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Comparison of B-splines and non-linear functions to describe growth patterns and predict mature weight of female beef cattle

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Submitted: 16 February 2015 Accepted: 29 May 2015 Published online: 9 July 2015

Abstract.

The objective of this study was to compare the ability of Basis spline (B-spline) models and five non-linear functions (Richards, Brody, Von Bertalanffy, Gompertz and Logistic) to describe the growth of females of a beef cattle breed and predict cow mature weight (A). Random regression models that included animal variation within function parameters were fitted using mixed model procedures. Comparisons were made among these functions for goodness of fit, standardised residuals and biological interpretability of the growth curve parameters. The B-spline function showed the best goodness of fit and within non-linear functions, the Richards and Von Bertalanffy functions estimated bodyweight at different periods accurately. The method of fitting the residual variance that provided the best goodness of fit in the model was the constant plus power variance function. The Richards function was found to be the best non-linear function and was compared with the B-spline function to predict mature weight. When the A parameter was estimated using fixed effects, it had a low correlation with the actual mature weight of the cow and the use of this estimate yielded no more gain in predictive accuracy of mature weight than the use of average breed mature weight. When A was estimated using fixed and random effects, it had a moderate correlation with actual mature weight for the B-spline and Richards functions. The use of both types of effects to estimate the maturity index reduced the error compared with the use of average mature weight, especially for the B-spline function, which is recommended as the best function to describe animal growth and predict mature weight.

Additional keywords: adult weight, B-spline, cows, growth curve, random regression.

Introduction

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The pattern of growth of beef and dairy cattle can be related to the efficiency of the production system and the longevity of the cow (Engelken 2008). The degree of maturity of a heifer [bodyweight (BW) related to mature weight] is used to estimate its sexual maturity and different thresholds are currently being discussed as optimal for first matings in beef heifers (Martin *et al.* 2008; Stockton *et al.* 2014; Titterton *et al.* 2015). Therefore, accurate knowledge concerning the growth of females of a breed in a given production system could be used to manage them to achieve a desired degree of maturity at key management events, such as first mating.

Non-linear models have been used to describe animal growth using BW recorded throughout the animal's lifespan (Fitzhugh 1976). Another approach to describe growth is using high order polynomial, which tend to produce a better fit but use model parameters that do not have biological meaning. A particular case of polynomial models is the spline, a piecewise polynomial of degree n whose function values and first $n-1$ derivatives agree at the points where they join (knots) (Meyer 2005b). Basis spline (B-spline) linear regression models can be used as an alternative to high order polynomials and complicated non-linear models (Boligon *et al.* 2012). A description of the mean growth curve (linear or non-linear) of a population is not enough if decisions have to be taken at the cow level. The environmental and animal effects that modify the mean growth curve could be estimated using random regression models (Schaeffer and Jamrozik 2008).

The aim of this study was to: (i) compare non-linear and B-spline models as tools to describe growth from birth to maturity of females of the Parda de Montaña breed; a beef cattle breed managed in extensive conditions, taking into account the variability between animals, and (ii) evaluate the ability of these models to predict mature weight of heifers based on individual data recorded until their first mating.

Materials and methods

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Data

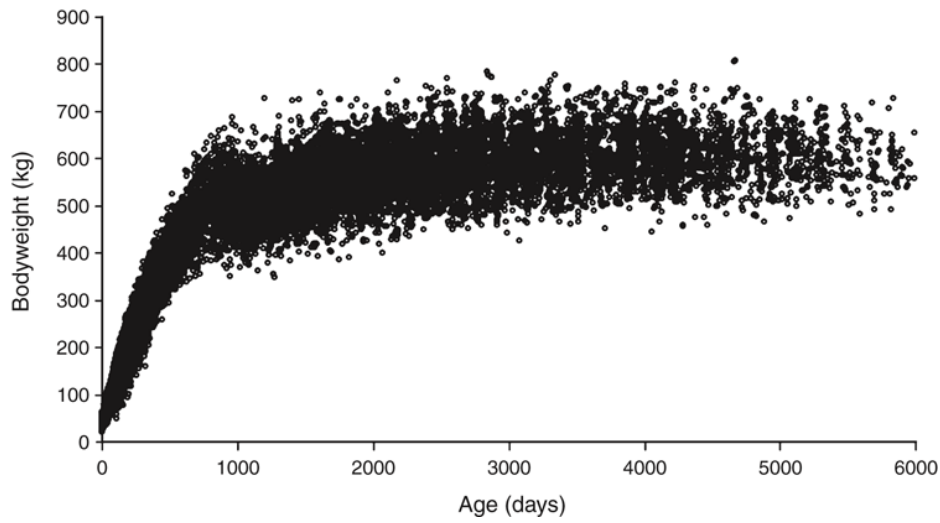
The data were collected at La Garcipollera Research Station (Spain, 42°37'N, 0°30'W; 945 m above sea level), in the mountain area of the southern Pyrenees (Spain), and at the CITA research centre in Zaragoza (41°43'N, 0°48'W; 225 m above sea level), for 23 years, between 1987 and 2010. The data comprised BW records of Parda de Montaña females (60–100 adult cows per year over the study period) that were within the experimental herd from birth to maturity. Parda de Montaña is a suckler cattle breed widely spread throughout northern Spain that came from the ancient Brown Swiss

