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Growth curves modeling of multirracial replacement milk heifers reared under pasture tropical conditions

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ADDITIONAL KEYWORDS

Dairy heifers' growth.
Nonlinear mixed models.
Crossbred animals.

SUMMARY

Nonlinear mixed models were used to describe the growth pattern of dairy replacement heifers from birth to conception age using the Gompertz, Von Bertalanffy, Verhulst and Logistic functions. The studied racial groups were Holstein-50% x Gyr-50% (HG), Holstein-50% x Jersey-50% (HJ) and Jersey-50% x Holstein-25% x Gyr-25% (JHG). Random effects were linked to asymptotic body weight (β0), constant of integration (β1) and maturation rate (β2) parameters in each mathematical function. Models with fixed effects and different combinations of random effects were compared according with their capacity to fit the data set. Residual variance, Akaike and Bayesian information criterion and residual plots were used to evaluate the models. In general, the addition of random effects in the models increased the accuracy in parameters estimates, however the best fit was achieved with the Von Bertalanffy function with random effects associated to β0, β1 and β2 parameters. This model improved the likelihood statistics and reduced the residual variance in 47% on average with respect to the fixed effects models. Compared with an optimal growth process under tropical condition, model predictions indicate that heifer within the three evaluated genotypes are reaching conception with inadequate weights as a consequence of the poor diet quality available during the rearing period. The results suggest that exist the opportunity to exploit the real potential growth of heifers improving the rearing management, nutrition and selecting for precocious animals.

Modelación de curvas de crecimiento de novillas lecheras de reemplazo criadas en condiciones tropicales de pastoreo

PALABRAS CLAVE ADICIONALES

Crecimiento en novillas lecheras.
Modelos mixtos no lineales.
Animales cruzados.

RESUMEN

Se usaron modelos mixtos no lineales para describir el patrón de crecimiento desde el nacimiento hasta la edad de concepción en novillas lecheras de reemplazo, utilizando las funciones de Gompertz, Von Bertalanffy, Verhulst y Logística. Los grupos raciales estudiados fueron Holstein-50% x Gyr-50% (HG), Holstein-50% x Jersey-50% (HJ) y Jersey-50% x Holstein-25% x Gyr-25% (JHG). En cada función matemática, se asociaron efectos aleatorios con respecto a los parámetros peso corporal asintótico (β0), constante de integración (β1) y tasa de maduración (β2). Modelos con efectos fijos y diferentes combinaciones de efectos aleatorios se compararon de acuerdo a la capacidad de ajustarse al conjunto de datos. Para evaluar los modelos se tuvo en cuenta la varianza residual, los criterios de información de Akaike y Bayesiano y los gráficos de residuos. En general, la adición de efectos aleatorios en los modelos, incrementó la precisión en las estimaciones de los parámetros, no obstante, el mejor ajuste se logró con la función Von Bertalanffy con efectos aleatorios asociados a los parámetros β0, β1 y β2. Este modelo mejoró las estadísticas de verosimilitud y redujo la varianza residual en 47% en promedio con respecto a los modelos de efectos fijos. En comparación con un proceso de crecimiento optimo bajo condiciones tropicales, las predicciones de modelo indicaron que las novillas dentro de los tres genotipos evaluados están alcanzando la concepción con pesos inadecuados como consecuencia de la baja calidad de la dieta disponible durante el periodo de cría. Los resultados sugieren que existe la oportunidad de explotar el verdadero potencial de crecimiento de las novillas al mejorar el manejo durante la crianza, la nutrición y a través de la selección de animales precoces.

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INTRODUCTION

Rearing replacement heifers is a fundamental process to determine the future productive and reproductive performance of animals (Wathes et al., 2014). An optimum growth rate during this phase is particularly important, as it determines an early onset of puberty and sexual maturity, reducing the age at first mating and ultimately at first calving (Wattiaux, 1997). Poorly grown animals usually have low conception rates, dystocia problems and inadequate lifetime productivity (Wathes et al., 2008). Similarly, overconditioned heifers also experience more dystocia cases and are more susceptible to fat deposition preventing mammary development, thereby affecting future milk yield potential (Cooke et al., 2013; Lohakare et al., 2012). Both, low and extremely high growth rates during the rearing period have been associated with delays in the age at first calving (Guedes et al., 2017), and thus an inefficient growth process since the non-productive period of the animals is extended, increasing the rearing cost which is considered one of the main expenses of dairy production systems (Pirlo et al., 2000; Cooke et al., 2013).

Research has shown that a moderate prepubertal growth rate followed by a more rapid postpubertal growth is an efficient strategy to breed replacement heifers with an adequate body weight and frame size at 15 months of age, expecting to calve at 24 months (Macdonald et al., 2005; Wattiaux, 1997). However, this is not a general rule, since under different production scenarios, the decision on when to start breeding will be determined by the quality of nutrition and growth rate during the rearing period (Wathes et al., 2008). In tropical regions, this mating age is not feasible because heifers are commonly underfed and receive poor management (Moss, 1993) leading to delay the beginning of their reproductive life and consequently increasing the age at first calving, usually above 30 months (Ugarte, 1991).

In order to improve heifers development through the rearing period under typical tropical conditions, monitor the growth pattern is fundamental to determine factors affecting production efficiency (Menchaca et al., 1996). Nonlinear models are an effective method to describe growth curves, as these functions allow to derive parameters with biological meaning, useful for understanding the growth behavior of animals under specific production conditions (Mazzini et al., 2003; Berry et al., 2005). Parameters as animal's age, growth rate and maturity can be obtained with these models, and be used for assessing different management factors regarding nutrition and reproduction. Also, growth curve parameters are highly heritable (Silva et al., 2002) and could be used in selection programs to genetically improve growth traits within heifers population (Lupi et al., 2015).

