A* and *B* were 0.12 and 0.04, respectively. The estimates of correlation among logistic variables, using the most appropriate model (model 5), are presented in Table 7.

Table 6. Estimates of variance components (± standard deviation) in model 5

	σ_a^2	σ_m^2	σ_{pe}^2	σ_{re}^2	σ_p^2	h_a^2	h_m^2	c^2	h_t^2
A	3.62	46.53	36.37	125.2	211.72	0.017	0.21	0.17	0.12
	±0.013	±0.17	±0.011	±0.3	±0.31	±0.02	±0.01	±0.01	±0.02
B	0.24	1.94	7.16	22.25	31.59	0.007	0.06	0.22	0.04
	± 0.002	± 0.012	± 0.01	±0.02	±0.04	±0.001	±0.02	±0.01	±0.03

σ_a^2: Direct additive genetic variance, σ_m^2: maternal genetic variance, , σ_{pe}^2: permanent environmental variance, σ_{re}^2: residual variance, σ_p^2: Phenotypic variance, h_a^2: direct heritability, h_m^2: maternal heritability, c^2: ratio of maternal permanent environmental effects to phenotypic variance, h_t^2: total heritability.

Table 7. Correlation estimates (± standard error) among variables of the Logistic model

Trait1- Trait2	r_a	r_p	r_c	r_m
A-B	0.15±0.002	-0.09±0.02	-0.05±0.008	-0.50±0.008

r_a: Direct genetic correlation; r_p: phenotypic correlation; r_m r_c: maternal and permanent environmental correlations.

The direct additive genetic correlations between *A-B* were not significantly different than 0. Bathaei and Leroy (1998) found negative genetic correlations between *A* and *B, and between A* and *K,* while Abegaz et al. (2005) reported a positive genetic correlation between *A* and *B* (0.39). Lewis et al. (2002) estimated negative genetic correlation between *B* and *K*. Lambe et al. (2006) showed that NLMIXED was superior to NLIN. In our study, the correlation between BV90 and BV35 was 0.5419 with a confidence interval of 0.469 - 0.608.

Our data were from the lambs before they reached their mature body weight. Furthermore, few records were available per animal in the studied period. Consequently, we had not sufficient data to estimate all parameters appropriately. These particularities induce difficulties in the fitting of the model. We were unable to reach the convergence of model with the estimation of three parameters simultaneously. We fixed one parameter to estimate the others and repeated the procedure for all three parameters (Supplementary Materials, Appendix). Researchers have previously used a similar approach in which they settled one parameter at a presumed value rather than estimating it. Lehodey and Leroy (1999) estimated growth parameters according to the Bertalanffy growth model with *K* fixed and *K* varying. In our study, we used a two-step approach as proposed by Petráš et al. (2014). They fixed one parameter while holding the other parameters accessible. Girondot and Kaska (2014) adjusted the parameter of *K* from the Gompertz model to achieve optimum convergence. The major drawback of the two-step approach is the uncertainty in the coefficient predicted in step one that is not considered. Austin et al. (2011) suggested that the most appropriate method to estimate the growth rate is the fixed *A* method. Motulsky and Christopoulos (2004) described fix parameters as part of the picking model. Han (1987) suggested that we can settled a parameter to have a non-zero constant.

Conclusions

We tried to predict BV at 90-age by sing the breeding values of 0-35 accurately in Romane lambs. Since BV90 and BV35 have a positive genetic correlation, BV35 could be used to select the lambs for best growth until the slaughter age using the Logistic model. The practical objective of selection was to obtain a higher BW at the slaughter age. Non-linear curve fitting results showed that the logistic function is suitable to describe the changes in weight change with time for Romane sheep at an early age. The estimated genetic parameters for the logistic growth curve showed a moderate heritability for the *A* parameter of the curve, indicating that, selection on mature weight is possible. Due to the significant environmental effects on bodyweight, curve parameters, as well as the maximum daily growth in this study, it is recommended that, environmental conditions must be optimized for the development of the animal capacity resulting in reduced breeding cost and thus increase the heard profitability. The practical purpose of this study was to increase the weight at the optimum slaughter age of 90 d. However, the possible negative relationship between body weight and other traits must be considered in practical selective breeding. This issue is perspective of the further investigations.