and its crosses with local breeds. It had been used as a dual-purpose breed, milk-beef (Álvarez-Rodríguez *et al.* 2010), but in recent decades it has been selected primarily for beef production and mothering abilities (calving ease and weaning weight). The maturing rate of this breed was considered intermediate between highly specialised, late-maturing beef breeds and lower meat-producing, early-maturing hardy breeds (Alberti *et al.* 2005).

The management of the experimental herd consisted of housing during winter, grazing on high mountain pastures (1500–2200 m above sea level) during summer and grazing on valley meadows and forest pastures (945–1500 m above sea level) during spring and autumn. The reproductive management of the herd consisted of two calving seasons; spring (March–May) and autumn (September–November). Further details of herd management can be found in Casasús *et al.* (2002). Cows remained in the herd until either natural death occurred or they were culled for sanitary reasons or reproductive failure. Calves were raised with their dams and weaned at ~5 (autumn-born calves) or 6 months of age (spring-born calves) (Villalba *et al.* 2000). After weaning, replacement heifers were raised on pasture and forage plus concentrates during winter, and were bred by natural service at ~2 years of age.

The dataset consisted of a total of 18 627 BW records from 1189 females. They were weighed within a week of birth, at weaning, during rearing, at calving, at the end of lactation, when they were turned-out to high mountain pastures and housed back at the farm facilities, and at other different times between these time points. On average each female had 16 BW records, but the number of records ranged between 2 (birth and weaning) and 73 (mature cows enrolled in several experimental tests involving serial weighing) per female. The distribution of BW records relative to age in the dataset is presented in Fig. 1.

Fig. 1. Bodyweights relative to age in a dataset containing records from Parda de Montaña females between birth and maturity.



Non-linear functions

Five non-linear functions frequently used for describing growth curves in cattle were tested: Richards, Brody, Von Bertalanffy, Gompertz and Logistic as proposed by Fitzhugh (1976). These non-linear functions are special cases of the four-parameter non-linear function,

$$y_t = A(1 - b^{-kt})^M \quad (1)$$

where y_t = observed BW (kg) at age t (day), A = the asymptotic limit of BW (kg) when age t approaches infinity, b = integration constant, k = fractional rate of maturation (1/day), M = shape parameter determining the position of the inflection point of the curve. When the M parameter is fixed at 1, 3, and -1 , the functions corresponds to the Brody, Von Bertalanffy, and Logistic functions, respectively. The Gompertz function has three parameters, with $M \rightarrow \infty$, and is defined as,

$$y_t = Ae^{(-be^{-kt})} \quad (2)$$

Some of the parameters obtained from these functions have biological interpretation. The A parameter is an estimate of mature BW (kg), k is the fractional rate of maturation (1/day) and Taylor (1965) referred to k^{-1} as the maturing interval; a standard time scale for measuring changes in degree of maturity. Further growth traits were obtained in addition to these aforementioned traits: birthweight (calculated at $t = 0$), BW (y^*) (kg) and age (t^*) (day) at the point of inflection, average absolute maturing rate (v) (kg/day), average absolute growth rate (v^*) (kg/day), age at puberty (estimated at 56% of mature BW, according to Freetly *et al.* (2011), $P^{56\%}$), and age to reach maturity [estimated at 98% of asymptotic BW, according to Johnson *et al.* (1990), $P^{98\%}$].