Usually, the adjustment of weight-age data through nonlinear models has been performed using ordinary least squares regressions, where errors are assumed to be homoscedastic and normally distributed (Wang and Zuidhof, 2004). Nevertheless, the unbalanced structure of the data, which is naturally generated by death or discard of animals during growth and the correlation of mesurements of an individual over time, tend to generate correlated errors and heterogeneous variances between observations from one age to another, violating some of the mentioned assumption and therefore, the parameters estimates may not be the most appropriate (Regadas-Filho et al., 2014; Tedeschi et al., 2000).

Another approach to model longitudinal growth data is the use of nonlinear mixed models. These models have the property to account for multiple sources of heterogeneity in data through the inclusion of random effects (Aggrey, 2009). In this way, mixed models separate the between and within animal variation allowing them to account for a portion of the heterogeneous variance of observations that increases over time, and with the covariance structure assumed with the random effects, some of the serial correlation between measurements is also controlled (Wang and Zuidhof, 2004). This methodology provides a flexible statistical framework useful to characterize growth curves at both, individual level as well as the population level (Harring, and Blozis, 2014; Aggrey, 2009). The objective of the present study was to identify the nonlinear function that best fit the growth data of multiracial dairy replacement heifers reared under tropical conditions, using the nonlinear mixed model metodology.

MATERIAL AND METHODS

DATA

The weight-age data used in the present study were collected from an intensive multirracial dairy production system, located at 926 m.a.s.l. in the municipality of Zarzal - Valle del Cauca, Colombia with an average temperature of 25 ºC, humidity of 70% and annual rainfall of 1200 mm/year. Registers of multirracial heifer's growth from birth to conception age were collected between 2003 and 2014. According to data availability three genetic groups were include in the study: Holstein-50% x Gyr-50% (HG – n=93), Holstein-50% x Jersey-50% (HJ – n=68) and Jersey-50% x Holstein-25% x Gyr-25% (JHG – n=35). A graphical analysis was conducted in each group, to identify and eliminate outliers. Only animals with coherent information and at least four records were maintained in the study. **Table I** shows the structure of the final data included in the analysis.

ANIMAL MANAGEMENT

Once the birth occurs, the calves were located in individual cribs where they were supplied with colostrum or milk and a calf concentrate until the day 15. Later, the calves were transferred to a bucket-stake system in paddocks with star grass (*Cynodon plectostachyus*), and they kept consuming milk (2 L morning and afternoon) and concentrate until 4 months of age. Between 4 and 8 months of age, the animals started a rotational grazing system in paddocks composed mostly of Pangola (*Digitaría decumbens*) and Guinea (*Megathyrsus maximus* Cv. Tanzania) grasses in association with *Leucaena leucocephala*. Animals were supplemented with 1-1.5 Kg of calf concentrate according to the body condition. Since 8 to 13 months of age,

Table I. Data summary used in the analysis (Resumen de los datos usados en el análisis)

		No. of weights		
Racial group	No. animals	Minimun	Maximum	Total
HG	93	4	20	1271
HJ	68	4	9	482
JHG	35	5	22	556
Total	196			2309

HG: Holstein-50% x Gyr-50%; HJ: Holstein-50% x Jersey-50%; JHG: Jersey-50% x Holstein-25% x Gyr-25%.

animals were moved to an extensive grazing system in large paddocks lacking of agronomics management and composed mainly of Pangola and Guinea grasses, native leguminous and weeds. Animals were supplemented with 0.5-1 Kg of heifer concentrate according to the body condition. From 13 months onwards, heifers were maintained under the extensive management without supplementation, until their first mating. **Table II** shows the proximate chemical composition of the diets consumed during the racial groups growth.

Mathematical models

The Gompertz, Von Bertalanffy, Verhulst and the Logistic growth functions were choosen to describe the growth of the genetic groups. These models (**Table III**) are commonly used to adjust growth curves data because their simplicity and the biological interpretation of their parameters (Forni et al., 2009; Macciotta et al., 2004; Lupi et al., 2015; Goldberg and Ravagnolo, 2015). In these models, y is the animal weight in an especific time; β0 represents the asymptotic body weight; β1 is the constant of integration; β2 is related to the maturation rate, M determines the point when the acceleration phase of growth ends and e is the base of the natural logarithms.

Estimation of growth curves

A first attempt was performed to adjust a general growth curve in each racial group using the NLIN procedure of SAS, and although convergence was achieved, the results lacked of biological significance and were not consistent with literature reports (data not shown). The correlation between mesurements on the same animal and the presence of animals with different numbers of body weight measurements, make the database heterogeneous and unbalanced. These data characteristics can lead to disrupt the basic assumptions of normality, variance homogeneity and independence of errors, and as a consequence the estimated parameters and their correspoding standard errors could be biased (Harring and Blozis, 2014). Another approach was then considered to adjust the overall nonlinear mean structure of the data and at the same time, take into account the variability between and within animals. This option was possible using the nonlinear mixed model methodology available through the NLMIXED procedure of SAS (Littell et al., 2006).

In a first step, using the mathematical models proposed (**Table III**), the individual growth curves of each animal in each genetic group were adjusted using ordinary least squares method (NLIN procedure). Individual estimates of the parameters (β0, β1 and β2) were used to estimate the variance-covariance matrix and residual variance. This information was required to be used by the NLMIXED procedure.

To control data heterogeneity, three random terms (0, 1 and 2) were established to account for between animals variations associated to β0, β1 and β2 parameters, respectively. The implementation of random effects in the models allows to account for parameters variation through estimate them individually by each animal within each racial group. These random effects are considered the difference between the individually fitted parameter for each animal and the population average (Aggrey, 2009).Models with fixed effects and different combination of random terms were evaluated according with their capacity to adjust the data set. The combinations were as follows: fixed effects models, random effects related to “β0”, “β0 and β1”, “β0 and β2”, or all random terms associated to “β0, β1 and β2”. To avoid problems with convergence (floating-point errors), the parameters were rescaled to bring their values to the same magnitude (Kiernan et al., 2012).

