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Modelling of growth curves and estimation of genetic parameters for growth curve parameters in Peruvian young llamas (*Lama glama*)

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ABSTRACT

The objectives of this study were to describe the growth of young llamas by the application of four non-linear functions (Gompertz, Logistic, Von Bertalanffy and Brody), evaluate the importance of fixed (environmental) effects (sex, type of llama, month and year of birth) on growth curve parameters and finally estimate the genetic parameters for growth curve parameters (A : asymptotic body weight and k : specific growth rate). A total of 35,691 monthly body weight records from birth up to 16 months of age from 2675 young llamas, collected from 1998 to 2008 in the Quimsachata Experimental Station of the Instituto Nacional de Innovación Agraria (INIA) in Peru were used. Growth curve parameters were estimated by non-linear procedures while genetic parameters were estimated by application of a bivariate animal model and the restricted maximum likelihood (REML) method. All non-linear functions closely fitted actual body weight measurements, while the Gompertz function provided the best fit in describing the growth data of young llamas. All environmental effects significantly influenced the asymptotic weight (A), while the specific growth rate (k) was only affected by the month and year of birth. Heritability estimates for parameters A and k were 0.10 and 0.01, respectively. Genetic correlation between A and k was high and negative (-0.82), indicating that a rapid decrease in growth rate after inflection point is associated with higher mature weight. Despite the low heritability estimates obtained herein, slight genetic gain(s) were observed in the current study suggesting that a selection program to change the slope of the growth curve of llamas may be feasible.

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1. Introduction

It is estimated that more than four million South American camelids live in Peru, of which, the llama (*Lama glama*) represents more than 24% of the total. Majority of the animals are found in the districts of Puno (35.7%), Cusco (17.7%) and Junin (11.2%) (FAO, 2005). The habitat of the llama and other South American camelids is mainly the high mountain areas and it

extends from northern Peru to northern Argentina, the respective highlands zones from Bolivia and Chile (Rossi, 2004), included. Llamas and alpacas constitute the most important social and economical species in Peru, where more than 2.9 million inhabitants (11% of the population) are dependent on these species through more than 100,000 producers (Brenes et al., 2001).

Llamas are very well adapted to the Andean highlands and provide the farm households with a variety of products such as fibre, meat and dung while being used as pack animals. A large part of the products is consumed within the local community, but are also source of some cash income from selling fibre and meat. In Peru, llamas are traditionally classified into two different types: Ch'accu, characterized by increased coverage

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Table 1

Number of animals, mean, standard deviation and coefficient of variation for body weight from young llamas at different ages.

Ages (months)	N° of animals	Mean (kg)	Standard deviation (kg)	Coefficient of variation (%)
0	2675	9.56	1.66	17.33
1	999	17.63	9.51	53.96
2	2272	18.10	4.31	23.83
3	2503	21.85	5.55	25.39
4	2628	24.71	5.63	22.79
5	2663	27.65	6.32	22.87
6	2560	29.79	7.11	23.87
7	2512	31.24	7.84	25.10
8	2510	32.56	8.06	24.76
9	2654	33.34	8.31	24.92
10	2550	34.82	8.88	25.50
11	2545	37.13	9.13	24.58
12	2462	39.52	9.94	25.16
13	2211	41.42	11.30	27.27
14	1315	43.09	12.37	28.71
15	415	43.22	13.59	31.44
16	216	46.06	9.68	21.01

of fleece, covering the extremities, the neck and the head and K'ara, with no fibre on extremities, head and ears and a reduced fibre growth on the neck, but of greatest strength often used by Andean people as a pack animal (Flores, 1988; Leyva, 1991). Both llama types provide meat with high protein content (San Martín, 1996) representing the main source of food of animal origin for the Andean people (Flores, 1988; Leyva, 1991).

More llama meat and fibre is progressively being marketed reflecting a growing demand for these products. The absence of infrastructure and standard quality and quantity of llama meat and fibre are, however, the main factors preventing a more market oriented husbandry. This problem occurs because llamas are handled and produced in small production systems and with low-income producers, confronting the aftermath of marginalization of livelihood systems (Quispe et al., 2009). On the other hand, the lack of production goals does not allow the application of breeding programs. Under these production conditions an important phenotypic indicator of the meat production capacity is the description of animals' body weight by time.

The most important characteristic of live material is growth, described as an increase in both the weight and size in a certain period of time (Thornley and Johnson, 1990). Meat production is therefore influenced by growth rate and the animals' body size, which are dependent on live weight or dimension for a period of time. Better understanding of animal growth using mathematical modelling of growth data allows better explanation and interpretation of growth events which in turn contributes to improving overall productivity (Efe, 1990).