B-spline functions

B-spline functions can be defined recursively (Meyer 2005b). Basis functions of degree $P = 0$ have values of unity for all points in a given interval, and zero otherwise. For the k th interval given by knots T_k and T_{k+1} with $T_k \leq T_{k+1}$,

$$B_{k,0}(t) = \begin{cases} 1 & \text{if } T_k \leq t \leq T_{k+1} \\ 0 & \text{otherwise.} \end{cases} \quad (3)$$

Higher degree basis functions, $B_{k,p}$ for $P > 0$, are then determined from the values of the lower degree basis functions, already evaluated, and the width of the adjoining intervals between knots. The general relationship is:

$$B_{k,p}(t) = \frac{t - T_k}{T_{k+p} - T_k} B_{k,p-1}(t) + \frac{T_{k+p+1} - t}{T_{k+p+1} - T_{k+p}} B_{k+1,p-1}(t) \quad (4)$$

According to similar analyses (Meyer 2005b; Boligon et al. 2012) linear, quadratic and cubic polynomials were considered for each individual segment, with basis functions of degree $P = 1, 2$ and 3 , respectively. Using spline functions with $P = 1$ can yield 'wiggly' estimates of curves but minimise the smoothly influence data outside the local interval has on the fitting of the polynomial within the local interval, whereas high degree polynomials produce smoother fit but with more influence in the local interval of data outside the interval (Meyer 2005b). The m knots divide the age at recording into intervals related to physiological events (i.e. age at knot of 180, 365, 700, 1000 days) and the external knots were located on ages 0 and 3000.

Statistical analyses

The models were fitted using the *nlme* and *splines* procedures in version 2.15.2 of the R statistical software package (Pinheiro et al. 2008). Mixed models were used to fit the functions (either non-linear or B-spline) to data with parameters of the function defined as fixed effects (i.e. describing the population) and as random effects (i.e. describing the individual deviation from the mean value of the population). The model used for the most complex non-linear function (Richards) was:

$$y_{ijlm} = (A_{season_i} + A_{dam_age_j} + \alpha_l)(1 - (b_{season_i} + b_{dam_age_j} + \beta_l)^{-(k_{season_i} + k_{dam_age_j} + \kappa_l)t})^{(M_{season_i} + M_{dam_age_j} + \mu_l)} + \varepsilon_{ijlm} \quad (5)$$

where y_{ijlm} is BW at age t , A_{season} , b_{season} , k_{season} , M_{season} and A_{dam_age} , b_{dam_age} , k_{dam_age} , M_{dam_age} are the fixed effects of birth season i (spring, autumn) and dam age j (≤ 4 years, >4 years) on the A , b , k and M parameters, and α_l , β_l , κ_l and μ_l are random effects of animal l on the A , b , k and M parameters, respectively.

The model used for B-splines functions was

$$y_{ijlm} = \sum_{r=1}^k (Season_{ri} + Dam_age_{rj} + \varphi_{rl}) B_r(t) + \varepsilon_{ijlm} \quad (6)$$

where y_{ijlm} is BW at age t , k is the number of regression coefficients fitted (depending on number of knots and polynomial order), $Season_{ri}$ and Dam_age_{rj} are the fixed effects affecting the coefficient r for season i and dam age j , and φ_{rl} is the random effect of animal l affecting coefficient r .

In all models, the random coefficients are modelled with an unstructured matrix of co-variances. The variance of residual error (ε_{ijlm}) was included in the models with no heteroscedasticity (constant residual variance), using the power variance function (variance related to BW) or the constant plus power variance function (equivalent to power variance function but with a constant value at low BW).

The models were compared using the lack of solution (no convergence in the iterative procedure) and goodness of fit. Goodness of fit was evaluated using $-2 \times \log$ -likelihood of the model (the lower the better), Akaike information criterion (AIC) (the lower the better) and Bayesian information criterion (BIC) (the lower the better). The AIC and BIC considered the lack of fit and the number of parameters estimated in the model. The AIC can be used to compare models including the same fixed effects but different variance structures. The BIC provides a similar assessment except it attributes a higher penalty to models containing a larger number of parameters than the AIC. Standardised residuals of the different functions were obtained as the difference between estimated BW and actual BW divided by the standard deviation of the actual BW at the age of estimation.