The analysis was carried up with the proc NLMIXED of SAS 9.4. This procedure fits nonlinear mixed models by numerically maximizing an approximation to the likelihood integrated over the random effects (Wolfinger, 1999). Although different approximations to the integral are available, in the present study, the approximation used in those models associated with random effects, was the first-order method of Beal and Sheiner (1982, 1988) available via METHOD=FIRO option. However, in the estimation of the fixed effects models, the approximation used was the adaptive Gaussian quadrature (Pinheiro and Bates 1995), since FIRO method is not appropriate if random effects are not considered in the model (Regadas-Filho et al., 2014). The estimated models were used to constructs

Table II. Chemical composition of diets available during the growth of the evaluated racial groups (Composición química de las dietas disponibles durante el crecimiento de los grupos raciales evaluados).

	Cynodon plectostachyus	Diet 1 (4-8 months)	Diet 2 (>8 months)	Calf concentrate	Heifer concentrate
DM %	21.1	21.3	29.0	90	90
CP % of DM	14.2	17	9.5	18	16
NDF % of DM	75.0	71.7	74.0	9.6	9.6
ADF % of DM	34.2	30.2	34.4	4.8	4.8
Lignin % of NDF	11.5	7.0	4.8	3.5	3.5
Ash % of DM	8.0	10.1	9.5	10.0	10.1
EE % of DM	0.6	0.2	0.9	6.3	6.4

DM: dry matter; CP: crude protein; NDF: neutral detergent fiber; ADF: acid detergent fiber; EE: ether extract.

Diet 1: samples of a forages mixture of pangola (*Digitaría decumbens*), guinea (*Megathyrsus maximus* Cv. Tanzania) and leucaena (*Leucaena leucocephala*), with a 35-40 days rest period.

Dieta 2: samples of a forages mixture of pangola (*Digitaría decumbens*) and guinea (*Megathyrsus maximus Cv.* Tanzania), with a 60-70 days rest period.

Table III. Nonlinear growth functions evaluated (Funciones de crecimiento no lineales evaluadas)

Model	Equation
Gompertz (Laird, 1965)	$y = \beta 0 e^{-\beta 1 e^{-\beta 2 t}}$
Von Bertalanffy (Von Bertalanffy, 1957)	$y = \beta 0 (1 - \beta 1 e^{-\beta 2 t})^3$
Verhulst (Macciotta et al., 2004)	$y = \beta 0 / (1 + \beta 1 e^{-\beta 2 t})$
Logistic (Nelder, 1961)	$y = \beta 0 (1 + e^{-\beta 2 t})^{-M}$

predictions for each observation in the data set using empirical Bayes estimates of the random effects (Littell et al., 2006). The predictions were obtained with the PREDICT statement available in the NLMIXED procedure.

Comparisons of models goodness of fit were evaluated according to the Bayesian information criterion (BIC), Akaike information criterion (AIC), residual variance (σ2e), non-singular and positive definite Hessian matrix and residuals against predicted values plot.

RESULTS AND DISCUSSION

Fitting nonlinear functions to animal growth data is a useful tool to describe factors affecting production efficiency within a particular environment and management system. This information can be used in the establishment of nutrition programs and genetic breeding to asses the genetic potential of the animals for growth traits (Menchaca et al., 1996; Marinho et al., 2013).

Table IV shows the information criteria for comparisson of fitted models. No problems with convergence and non-singular and positive definite Hessian matrix were found in the analysis. In general, the inclusion of random effects in the models improved the adjustment to the data set (low values of BIC, AIC and σ2e) compared with the fixed effect models. The best goodness of fit was achieved by the inclusion of random effects associated to "β0, β1 and β2" parameters in the Von Bertalanffy function (VB-012), followed by the Gompertz (G-012), Logistic (L-012) and Verhulst (V-012) functions. The residual variance with VB-012 was reduced in 47.6, 48.4, and 44.2 % for HG, HJ and JHG respectively, compared with the respective fixed effect models. This observed reduction in the residual variance is because the heterogeneity associated with the random effects allowed for the separation of the between and within animal variation (Littell et al., 2006).

Table IV. Fit criteria for model comparison (Criterios de ajuste para la comparación de modelos).

Model	Random Variables	HG			HJ			JHG		
		σ^2e	AIC	BIC	σ^2e	AIC	BIC	σ^2e	AIC	BIC
Gompertz	Fixed	22,6	11536	11557	27,0	4552,7	4569,4	23,7	5105,5	5122,8
	G-0	14,3	10684	10696	17,2	4284,3	4295,4	15,3	4724,7	4732,5
	G-01	13,3	10610	10627	16,4	4279,8	4295,3	14,2	4684,5	4695,4
	G-02	13,8	10649	10667	15,1	4241,8	4257,4	14,6	4707,0	4717,9
	G-012	12,8	10578	10603	14,6	4208,2	4230,4	13,7	4679,0	4694,6
Von Bertalanffy	Fixed	22,3	11501	11522	26,6	4539,2	4555,9	23,3	5085,3	5102,6
	VB-0	13,7	10577	10590	16,1	4230,3	4241,4	14,5	4665,1	4672,9
	VB-01	12,6	10496	10513	15,7	4230,0	4245,5	13,3	4623,2	4634,1
	VB-02	13,2	10547	10565	14,2	4187,8	4203,3	13,7	4647,2	4658,1
	VB-012	12,2	10459	10485	13,7	4150,4	4172,6	13,0	4616,8	4632,3
Verhulst	Fixed	23,5	11644	11665	28,4	4601,7	4618,4	25,1	5169,7	5186,9
	V-0	16,2	10968	10981	20,4	4420,8	4431,9	17,7	4877,8	4885,6
	V-01	15,4	10926	10944	18,6	4407,4	4423,0	16,6	4847,8	4858,7
	V-02	15,7	10937	10955	18,3	4389,9	4405,4	17,1	4863,1	4874,0
	V-012	14,9	10892	10917	17,6	4361,1	4383,3	16,0	4839,0	4854,5
Logistic	Fixed	22,9	11563	11591	27,4	4568,9	4585,7	24,1	5125,7	5143,0
	L-0	14,9	10780	10793	18,4	4337,1	4348,2	16,1	4777,5	4785,3
	L-01	13,9	10735	10717	17,6	4333,5	4349,0	15,0	4743,1	4754,0
	L-02	14,4	10746	10764	16,2	4297,4	4312,9	15,4	4760,7	4771,6
	L-012	14,9	10892	10917	15,6	4264,6	4286,8	14,5	4735,9	4751,5