Growth curves are one way of describing growth in a certain period of time. There are many non-linear mathematical functions (e.g., Gompertz, Richards, Von Bertalanffy and Logistic) that have been extensively used in different livestock species to describe the development of body weight (e.g., Kaps et al., 2000; Menchaca et al., 1996, in cattle, Bathaei and Leroy, 1998, in sheep, Schinckel et al., 2004, in pigs and Mignon-Grasteau et al., 2000, in chicken). However, little information in the literature on the growth curve modelling as well as estimation of genetic parameters of the growth curve parameters is found in llamas. Furthermore, the growth characteristics of llamas from birth to first year-old have not been adequately studied. Most investigations are limited to the prediction of live weight from body measurements (Wurzinger et al., 2005; Llacsá et al., 2007). Riek and Gerken (2007) fitted growth curves in llamas using both simple linear regression and the Gompertz equation and concluded that that a linear regression may be adequate to describe body weight development from birth to 27 week post partum.

Several studies have reported significant heritability estimates for growth curve parameters in different livestock species (Mignon-Grasteau et al., 2000; Koivula et al., 2008; Silva et al., 2012; Lopes et al., 2012), demonstrating that these parameters are heritable and thus could be modified by selection through the implementation of an effective breeding program. In that sense, it is important to know the relationship between the growth curve parameters to properly define the breeding objectives. However, this knowledge does not exist for many breeding populations, including the South America's Camelids.

Aiming at providing more knowledge on body weight development of llamas we have elaborated the present study. The goals of the present study are: (a) to describe growth from birth to 16 months of age by application of four non-linear functions, (b) to evaluate the environmental effects on growth curve parameters and (c) to estimate the genetic parameters and genetic trend for growth curve parameters in a population of young llamas.

2. Materials and methods

2.1. Data

Data comprised individual body weights of males and females llamas belonging to two types: K'ara and Ch'accu. Data were made available by the Quimsachata Experimental Station, of the National Institute of Agricultural Research (INIA) located in Puno, Peru. The Quimsachata Station is located at 4025 meters above sea level, 15°45'38.9" south latitude, 70°34'18.9" western length, whose temperatures vary between –5 and 18 °C and rainfall reaching 700 mm/year. The database consists of 35,691 records of body weight of 2675 young llamas (Table 1). Individual body weight of animals was obtained by using a digital weighing scale at monthly intervals from birth to 16th month of age, collected during 1998–2008. The total number of records and animals used in the present study are shown in Fig. 1.

2.2. Statistical analysis

2.2.1. Growth curves parameters

The description of the growth trajectory of animals was performed by application of four non-linear models of Brody, Von Bertalanffy, Logistic and Gompertz (Table 2), where y_{ij} is the observed body weight of individual i ($i = 1, \dots, n$) at measurement time j ($j = 1, \dots, n_i$) for animal i , t_{ij} is age of animal i in days at time j and ε_{ij} is the random residual term. The growth curve parameters for the i th animal are: A_i , the asymptotic body weight of animal i , which is interpreted as mature weight; B_i , the proportion of the asymptotic mature weight to be obtained after birth for animal i ; k_i , the maturation rate of animal i , which is interpreted as weight change in relation to mature weight to indicate how fast the animal approaches adult weight. The NLIN procedure from the SAS software package was used to estimate the least-squares estimates and the standard errors of

Table 2

Equations of non-linear models will be used to describe the growth of young llamas.

Model	Formula
Brody (Brody, 1945)	$Y_{ij} = A_i(1 - B_i e^{-k_i t_{ij}}) + \varepsilon_{ij}$
Von Bertalanffy (Von Bertalanffy, 1957)	$Y_{ij} = A_i(1 - B_i e^{-k_i t_{ij}})^3 + \varepsilon_{ij}$
Logistic (Nelder, 1961)	$Y_{ij} = A_i(1 - B_i e^{-k_i t_{ij}})^{-1} + \varepsilon_{ij}$
Gompertz (Laird, 1965)	$Y_{ij} = A_i e^{-B_i e^{-k_i t_{ij}}} + \varepsilon_{ij}$