To determine the predictive ability of the non-linear and B-spline models 100 animals were selected at random that had: (i) actual mature BW data (more than two weights after 1500 days) and, (ii) at least four weights distributed between birth and 700 days (key date surrounding the first mating decision) available. A new subset of data (TEST_HF) was constructed excluding the records above 700 days for these 100 animals (HF females) simulating the data available for heifers before first mating, and including all BW records from the remaining females in the dataset. Predictions of mature BW and maturity index (BW/mature BW) for HF females obtained from the non-linear and B-spline models were compared with actual mature BW (average calving weights above 1500 days) using the Pearson correlation coefficient. The slope obtained from the linear regression of actual values (Y) on estimated values (X) was tested to be equal to 1 using a t -test in order to check the accuracy of prediction (Tedeschi 2006). Mean absolute

percent error (MAPE, $\frac{|estimated\ value - actual\ value|}{actual\ value} \times 100$) was also calculated as proposed by Stockton et al. (2013).

Results and discussion

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Goodness of fit of the models

Results comparing the goodness of fit for the different models are presented in Table 1. The best fitting B-spline function included three internal knots located at 365, 700, and 1000 days of age, and two external knots located at 0 and 3000 days. The internal knots were associated with events in the female's life, such as puberty, breeding and first calving, similar to the knots described by Boligon et al. (2012). In comparison Blanco et al. (2010), when analysing insulin-like growth factor-1 plasmatic concentrations in Parda de Montaña males from birth to slaughter at 1 year, described a single knot at weaning corresponding to the point of maximum change in growth rate. The different feeding systems used for males and females from weaning up to 365 days of age may explain why the inclusion of the weaning knot in the B-spline curve describing female's growth did not improve the goodness of fit. The male feeding system from weaning was based on *ad libitum* concentrate whereas the female diet was restricted and based on hay.

Table 1. The log-likelihood, Akaike information criterion (AIC), and Bayesian information criterion (BIC) for different non-linear functions and the B-spline function when fitting data from Parda de Montaña females

Function	Criteria		
	-2 log-likelihood	AIC	BIC
Non-linear			
Richards	183 333	183 379	183 560
Brody	183 684	183 715	183 841
Von Bertalanffy	184 590	184 623	184 749
Gompertz	185 666	185 670	185 825
Logistic	184 592	184 623	184 749
B-spline	180 430	180 471	180 578

A linear polynomial adjustment had the best agreement with data for the basis function of the B-spline. Higher order polynomials yielded slightly better likelihood and lower residuals (data not shown) but the linear model had lower AIC and BIC with less parameters. Thus, the first degree B-spline model was compared with the five non-linear models.

The model for the Richards function that contains four parameters (A , k , M and b) as random effects did not converge in the iterative procedure. A possible reason could be that there was a strong correlation among these parameters in the fittings process (in both the random and fixed component, $r > 0.9$) as described in other studies (Fang and Bailey 2001; Giraldo *et al.* 2002). In subsequent analyses of the non-linear functions, only the A , k , and M (if included in the model) parameters were included as random.

The B-spline function had better values of agreement with data than any of the non-linear functions. Conversely, Aggrey (2002) reported that non-linear models had better fit than splines for poultry growth data; however, their model did not include the random regression coefficients, in contrast to the approach presented in this study. Spline functions have been used to describe growth in Angus (Meyer 2005b), Gelbvieh (Iwaisaki *et al.* 2005), Polled Hereford (Meyer 2005a), Canchim (Baldi *et al.* 2010) and Nelore (Boligon *et al.* 2012) cattle, but were not compared with other functions in any of these studies.

In female beef cattle, different non-linear models have been used and compared, but the best equation to describe growth or the method to model residual variance is not clear as they both depend on breed (Freetly *et al.* 2011) and sometimes on data structure (Forni *et al.* 2009). In the present study, the Richards function provided the best goodness of fit with the lowest AIC and BIC values among the non-linear functions (Table 1). Similarly, Tj rve and Tj rve (2010) found that the Richards function or some reparametrisation of it was the best function to fit simulated data. The Von Bertalanffy function had good agreement with data whereas the Logistic function had the worst fit. The Richards and Brody functions were used in Hereford data (Brown *et al.* 1976; DeNise and Brinks 1985; Doren *et al.* 1989) because they produced the best goodness of fit to actual data according to the sum of squared deviations. Likewise, these two equations were chosen to describe the growth of Angus females because of their goodness of fit and the parameter estimates are easily interpreted (Beltran *et al.* 1992). In Nelore growth data the Brody function provided a more accurate fit whereas the Logistic function was found to be the least accurate based on AIC and BIC (Forni *et al.* 2009).