σ^2e: residual variance; AIC: akaike information criterion; BIC: bayesian information criterion
HG: Holstein-50% x Gyr-50%; HJ: Holstein-50% x Jersey-50%; JHG: Jersey-50% x Holstein-25% x Gyr-25%.

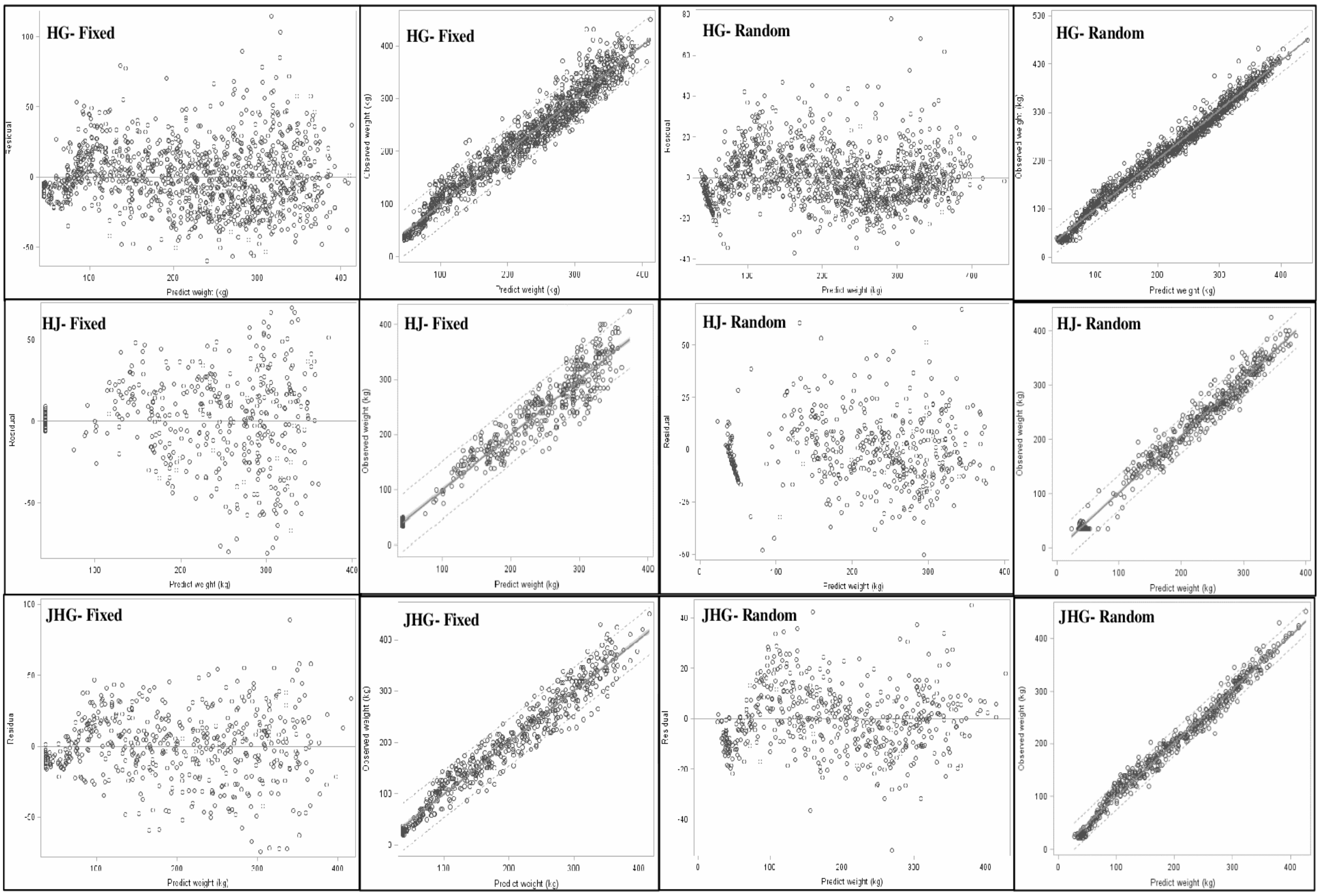

Figure 1. Residuals plots and linear relationship between predicted and observed weigths obtained with the Von Bertalanffy model, using fixed and random effects (VB 012 Gráficos de residuos y relación lineal entre los pesos observados y los predichos con el modelo Von Bertalanffy usando efectos fijos y aleatorios VB-012).

The variance partition is important because parameters estimates can vary from animal to animal even within each racial group, especially those related with asymptotic body weight and maturation rate (Regadas-Filho et al., 2014). In the case of VB-012, the error variation was partitioned in within animal variation and the between animal variation was further divided into variance due to asymptotic weigth (β0), constant of integration (β1), maturation rate (β2) and the covariance among them (Aggrey, 2009).