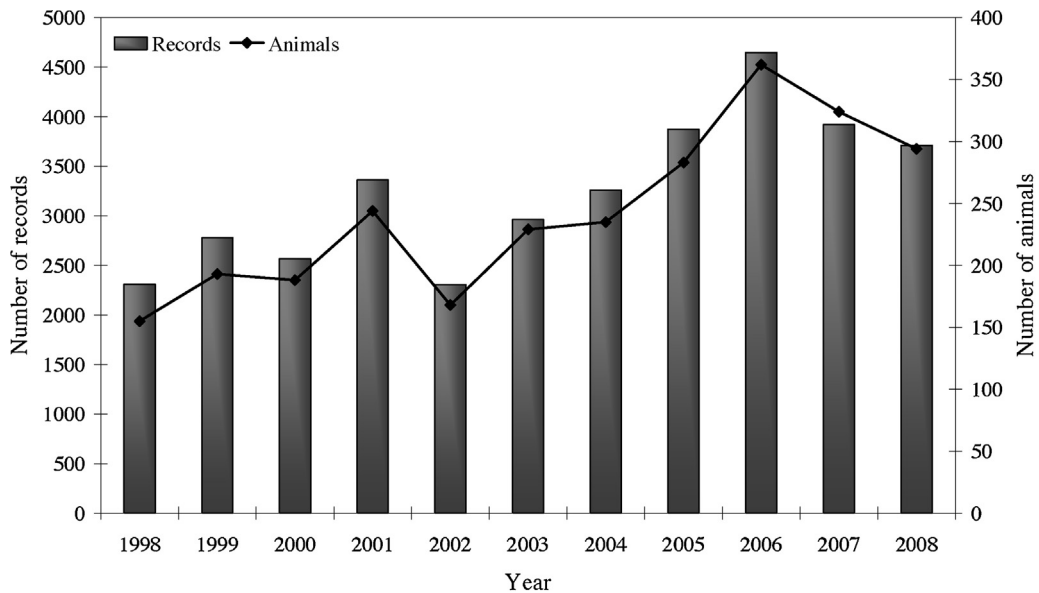


Fig. 1. Total number of records (first vertical axis, gray bars) and animals (second vertical axis, ♦) per year.

the parameters A_i , B_j and k_i . The goodness of fit was assessed by using four criteria: the determination coefficient (R^2), the mean squared error (MSE), the mean absolute deviation (MAD) and the percentage of convergence (C%). R^2 was calculated through a linear regression analysis between observed and estimated weights; the MSE was calculated by dividing the residual sum of squares by the number of observations, which represents the estimator of the maximum likelihood of the residual variance; the MAD was calculated as $MAD = \sum_{i=1}^n |Y_i - \hat{Y}_i| / n$, where Y_i is the observed value, \hat{Y}_i is the estimated value, and n was the sample size (Sarmiento et al., 2006). C% indicates the percentage of convergence in relation to the individual dataset evaluated. The lower the MSE and MAD values are, the better the adjustment.

After selecting the best model, the absolute growth rate (AGR) for body weight was calculated based on the first derivative from the adjusted function in relation to time ($\partial y / \partial t$). The AGR represents the weight gained per time unit (Malhado et al., 2009).

2.2.2. Environmental effects on growth curve parameters

To assess the influence of fixed effects, such as sex ($i=1$ and 2), animal type ($j=1, 2$ and 3), month of birth ($k=1, \dots, 5$) and year of birth ($l=1997, \dots, 2008$) on growth curve parameters of the selected model, a mixed model was employed as follows:

$$y_{ijklm} = \mu + \alpha_i + \beta_j + \delta_k + \gamma_l + \varepsilon_{ijklm}$$

where y_{ijklm} = m th growth parameter estimate of i th sex, j th type, k th month of birth, and l th year of birth; μ = population mean; α_i = i th sex effects; β_j = j th type effects; δ_k = k th month of birth effects; γ_l = year of birth effects and ε_{ijklm} = random error attributed with each observation. This analysis was performed by procedure MIXED in SAS (SAS, 2001). Only the parameters A and k were evaluated during this analysis since they have biological interpretation.

2.2.3. Estimation of genetic parameters and genetic trend

A bivariate animal model was employed to estimate (co)variance components of as follows:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where y_1 and y_2 are the vectors of observations for traits 1 (parameter A) and 2 (parameter k), respectively; β_1 and β_2 are the vectors of fixed effects (sex, type, month of birth and year of birth) for traits 1 and 2, respectively; u_1 and u_2 are vectors of random additive genetic effects, and e_1 and e_2 are the residual effects for the traits 1 and 2, respectively; X_1 and X_2 and Z_1

and Z_2 are the incidence matrices that associate the elements of β_1 and u_1 and β_2 and u_2 , respectively, with y_1 and y_2 . The variances and covariances of all random vectors are equal to:

$$\text{Var} \begin{bmatrix} u_1 \\ u_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{a_1}^2 & A\sigma_{a_1a_2} & 0 & 0 \\ A\sigma_{a_1a_2} & A\sigma_{a_2}^2 & 0 & 0 \\ 0 & 0 & I\sigma_{e_1}^2 & I\sigma_{e_1e_2} \\ 0 & 0 & I\sigma_{e_1e_2} & I\sigma_{e_2}^2 \end{bmatrix}$$

where A is a Wright's numerator relationship matrix, calculated in our study on base of offspring–mother relationships, $\sigma_{a_1}^2$ and $\sigma_{a_2}^2$ are the variances of the direct additive genetic effect; $\sigma_{e_1}^2$ and $\sigma_{e_2}^2$ are the residual variances for traits 1 and 2, respectively; and I is the identity matrix. The genetic and environmental covariance between both traits are $\sigma_{a_1a_2}$ and $\sigma_{e_1e_2}$, respectively.