Observed BW and mean predicted growth curves obtained from different functions are shown in Fig. 2. The accuracy of prediction varied over the different time periods: at birth, during suckling (until ~140–170 days of age, depending on the calving season), during rearing from weaning until first mating (until 700 days), then from first mating until first calving (up to 980 days) and finally to maturity. The B-spline function had the lowest standardised residuals for all periods and, thus best described actual cow BW (Fig. 3). Among the non-linear functions, the Richards and Von Bertalanffy functions had the most accurate estimate of BW at all ages. Both non-linear functions had residuals similar to the B-splines function before 365 days of age with slightly higher residuals around first calving. Similarly, Brown *et al.* (1976) reported that the Richards function gave a generally unbiased fit at all ages and the Von Bertalanffy function fitted reasonably well over all ages, although it usually overestimated BW until 6 months in Hereford and Jersey cattle.

Fig. 2. Weekly average observed bodyweight (BW) and mean breed growth curve for the different functions tested during (a) the first year of age and (b) after the first year of age.

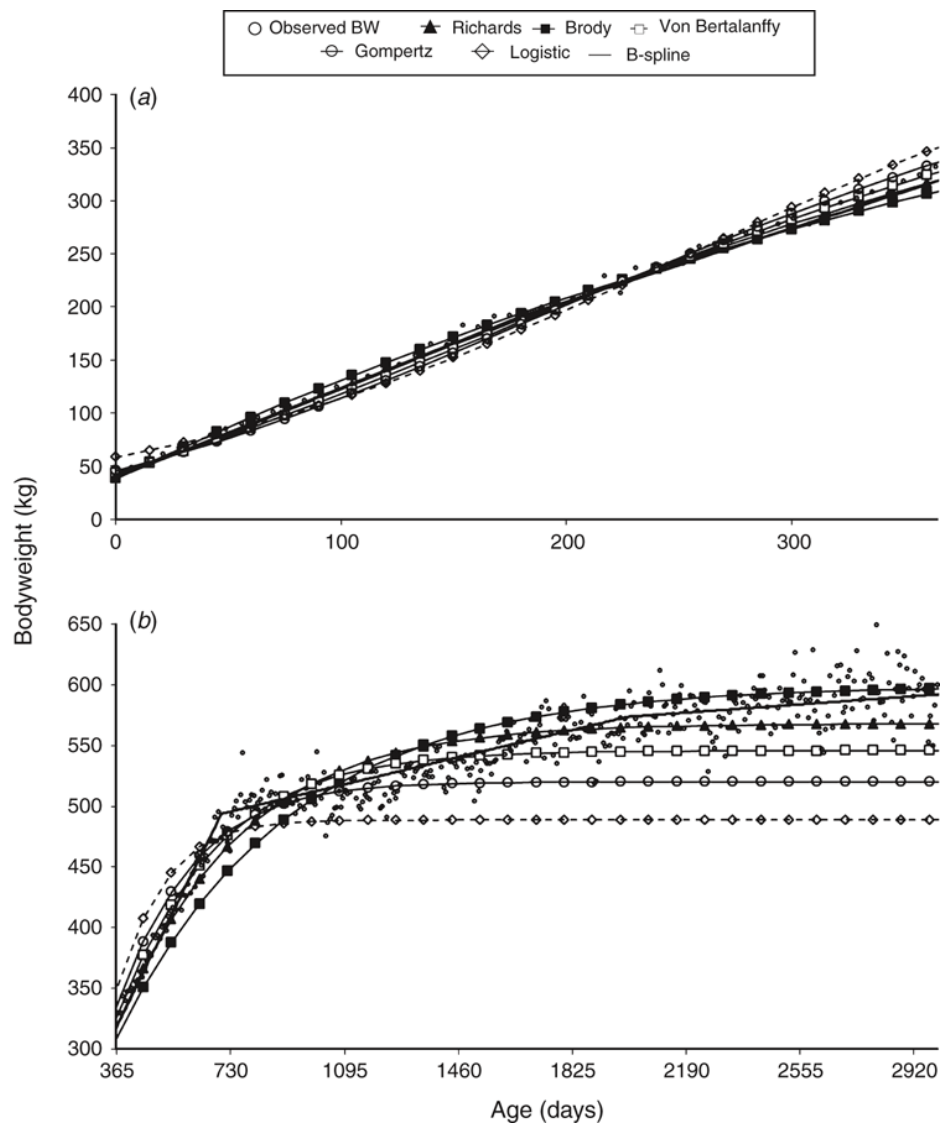
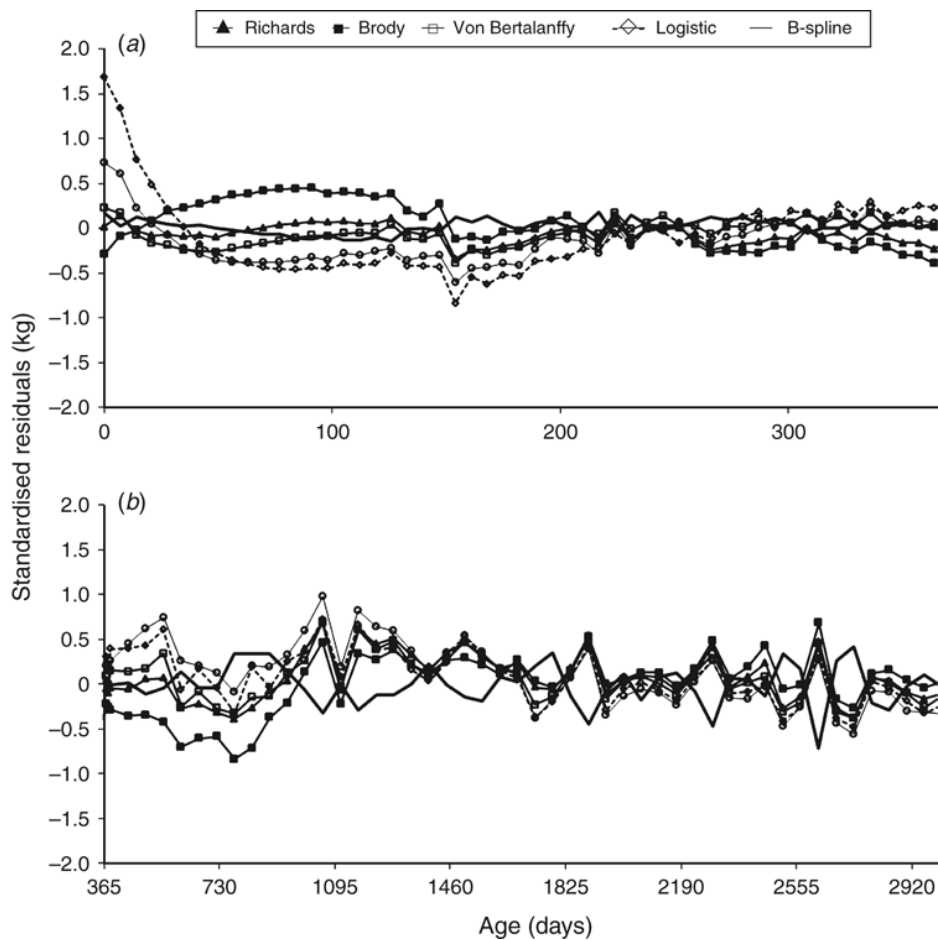


Fig. 3. Standardised residuals of predictions made by the different functions during (a) the first year of age and (b) after the first year of age.



Among the remaining functions tested in this analysis, the Brody function estimated birthweight accurately whereas the Logistic and Gompertz functions tended to overestimate birthweight. Similarly in Nelore cattle, the Brody function provided more accurate estimates of birthweight whereas the Logistic function overestimated birthweight (Forni *et al.* 2009). During the suckling period, the Brody function overestimated BW whereas the Gompertz and Logistic underestimated it. Conversely from 360 days to first mating, the Logistic and Gompertz functions overestimated BW and the Brody function underestimated BW. Towards maturity (98% BW), all functions either underestimated or overestimated BW to a greater or lesser extent. The results partially agree with those reported by Brown *et al.* (1976), where the Gompertz function consistently overestimated early BW, the Brody function tended to either over- or underestimate BW before 6 months but fitted the observed data well after 6 months whereas the Logistic function tended to overestimate early BW and underestimate mature BW. The differences between studies could be partially related to the different maturing rate of the breeds studied and the effect that feeding management can have on the shape of the growth curve (Freetly *et al.* 2011).