Residuals plots and the linear relationship between predicted and observed weights obtained with the fixed and VB-012 models, in each racial group are shown in **Figure 1**. The plots confirm the general trend in which the inclusion of random effects reduce the magnitude of the residuals (scattered observations closer to the zero line) and increase the predictive capacity of the model. In the HJ group, an apparent heteroscedasticity was corrected by the inclusion of random variables. In this case, to account for serial correlation between mesurements within the same animal and heterogeneity, the covariance structure of the residuals that are assumed to be independent with homogeneous variances (Harring and Blozis, 2014) apparently was enough to solve the problem.

The best fit to age-weight data achieved with the Von Bertalanffy function is similar to the reports found in other studies evaluating growth curves in Holstein Friesian cows (García-Muñiz et al., 1998; Berry et al., 2005), Nerolle cows (Marinho et al., 2013), Hereford males (Mazzini et al., 2003), Retinta cows (López de Torre et al., 1992) and Guzera animals and their crossbreds with Brown Swiss, Nellore, Chianina and Caracu breeds (Tedeschi et al., 2000).

The estimated parameters by the evaluated mathematical functions can be found in **Table V**. In the nonlinear mixed model methodology, the estimation of fixed effects is considered the mean value of each parameter (β0, β1 or β2) within the studied population, meanwhile, as individual growth curve parameters are adjusted for each animal at the same time, the random effects represent differences between the individually fitted parameter for each animal and the population average (fixed effect). The random effects are modeled assuming a normal distribution with zero mean and unstructured covariance matrix G (Aggrey, 2009; Regadas-Filho et al., 2014).

Figure 2 presents the general adjusted growth curve and an example of individual adjustment of a random animal obtained with VB-012 model. Although it has been reported that Von Bertalanffy function tends to overestimate initial weights (Freitas, 2005), this trend was only observed in the HJ group. In the other racial groups, the birth weights were in agreement with the observed data.

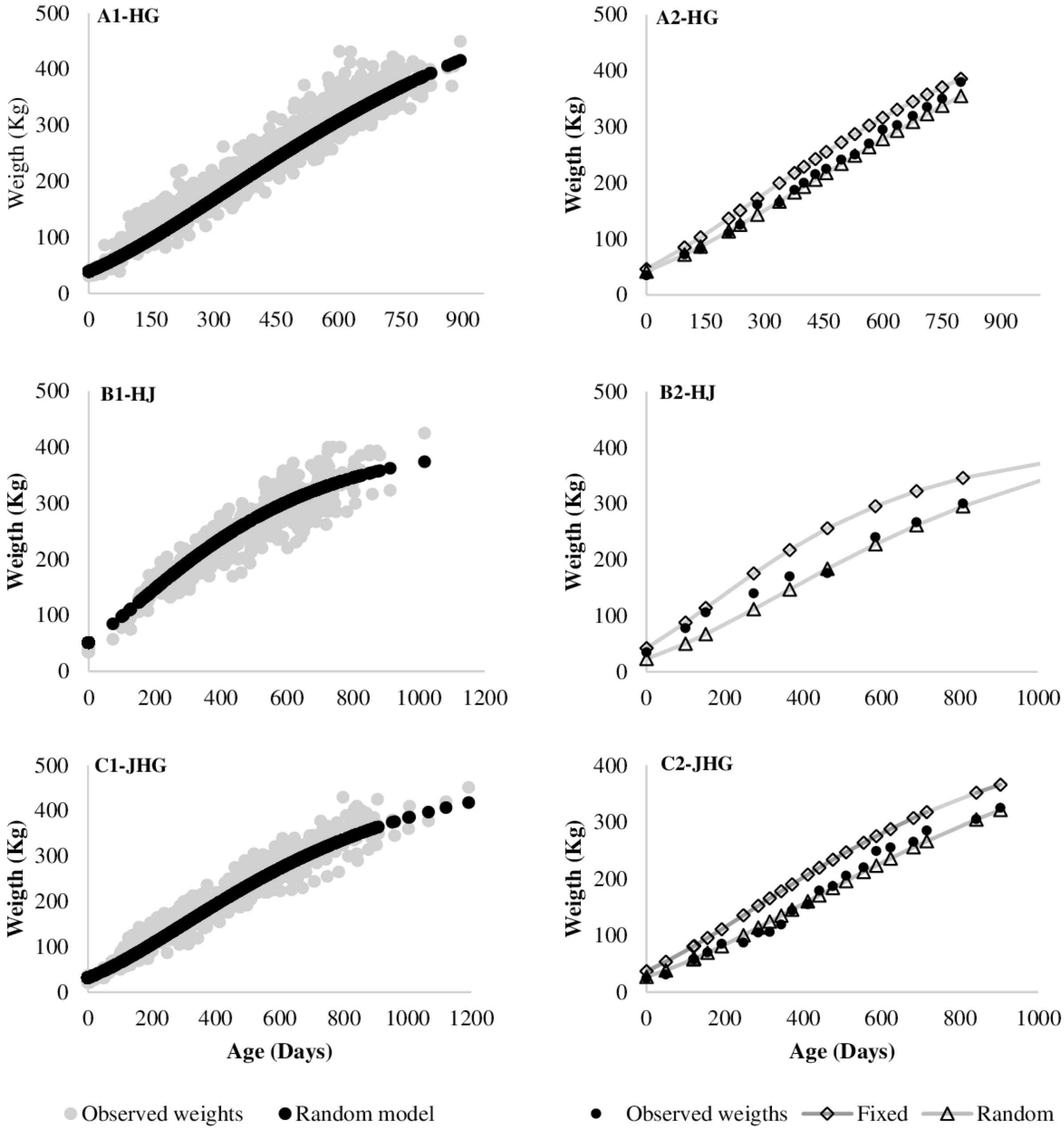

Figure 2. General fit of Von Bertalanffy model with random effects associated to β0, β1, β2 (A1, B1, Cl) and comparison of individual adjustment against its respective fixed effect versión of the mode1, using data of a random animal within each genetic group (A2, B2, C2) (Ajuste general del modelo Von Bertalanffy con efectos aleatorios asociados a f30, f31 y f32 (A1, B1, C1) y comparación del ajuste individual con su respectiva versión de efectos fijos, utilizando los datos de un animal aleatorio dentro de cada grupo genético (A2, B2, C2).