The (co)variances and genetic parameters were estimated by the Average Information Restricted Maximum Likelihood method (AI-REML) using the software WOMBAT (Meyer, 2007). Based on the estimated (co)variance components, heritability of A and k and the genetic correlation between the two were calculated.

2.2.4. Genetic trend

Genetic trends were estimated by averaging the EBVs of the parameters A and k within year of birth and regressing these values on year of birth. The model used was:

$$y_d = b_0 + b_1 X_d$$

where y_d is the average of EBV of d th year of birth; X_d is the d th year of birth; b_0 and b_1 , are the intercept and the linear regression coefficient, respectively (genetic trend).

3. Results and discussion

3.1. Model parameters and goodness of fit

Least-squares means of the growth curve parameters as well as goodness of fit in the four growth models are in Table 3. The asymptotic body weight (A) was highest in the Brody model (55.9 kg) and lowest in the Logistic model (46.7 kg). The estimate of the parameter B was smallest

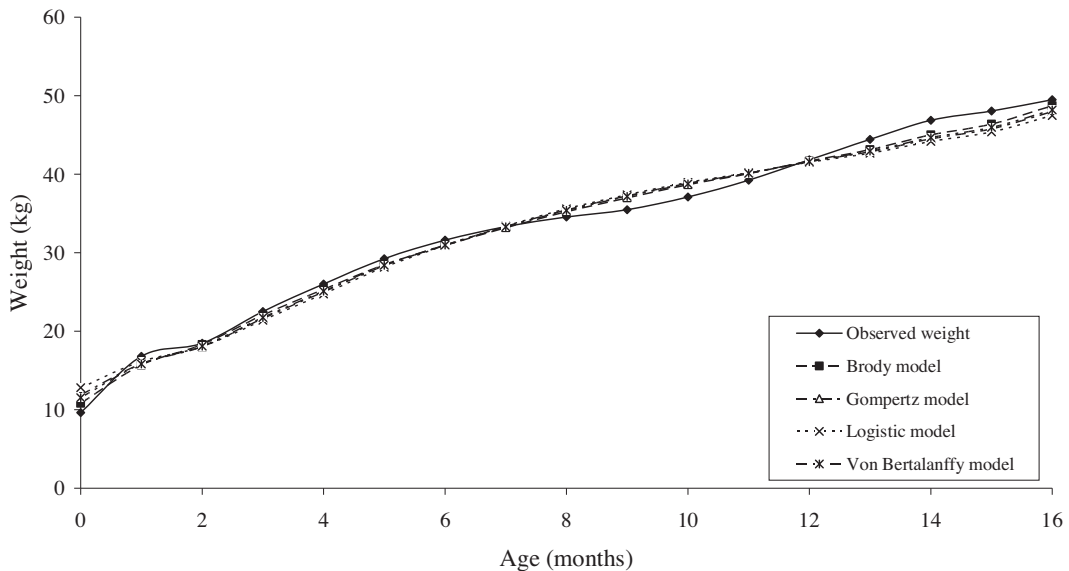


Fig. 2. Body weight observed and estimated by Gompertz, Logistic, Von bertalanffy and Brody functions in young llamas.

in the Von Bertalanffy (0.387 kg) and highest in the Logistic (2.775 kg). The maturation rate (k), ranged from 0.007 (Brody model) to 0.016 (Logistic model). There are a limited number of published studies on growth curve modelling in llamas in literature. Wurzinger et al. (2005), applying Brody growth model for the Bolivian adults llamas, reported values 74.3–101.1, 0.851–0.934 and 0.258–0.614 for A , B and k , respectively. The differences between these estimates and the present results could be attributed to several factors such as age and strain of animal, adjustment or not to environmental effects etc. In fact, in the study of Wurzinger et al. (2005), animals of the K'ara type were excluded from analysis. Overall all the models were reasonably fitted the observed weights (Fig. 2) with overestimation observed at the initial (2–6 months), middle stage (8–11 months of age) and final stage (13–16 months).

With respect to goodness of fit, all models had high R^2 (from 0.94 to 0.95), suggesting an overall good fit to the data (Table 3). More specifically, the R^2 of Gompertz (0.947) was slightly greater than Von Bertalanffy and Brody (0.946), and these models were greater than Logistic (0.944). According to MSEs, the ranking of the models was: Von Bertalanffy > Brody > Logistic > Gompertz, with the Gompertz model showing the lowest MSE value

and therefore the best fit. However, when MAD values were used to compare models, the Logistic model had the least value, suggesting that this model is best for predicting growth. Moreover, the percentage of convergence in the Logistic function was considerably higher (~100%) compared to other models, suggesting that this model would be the best model. Note that such divergent findings between model comparison criteria with respect to the choice of the best model, are common in the literature (Forni et al., 2009; Malhado et al., 2009; Silva et al., 2012).