Declaration of interest

Authors have not any conflict of interest.

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Supplementary materials

Table S1 Growth functions descriptions

Growth function	Parameters	Formula
Brody	*A, B, K*	$W_t = A(1-B)\exp(-kt) + e$
Gompertz	*A, B, K*	$W_t = A\exp(-B\exp(-kt)) + e$
Logistic	*A, B, K*	$W_t = A/[1 + B\exp(-kt)] + e$
Richards	*A, B, K, M*	$W_t = A[1 - B\exp(-kt)]^M + e$
Linear Regression	$\beta_\circ, \beta_1$	$W_t = \beta_\circ + \beta_1 t + e$

W_t is the weight measured at age *t* (day) expressed in kg

Table S2 The Pedigree structure

No. of records	3,446
No. of sires	12
No. of dams	198
Individuals with progeny	210
Individuals with no progeny	661
Founders	210
Non-founders	661
Full-sib groups	243

Table S3 Piecewise regression results show that 35-days old is a crucial breakpoint.

	Probability	R^2	Intercept (±SE)	Slope
All 0-90	**<.0001**	**0.90**	**1326.06±91.66**	**346.39±2.05**
0-35	<.0001	0.72	3635.31±59.02	205.62±2.75
35-60	<.0001	0.63	-2005.04±404.99	364.91±8.31
60-90	<.0001	0.78	-11931.00±669.40	530.33±8.93

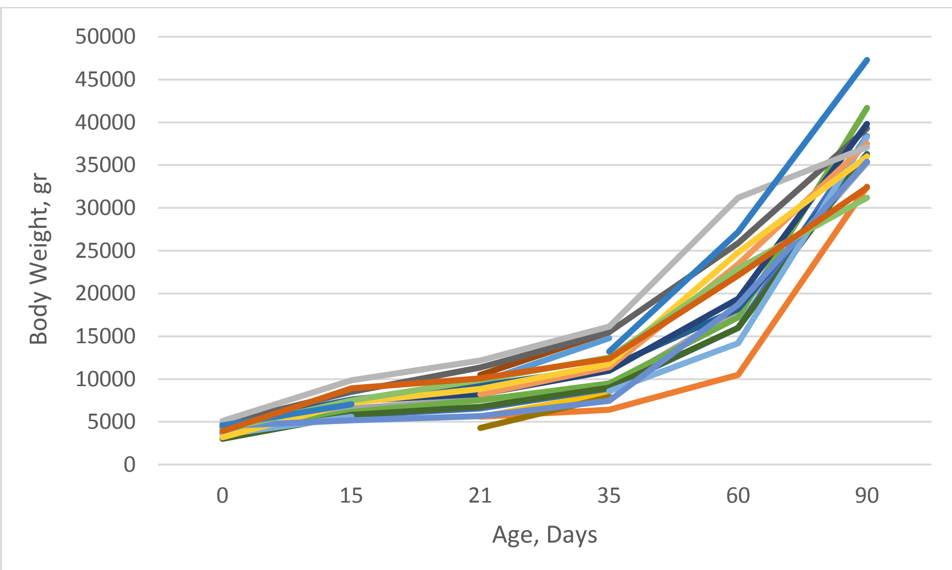

Figure S1. Shows raw data trajectories for 20 lambs selected at random from the data.