The estimates of β0 parameter obtained with the VB-012 model were 611 (± 15), 413 (± 10) and 495 (± 15) Kg for HG, HJ and JHG respectively. Since heifers' growth curves were estimated from birth to conception age (average 25 months), the values of β0 parameter do not represent the real asymptotic body weight (or mature weight) because the animals did not reach maturity (Marinho et al., 2013). Reliable estimates of asymptotic body weight only are possible when weight-age data available include animals older than 4-4.5 years old (Goldberg and Ravagnolo, 2015; Fox et al., 2004). Even when β0 estimates were obtained under the same environmental conditions, they are not comparable, because the racial groups evaluated do not present the same mature weights, given the genetic variation in live weight and body size of the breeds involved in the crosses (Berry et al., 2005). Similar β0 values were found compared with other reports in dairy cattle

Table V. Estimates of growth parameters and their standard error obtained with the evaluated nonlinear regression functions in each racial group (Estimaciones de parámetros de crecimiento y su error estándar obtenidos con las funciones de regresión no lineal evaluadas en cada grupo racial)

Model	Random Variables	HG[1]			HJ[2]			JHG[3]		
		β0 (s.e.)	β1/M (s.e.)	β2 (s.e.)	β0 (s.e.)	β1 /M (s.e.)	β2 (s.e.)	β0 (s.e.)	β1 /M (s.e.)	β2 (s.e.)
Gompertz	Fixed	500 (10)	2,3 (0,02)	0,0027 (7,3x10^{-5})	385 (8)	2,1 (0,05)	0,0036 (1,6x10^{-4})	444 (11)	2,4 (0,03)	0,0027 (1,0x10^{-4})
	G-0	530 (8)	2,4 (0,01)	0,0026 (4,4x10^{-5})	395 (8)	2,1 (0,03)	0,0034 (1,1x10^{-4})	464 (10)	2,4 (0,02)	0,0026 (6,5x10^{-5})
	G-01	541 (9)	2,4 (0,02)	0,0025 (4,2x10^{-5})	394 (8)	2,1 (0,04)	0,0034 (9,9x10^{-5})	459 (10)	2,4 (0,04)	0,0026 (6,4x10^{-5})
	G-02	516 (12)	2,3 (0,01)	0,0027 (8,5x10^{-5})	382 (8)	2,1 (0,03)	0,0036 (1,3x10-^{4})	431 (14)	2,4 (0,02)	0,0029 (1,4x10^{-4})
	G-012	526 (12)	2,4 (0,02)	0,0026 (7,8x10^{-5})	385 (8)	2,1 (0,03)	0,0035 (1,2x10^{-4})	448 (12)	2,3 (0,04)	0,0027 (9,1x10^{-5})
Von Bertalanffy	Fixed	556 (16)	0,6 (0,00)	0,0019 (6,8x10^{-5})	409 (11)	0,5 (0,01)	0,0028 (1,4x10^{-4})	485 (15)	0,6 (0,01)	0,0021 (9,3x10^{-5})
	VB-0	612 (11)	0,6 (0,00)	0,0018 (3,7x10^{-5})	423 (9)	0,5 (0,01)	0,0026 (8,5x10^{-5})	514 (13)	0,6 (0,00)	0,0019 (5,5x10^{-5})
	VB-01	632 (12)	0,6 (0,00)	0,0018 (3,5x10^{-5})	423 (10)	0,5 (0,00)	0,0026 (8,2x10^{-5})	512 (12)	0,6 (0,01)	0,0019 (5,3x10^{-5})
	VB-02	593 (16)	0,6 (0,00)	0,0019 (6,3x10^{-5})	406 (9)	0,5 (0,00)	0,0028 (1,1x10^{-4})	463 (24)	0,6 (0,00)	0,0022 (1,7x10^{-4})
	VB-012	611 (15)	0,6 (0,00)	0,0018 (5,4x10^{-5})	413 (10)	0,5 (0,00)	0,0027 (1,0x10^{-4})	495 (15)	0,6 (0,01)	0,0020 (7,8x10^{-5})
Verhulst	Fixed	421 (5)	6,3 (0,11)	0,0050 (9,3x10^{-5})	352 (6)	5,5 (0,26)	0,0059 (2,3x10^{-4})	391 (7)	6,6 (0,20)	0,0048 (1,4x10^{-4})
	V-0	438 (6)	6,4 (0,08)	0,0049 (6,3x10^{-5})	357 (6)	5,2 (0,17)	0,0056 (1,7x10^{-4})	402 (8)	6,5 (0,14)	0,0046 (9,9x10^{-5})
	V-01	440 (6)	6,5 (0,12)	0,0049 (6,2x10^{-5})	355 (6)	5,5 (0,26)	0,0057 (1,6x10-4)	396 (7)	6,4 (0,20)	0,0047 (9,8x10^{-5})
	V-02	430 (5)	6,4 (0,08)	0,0049 (8,7x10^{-5})	349 (6)	5,3 (0,16)	0,0058 (1,9x10^{-4})	387 (9)	6,5 (0,14)	0,0048 (1,5x10^{-4})
	V-012	433 (5)	6,4 (0,13)	0,0049 (8,8x10^{-5})	349 (6)	5,4 (0,17)	0,0057 (1,8x10^{-4})	392 (8)	6,4 (0,23)	0,0047 (1,4x10^{-4})
Logistic	Fixed	464 (8)	3,1 (0,03)	0,0034 (8,2x10^{-5})	369 (7)	2,9 (0,07)	0,0044 (1,7x10^{-4})	420 (9)	3,2 (0,05)	0,0034 (1,1x10^{-4})
	L-0	488 (7)	3,2 (0,02)	0,0033 (5,2x10^{-5})	376 (7)	2,9 (0,04)	0,0042 (1,3x10^{-4})	436 (9)	3,2 (0,03)	0,0032 (7,7x10^{-5})
	L-01	496 (8)	3,2 (0,03)	0,0033 (5,1x10^{-5})	376 (7)	2,9 (0,06)	0,0042 (1,2x10^{-4})	432 (9)	3,2 (0,05)	0,0033 (7,4x10^{-5})
	L-02	477 (8)	3,2 (0,02)	0,0034 (7,3x10^{-5})	366 (7)	2,9 (0,04)	0,0044 (1,4x10^{-4})	412 (11)	3,2 (0,03)	0,0035 (1,3x10^{-4})
	L-012	433 (5)	6,4 (0,13)	0,0049 (8,5x10^{-5})	367 (7)	2,9 (0,04)	0,0029 (1,3x10^{-4})	422 (10)	3,2 (0,05)	0,0033 (1,0x10^{-4})