In the present study, the Gompertz model showed the highest R^2 and lowest MSEs even though its convergence rate was lower when compared to other models (Table 3). Therefore, it was chosen to the growth curve modelling.

Different growth non-linear functions have been used in modelling the growth in various livestock species. A main feature of these functions (e.g. Gompertz, logistic, von Bertalanffy) is that they have a fixed inflection point, in relation to mature weight and are easier to apply in practice. The Gompertz growth model has been shown to accurately describe the growth of sheep (Lewis et al., 2002; Sarmiento et al., 2006; Lambe et al., 2006; Malhado et al., 2009) and cattle (Silva et al., 2004; Forni et al., 2009).

Table 3

Mean growth curve parameters (\pm standard deviation), coefficient determination (R^2), mean square error (MSE), mean absolute deviation (MAD) and percentage of convergence (C%) of four growth functions that describe the growth curve of young llamas.

Model	Parameters			R^2	MSE	MAD	C%
	A	B	k				
Gompertz ^a	49.611 \pm 0.281	1.427 \pm 0.006	0.010 \pm 0.001	0.947	7.256	1.941	92.79
Logistic	46.723 \pm 0.225	2.775 \pm 0.019	0.016 \pm 0.002	0.944	7.359	1.071	99.89
Von Bertalanffy	51.067 \pm 0.304	0.387 \pm 0.001	0.013 \pm 0.001	0.946	7.393	1.908	93.01
Brody	55.876 \pm 0.367	0.794 \pm 0.002	0.007 \pm 0.001	0.946	7.379	1.836	87.96

^a Selected model, A is the predicted asymptotic body weight (kg), B is the proportion of the asymptotic mature weight to be obtained after birth, k is the maturing rate.