Appendix:

<u>Non-linear model</u>

<u>1: Brody</u>

1-1) Overall method

Variable	Value
A	16.00
B	0.129
K	0.01

1-2) By ANIMAL Method

Variable	Mean	SD	SE	Min	max
A	16.00				
B	0.139	0.213	0.008	-0.278	0.926
K	0.008	0.006	0.0002	-0.037	0.01

1-3) Overall method

Variable	Value
A	16.00
B	0.129
K	0.01

Variable	Value
A	16.36
B	0.15
K	0.01

1-4) By ANIMAL Method

Variable	Mean	SD	SE	Min	max
A	16.34	3.64	0.15	1.38	24.07
B	0.15				
K	0.009	0.003	0.0001	-0.037	0.01

1-5) Overall method

Variable	Value
A	16.99
B	0.18
K	0.01

1-6) By ANIMAL Method

Variable	Mean	SD	SE	Min	max
A	16.44	3.93	0.164	2.98	25.01
B	0.145	0.086	0.003	0.008	0.3
K	0.01				

2: Gompertz

2-1) Overall method

Variable	Value
A	35.00
B	3.02
k	0.03

2-2) By ANIMAL Method

Variable	Mean	SD	SE	Min	max
A	35.00				
B	3.38	1.36	0.064	1.83	17.04
K	0.035	0.012	0.0005	0.006	0.263

2-3) Overall method

Variable	Value
A	40.0
B	6.0
k	0.03

2-4) By ANIMAL Method

Variable	Mean	SD	SE	Min	max
A	38.54	16.15	0.71	10.29	99.92
B	6.0				
K	0.05	0.019	0.0008	0.02	0.13

2-5) Overall method

Variable	Value
A	32.01
B	5.0
k	0.05

2-6) By ANIMAL Method

Variable	Mean	SD	SE	Min	max
A	31.72	7.74	0.32	3.73	51.49
B	6.09	5.03	0.21	0.07	34.15
K	0.05				

3: Logistic

3-1) Overall method

Variable	Value
A	70
B	0.88
k	-3.0

3-2) By ANIMAL Method

Variable	Mean	SD	SE	Min	max
A	70				
B	9.51	5.89	0.26	-3.26	19.97
K	-0.99	1.71	0.07	-10.83	0.03

3-3) Overall method

Variable	Value
A	66.14
B	15
k	0.03

3-4) By ANIMAL Method

Variable	Mean	SD	SE	Min	max
A	69.16	19.40	0.81	18.28	160.51
B	15				
K	0.03	0.006	0.0002	0.0009	0.056

3-5) Overall method

Variable	Value
A	77.17
B	17.25
k	0.03

3-6) By ANIMAL Method

Variable	Mean	SD	SE	Min	max
A	90.34	7.45	1.03	58.98	99.03
B	23.9	4.29	0.59	20.01	44.20
K	0.03				

4: Richards

4-1) Overall method

Variable	Value
A	30
B	0.023
k	0.019
M	42.90

4-2) By ANIMAL Method

Variable	Mean	SD	SE	Min	max
A	30				
B	0.023	0.0004	0.000017	0.021	0.026
K	0.019	0.005	0.00021	0.0002	0.033
M	42.74	1.38	0.057	37.32	47.31

4-3) Overall method

Variable	Value
A	26.67
B	0.02
K	0.01
M	35

4-4) By ANIMAL Method

Variable	Mean	SD	SE	Min	max
A	27.1	5.44	0.26	7.36	68.31
B	0.02				
K	0.016	0.003	0.0001	0.0008	0.074
M	35.05	1.08	0.052	27.1	47.61

4-5) Overall method

Variable	Value
A	30.66
B	0.02
K	0.01
M	35

4-6) By ANIMAL Method

Variable	Mean	SD	SE	Min	max
A	30.63	6.73	0.28	4.005	57.41
B	0.02	0.0015	0.00006	0.003	0.028
K	0.01				
M	35.01	0.22	0.009	35.00	39.79

4-7) Overall method

Variable	Value
A	26.67
B	0.02
K	0.01
M	35

4-8) By ANIMAL Method

Variable	Mean	SD	SE	Min	Max
A	27.1	5.44	0.26	7.36	68.31
B	0.02	0.0006	0.00003	0.015	0.027
K	0.01	0.003	0.0001	0.0008	0.074
M	35				