[1] Holstein-50% x Gyr-50%
[2] Holstein-50% x Jersey-50%
[3] Jersey-50% x Holstein-25% x Gyr-25%.

where maturity ages were included in the evaluation (Perotto et al., 1992; García-Muñiz et al., 1998) suggesting that some individuals within each racial group achieved their conception in very late ages.

The values of β1 parameter for the HG, HJ and JHG racial groups were 0.6 (± 0.004), 0.5 (± 0.005) and 0.6 (±0.006) respectively, similar to those found by Berry et al. (2005) and García-Muñiz et al. (1998) with the Von Bertalanffy function in dairy cattle. This parameter correspond to the constant of integration and although it has no biological interpretation, it is used to calculate the inflection point and adjust the values of initial weight, so it is usually associated with birth weights (Tedeschi et al., 2000; Lupi et al., 2015).

The obtained estimates of β2 parameter were 0.0018 (± 0.000054), 0.0027 (± 0.00010) and 0.0020 (± 0.000078) for HG, HJ and JHG respectively. This value represents the relative growth rate at which the animal approaches the asymptotic body weight, for this reason it is known as maturity or precocity rate. Large β2 values indicate early maturing animals as they reach the asymptotic weight in less time, meanwhile, small values indicate animals that tend to mature more slowly (Berry et al., 2005; Tedeschi et al., 2000; Lupi et al., 2015; Goldberg and Ravagnolo, 2015). Precocity has an extremely important effect on puberty and sexual maturity of dairy replacement heifers, because precocious females reach these growth phases earlier and start their reproductive life sooner (Moreira et al., 2016). The results suggest that of the three racial groups, HJ is the most precocious group. However, as mentioned before, this parameter is also not comparable between the racial groups studied, due to the difference between mature body weights. It is well known the negative correlation between mature body weight and maturation rate parameters, suggesting that early maturing animals have lower mature weight. Thus, to identify precocious heifers, it is necessary to study animals with similar mature body weight. Nevertheless, these values are lower than those found in other studies in dairy cattle (0.0030-0.089; Berry et al., 2005; Perotto et al., 1992), suggesting that the current diet (**Table II**) characterized by high levels of fiber and low protein, does not allow the proper development of heifers. Therefore, there is potential for growth in the racial groups that can be exploited in a better way through a better nutrition.

The heifers rearing period is a fundamental process that influence their future perfomance in terms of productivity, fertility and longevity (Teodoro et al., 2013). The most important consideration is to ensure an adecuate growth rate that allows to obtain an appropriate body weight (according to the maturity weight of each breed) and frame size at first calving (Wathes et al., 2014). There is a general agreement that heifers should present their first breeding at about 13-15 months of age with 50-60% of their mature weight, to ensure a first calving between 22-24 months with 85-90% of the mature weight (Wattiaux, 1997; Fox et al., 2004; Hoffman, 1997; Wathes et al., 2014). Under tropical conditions is difficult to meet these standards because heifers' nutrition and management is often overlooked. Heifers usually graze on low quality pastures with little or none supplementation, avoiding that animals can fulfill their nutritional requirements. In addition of the inadequate nutrient intake, the adverse environmental conditions and the presence of diseases and parasites also have restricted heifers' growth rates delaying first breeding and first calving (Moss, 1993; Ugarte, 1991). Haworth et al. (2008) suggest that the optimal age at first calving in tropical conditions should be between 24-30 months, as these animals have the highest lifetime production and spent more life time producing milk.