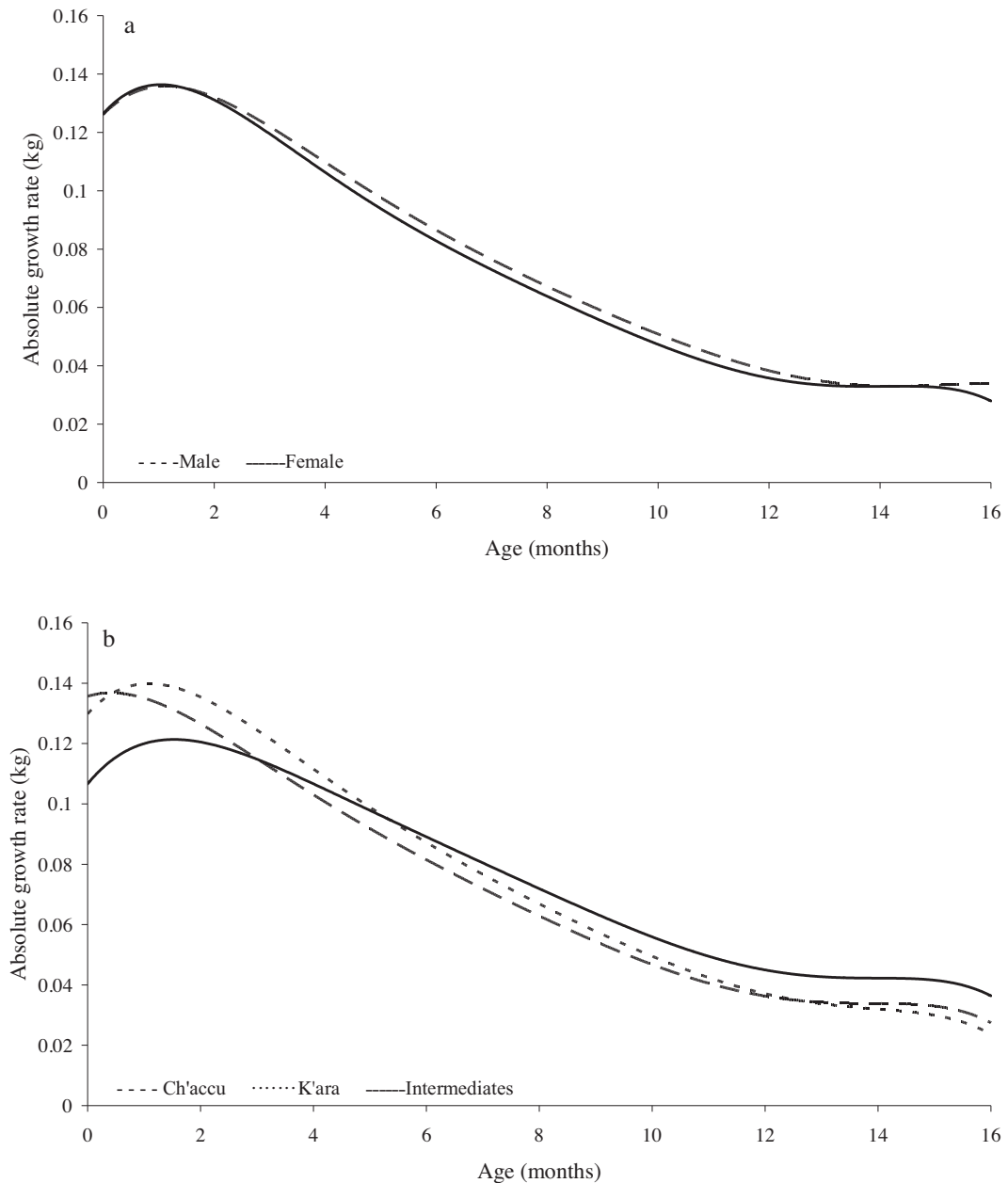


Fig. 3. Absolute growth rate for sex (a) and type (b) effects based on Gompertz model of young llamas.

The absolute growth rate (AGR), based on the first derivative of Gompertz function, by time, sex and type effects are shown in Fig. 3. Notably the maximum AGR was estimated at very early ages (30 days) in both sexes and the three types. More specifically, AGR was estimated as high as 140.2 and 138.9 g/days, for males and females, respectively. The AGR for the K'ara type, Ch'accu and the intermediate types was 142.2, 137.7 and 121.4 g/days, respectively. The AGR indicates the maximum age at which an animal presents satisfactory gains and provides information on animal performance during development, making it possible to establish an optimum slaughter age (Silva et al., 2012).

3.2. Environmental effects on growth curve parameters

Table 4 shows the least-square means for the parameters A and k . Sex had a significant effect on A , which was estimated to be 2.17 kg higher in females than in males ($p < 0.05$) (males = 45.47 kg and females = 47.64 kg). A higher value of A for females may be reasonably expected, due to the hormonal and physiological differences that stimulate the early onset of sexual activity, resulting in the increased body development of females than males (Otuma and Osakwe, 2008). Significant effects of sex on mature weight of llama have been reported in previous studies (Wurzinger et al., 2005; Zea, 2006; García and Leyva, 2007;

Table 4

Number of observations (N), least-squares mean \pm standard error of asymptotic body weight and maturation rate of Gompertz model, according to environmental fixed effects in young llamas.

Fixed effects	N	Asymptotic body weight	Maturation rate
Sex			
Male	1223	45.47 \pm 0.63 ^a	0.0234 \pm 0.0020 ^a
Female	1194	47.64 \pm 0.64 ^b	0.0210 \pm 0.0020 ^a
Type			
Ch'accu	965	45.41 \pm 0.60 ^a	0.0242 \pm 0.0019 ^a
K'ara	1327	47.34 \pm 0.55 ^b	0.0212 \pm 0.0017 ^a
Intermediates	125	46.92 \pm 1.16 ^b	0.0213 \pm 0.0036 ^a
Month of birth			
January	644	50.24 \pm 0.62 ^a	0.0183 \pm 0.0019 ^c
February	1078	47.35 \pm 0.53 ^b	0.0180 \pm 0.0016 ^c
March	515	45.24 \pm 0.66 ^c	0.0232 \pm 0.0020 ^b
April	141	39.69 \pm 1.09 ^d	0.0304 \pm 0.0034 ^a
May–December	39	50.26 \pm 1.93 ^{ab}	0.0211 \pm 0.0060 ^{abc}
Year of birth			
1998	151	62.19 \pm 1.09 ^a	0.0054 \pm 0.0034 ^c
1999	189	45.13 \pm 0.98 ^e	0.0119 \pm 0.0031 ^{bc}
2000	174	53.95 \pm 1.01 ^{bc}	0.0073 \pm 0.0032 ^{bc}
2001	239	41.60 \pm 0.95 ^f	0.0138 \pm 0.0029 ^b
2002	24	12.24 \pm 2.50 ^g	0.1418 \pm 0.0078 ^a
2003	219	51.65 \pm 0.97 ^{cd}	0.0098 \pm 0.0030 ^{bc}
2004	228	54.03 \pm 0.91 ^b	0.0091 \pm 0.0028 ^{bc}
2005	268	52.71 \pm 0.87 ^{bc}	0.0101 \pm 0.0027 ^{bc}
2006	342	49.73 \pm 0.83 ^d	0.0108 \pm 0.0026 ^{bc}
2007	297	46.24 \pm 0.85 ^e	0.0135 \pm 0.0026 ^{bc}
2008	286	42.65 \pm 0.85 ^f	0.0107 \pm 0.0027 ^{bc}

Within a column (and within each factor), values with different superscript letters differ significantly at $p < 0.05$.