Observing the average conception age of studied population (25 months), it is evident that the racial groups presented an inefficient rearing period, since age at first calving is expect to ocurr at 34 months on average, well above of that proposed by Haworth et al. (2008). To understand the growth behaviour of the racial groups, a possible comparison could be made with the weight at breeding and conception of a reference Holstein animal, given the large sizes of most of the breeds involved in the studied crosses. Assuming the upper limit of the proposed optimal age at first calving in tropical conditions (30 months), the conception must occur at 21 months of age with an expected body weight between 360-400 Kg (Wattiaux, 1997).According with the adjusted model, the estimated body weights at 21 months of age were 321, 310 and 283 kg for HG, HJ and JHG respectively. With the current management of the evaluated productive system, all racial groups would attain the conception in an underdevelopment state, with 39, 50 and 77 kg of body weight below the recommended value in the case of HG, HJ and JHG respectively. These estimates in conception body weight could be different if comparisons are made with the real maturity weight of each racial group, however they are useful as indicators that animals might calve at 30 months but also in underdevelopment state, increasing the risk of dystocia cases due to suboptimal skeletal growth (Hoffman, 1997), besides, taking into account that younger cows continue to growth after their first calving, the nutrients required for growth will be obtained at the expense of fertility (Cooke et al., 2013). Thus, an inadequate growth rate during rearing has greater detrimental effects on postpartum reproduction and lactation performance in primiparous cows (Ciccioli et al., 2003).

Table VI. Variance and covariance components obtained with the Von Bertalanffy function in each racial group (Componentes de varianza y covarianza obtenidos con la función Von Bertalanffy en cada grupo racial)

Racial group	Random variables	σ^2 b0	σ^2 b1	σ^2 b2	Cov b0,b1	Cov b0,b2	Cov b1,b2
HG	b0, b1, b2	94,13	0,0296	0,00036	2,0583	0,0278	0,000005
	(p-value)[1]	(<0,0001)	(<0,0001)	(<0,0001)	(0,0004)	(0,0328)	(0,0043)
HJ	b0, b1, b2	68,15	0,0152	0,00070	2,0553	0,0377	0,000015
	(p-value)	(<0,0001)	(0,1517)	(<0,0001)	(<0,0001)	(0,0025)	(<0,0001)
JHG	b0, b1, b2	58,53	0,0273	0,00028	0,8867	0,0125	0,000004
	(p-value)	(0,0008)	(<0,0001)	(0,0020)	(0,0893)	(0,1607)	(0,1511)

[1] P-value significant with P<0.05.

Animals with a late first calving (>30 months) as in the analized genetic groups, have a inneficient performance in terms of productivity, fertility and longevity. Inefficiencies in reproductive performance are characterized by low conception rates, higher days to first service and longer intervals from calving to conception. At the same time, the survival rate is low leading to reduce the longevity, resulting in a short productive life and thus an uneconomic process since the high rearing costs are unlikely to be repaid (Cooke et al., 2013; Wathes et al., 2008; Hultgren and Svensson, 2009; Oliveira Júnior et al.,2016). Most of the experiences show that 23 to 25 months is the optimal age range at first calving where heifers can express their productive potential without any adverse consequences in the long term, as long as the heifers are of an appropiate weight and body size (Wathes et al., 2014; Ettema and Santos, 2004; Cooke et al., 2013). Dobos et al. (2004) reported that for each month's delay in the age at first calving from 34 to 25 months in grazing Holstein heifers, an increase in milk production (56.7 L), milk fat (1.78 Kg), milk protein (1.45 kg) over the first 3 lactations were observed. The evidences suggest that within the studied population, improvements in management and nutrition to exploit the real potential growth of heifers during their rearing, offers the opportunity to maximize milk yield, fertility and productive life, and at the same time reduce the costs associated with this productive phase.

The variance and covariance components of the random effects estimated with VB-012 model are shown in **Table VI**. In general, the variance components associated to β0, β1 and β2 parameters were significant ($P<0.05$), except for β1 in the case of HJ group. These results indicate that random effects accounted for between animal variation related with these parameters allowing them to vary around from its corresponding mean parameter within the evaluated racial groups, which is appropriate, because the growth pattern among heifers is not identical (Wang and Zuidhof, 2004). All covariance components between the random effects were positive and only in the JHG group did not show to be significant ($P>0.05$).

The variance components significance yields important information suggesting variability in growth patterns within the racial groups. A special emphasis must be placed on variability related to asymptotic body weight (β0) and maturation rate (β2) parameters since it can be used in genetic programs to select the individuals with the best perfomance associated with these traits (Regadas-Filho et al., 2014; Menchaca et al., 1996).

In the present study, selecting animals with the highest asymptotic weights (equivalent to the conception weight) would be advantageous because the sexual maturity of heifers depends mainly on body weight. Also, research has shown a positive relationship between body weight at first calving and the subsequent milk production potential of the animals (Wattiaux, 1997; Moss, 1993; Hoffman, 1997; Dobos et al.,2004). Heifers could also be selected by maturation rate, in order to identify the most precocious females with an adequate pre and postpubertal growth rates allowing to reduce the conception age and therefore the first calving (Menchaca et al., 1996). In this way, the establishment of animal genetic programs for growth traits improvement through selection processes within each genotype, becomes another alternative to make the rearing process more efficient.

The significance of variance components shown in **Table VI** also suggest that inclusions of random effects to account for population variability, especially regarding to asymptotic weight and maturation rate parameters are fundamental to reduce the residual variance and therefore improve the predictive capacity of the model. Thus, the nonlinear mixed model methodology becomes a useful tool to handle longitudinal unbalanced growth data, because allows to control in part autocorrelation in repeated measures and trough the inclusión of random effects is possible to account for parameters heterogeneity before testing for fixed effects. Also, the predicted body weights are expected to be closer to the observed values because during random effects estimation all data is used (Aggrey, 2009).

CONCLUSIONS

The Von Bertalanffy function with random effects, associated to asymptotic body weight, constant of integration and maturation rate, was the function that best fit the heifers growth data within each racial group studied. The inclusión of random effects in the model controlled, in part, the heterogeneous variances and covariance effects present in the data, reducing the residual variance and improve the accuracy in parameters estimation.

Estimated growth curves indicate that animals are reaching conception in underdevelopment state, however there is potential to improve growth efficiency trough a better rearing management, nutrition and the stablishment of genetic programs to select individuals with the best behavior in growth characteristics.

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