Cortez and Copa, 2008). Wurzinger et al. (2005) reported higher mature weights for Bolivian llamas estimated as high as 101 and 75 kg, for males and females, respectively in the Th'ampulli strain. Conversely, Riek and Gerken (2007) reported no sex difference ($p > 0.05$) for mature bodyweight in llamas raised in Germany.

The K'ara and intermediate types had significantly higher mature weight (A) compared to the Ch'accu type (Ch'accu = 45.41 kg, K'ara = 47.34 kg and intermediate = 46.92 kg). The respective values for k were 0.0242, 0.0212 and 0.0213 for Ch'accu, K'ara and intermediate respectively, suggesting that The K'ara and intermediate types were later maturing than Ch'accu type. In contrast, Wurzinger et al. (2005) found no significant effect of type on asymptotic weight in their study with Bolivian llamas. Llaca et al. (2007) have not reported significant effect of animal types (K'ara and Ch'accu) on body weight from third to seventh month of age. Differences between the present results and those reported by these authors might be due to samples sizes used. For instance, in the study of Wurzinger et al. (2005), there were a few K'ara animals and females only, compared to Th'ampulli type (or Ch'accu type).

Month of birth had a significant effect on both A and k parameters. During the month of January animals reached maximum mature weights, decreasing gradually over the following months. This effect is likely due to better forage availability in the highlands of Peru during the rainy season (December–March) leading to better nutrition for the animals. In fact, the largest concentration of births (92.6%) was during the first three months of the year (Table 4). These results are in agreement with those reported by Agramonte

and Leyva (1991), who also found significant effects of season of birth on mature weight in alpacas.

The mature weight was also influenced by year of birth effect. In 2005, higher A values were achieved, except in 2001 and 2002, followed by a negative trend in the last years. This effect might be attributed by the changes in management conditions and undefined environmental factors such as differences in feed supply, protein composition, and nutritional quality over the years (Gbangboche et al., 2008).

The maturation rate indicates the growth speed to reach the mature weight. Animals with high values of this parameter present early maturity compared to those with lower values and similar initial weight. In this study, both month and year of birth had significant effects on maturation rate. These results could indicate that animals born at April would show higher maturation rates ($k = 0.03$) than those born during January and February ($k = 0.018$). In the present study, no significant effect of sex and/or type was established on k ($p < 0.05$). Wurzinger et al. (2005), showed significant effect of sex on this parameter that could be attributed to the age of llamas used.

3.3. Genetic parameters of the parameters of the growth curve

The phenotypic and genetic parameters estimates for Gompertz growth curve parameters are shown in Table 5. Both parameters displayed low heritabilities, with estimates as low as 0.10 for A and 0.01 for k , respectively. These estimates indicate that there is no or very little genetic

Table 5

Phenotypic and genetic parameters estimates and genetic gain for Gompertz growth curve parameters obtained from a bi trait analysis of young llamas records.

Model	Parameter	σ_p^2	σ_a^2	σ_e^2	h^2	$\sigma_{p_{A,k}}$	$r_{g_{A,k}}$	Δg
Gompertz	A	97.1383	9.564780	87.5735	0.10 ± 0.06	-0.41536	-0.82	0.28
	k	0.00813	0.000067	0.00807	0.01 ± 0.05			0.000259

σ_p^2 = phenotypic variance, σ_a^2 = additive genetic variance, σ_e^2 = environmental variance, h^2 = heritability, $\sigma_{p_{A,k}}$ = phenotypic covariance, $r_{g_{A,k}}$ = genetic correlation between asymptotic weight (A) and maturation rate (k), Δg = annual genetic progress calculated assuming a selection intensity of 1.65 and generation interval of 5.75 years.

variation or that certain environmental factors have significantly increased the phenotypic variation. Possible factors for low heritability estimate include: the use of data on only young llamas (1.5 year-old) and the lack of sire information in the pedigree that allowed for the use of only offspring–mother relationships during analysis. The fact that sire information was not accounted for in the current study may also be underestimating the additive genetic variance and so the heritability estimates obtained (Van Vleck, 1970; Harder et al., 2005; Sanders et al., 2006). Other of the reasons for the low heritability estimates can be attributed to the low nutritional level and poor quality of the pasture at the Quimsachata Experimental Station, creating large environmental variations.

No heritability estimates of growth curve parameters of young llamas could be found in the literature, and heritabilities of body weight of this species were also scarce. Choque and Rodríguez (1998) reported heritability estimates for birth weight, weaning weight and first shearing weight in Peruvian llamas of 0.047, 0.14 and 0.53, respectively. However, Wurzinger et al. (2005), evaluating the growth and body measurements traits in Bolivian llamas, reported moderate values of heritability (0.36) for body weight. García and Leyva (2007) working with both llama

strains, obtained estimates for live weight from birth to second shearing, ranging from 0.31 to 0.68 and 0.28 to 0.59 for K'ara and Ch'accu strains, respectively. The disagreement between our results and those of other authors may be explained by differences in methods of estimation, sample size used, biological or genetic differences between llama strains, etc.

Genetic correlation between the parameters A and k was relatively high and negative (Table 5). Negative correlation between these two growth parameters has been commonly reported from analyses of data from other livestock species (e.g., chicken: Mignon-Gasteau et al., 2000; pigs: Koivula et al., 2008; sheep: Silva et al., 2012; beef cattle: Lopes et al., 2012). The negative correlation between both parameters observed in the present study indicates that a rapid decrease in growth rate after inflection would result in a lower mature weight. Thus, from the standpoint of selection, the antagonism between both parameters would be favourable since animals with high mature weight values will take less time to reach their inflection point making it easier to identify high mature weight individuals earlier.

Despite the low estimates of heritability for the parameters A and k reported in the present study, some genetic gain through selection could be achieved for mature

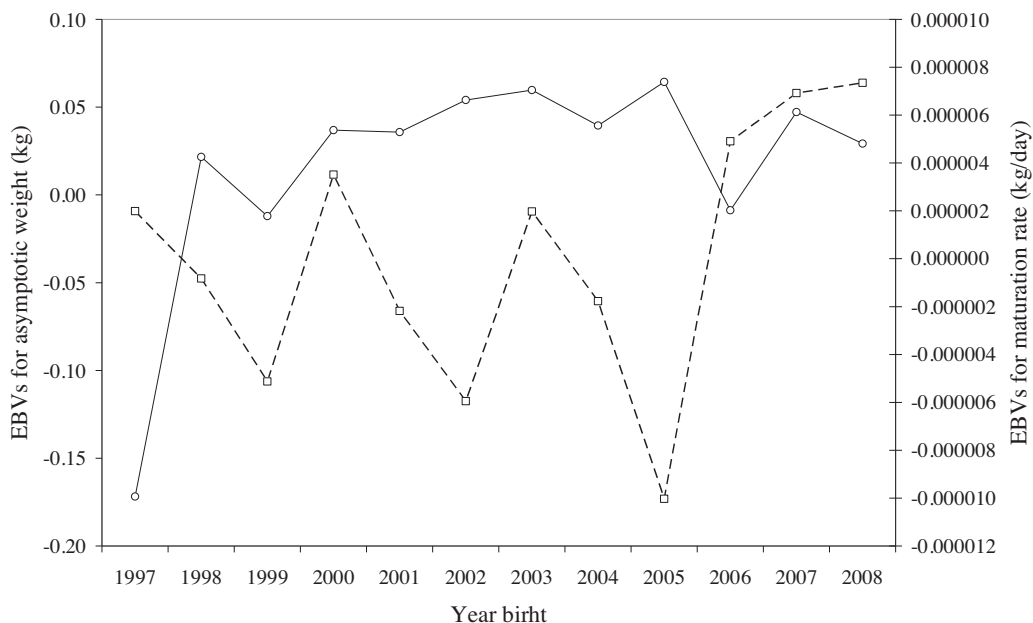


Fig. 4. Means of estimated breeding values (EBVs) for Gompertz functions of asymptotic weight (○) and maturation rate (□) by birth year from young llamas.

weight (Table 5). This parameter showed high genetic gain (0.28 kg/year) that k value ($0.00026 \text{ kg d}^{-1}$), suggesting that a selection program to change the slope of the growth curve from llamas would be feasible.

3.4. Genetic trend for parameters of the growth curve

Means of estimation breeding values (EBVs) by year for the parameters A and k by birth year of the young llamas are shown in Fig. 4. The EBVs for A have increased during the past 9 years. The main peaks were observed at 1998, 2000, 2003 and 2005, thereafter, these values decreased drastically up to 2006, and only turned positive in 2007. This is in agreement with the slightly genetic change for A (Table 5). Meanwhile, no clear pattern was observed for the parameter k from 1997 to 2005, but from 2006 to 2008 there was a marked increase. This trend confirms the slight improvement, if any, observed for k .

4. Conclusion

The Gompertz growth model was adequate in describing the growth pattern in Peruvian young llamas. The asymptotic weight was influenced by all fixed effects, but the maturation rate only by birth and year of birth. Animals from K'ara type reached higher weights at maturity and low precocity, whereas their maximum absolute growth rate occurred at an earlier moment than those for animals from the Ch'accu type. The heritabilities for asymptotic body weight and maturation rate were of low magnitude, indicating low genetic variability in young Peruvian llamas. Despite this, both parameters showed slight genetic gain, suggesting that a selection program to change the slope of the growth curve from llamas would be feasible. However, our results caution that factors such as sire information and sample size used should be accounted for in heritability estimates, and should make an effort to collect more reliable information.

Conflict of interest statement

The authors declare that no conflict of interest exists.

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