Using the Richards function, Forni *et al.* (2009) found a poor fit until 48 months of age. In the present analysis, the greater variability in fit was found after first calving (~33 months). This can be explained as BW of cows can vary: (i) due to their physiological state, for example, a dry, non-pregnant cow could be 10% lighter than the same cow that was 9 months pregnant, and (ii) as a response to grazing in the management system where the data were recorded, for example, a cow could gain 12% of BW in the summer grazing period (Casasús *et al.* 2002).

Estimates of curve parameters and derived growth traits

The parameters of the different non-linear functions are given in Table 2. According to the different models, mature BW ranged between 489 and 599 kg, with the Logistic function estimating the lowest and the Brody function the highest, respectively. The average BW of multiparous Parda de Montaña cows at calving was 574 and 599 kg in spring and autumn calving seasons, respectively (Casasús *et al.* 2002). The A parameter estimated with the Brody function was closest to the aforementioned values, followed by the Richards function, which underestimated adult BW. Conversely, better estimates of mature BW were obtained with the Richards function than with the Brody function in Angus cattle (Beltran *et al.* 1992) or with the Von Bertalanffy function than with the Brody function in Retinta cattle (Lopez de Torre *et al.* 1992). The Von Bertalanffy function was also chosen to define adult BW of different strains of Holstein-Friesian cattle (Berry *et al.* 2005). In the present analysis, the least accurate estimate was given by the Logistic function, as has been reported in Nelore (Forni *et al.* 2009) as well as Holstein and Ayrshire cattle (Perotto *et al.* 1992).

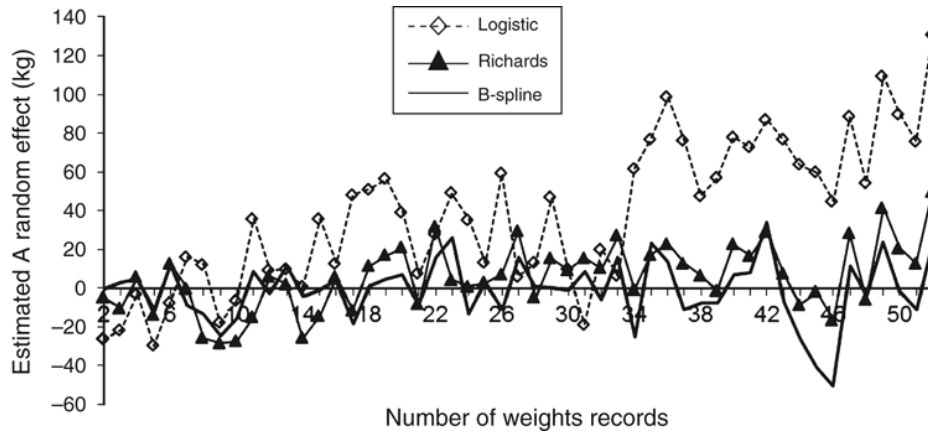
Table 2. Statistics of the estimated growth curve parameters for five non-linear models [mean (s.e.)] when fitted to data from Parda de Montaña females

A = the asymptotic limit of bodyweight when age t approaches infinity; b = integration constant; k = ratio of the relative intensity of growth; M = shape parameter determining the position of the inflection point of the curve

Function	Parameter			
	<i>A</i>	<i>b</i>	<i>k</i> (×1000)	<i>M</i>
Richards	568 (2.5)	-0.798 (0.0041)	2.713 (0.0209)	-0.611 (0.0075)
Brody	599 (2.1)	0.936 (0.0003)	1.805 (0.0069)	–
Von Bertalanffy	546 (2.2)	0.569 (0.0005)	3.531 (0.0262)	–
Gompertz	520 (2.3)	2.427 (0.0033)	4.704 (0.0379)	–
Logistic	489 (2.8)	7.349 (0.0329)	8.011 (0.0780)	–

The average predicted growth curve obtained from the Logistic function was below the observed values (Fig. 2) and underestimated breed mature weight (Table 2). This function consistently yielded biased estimates of the random effects for cows depending on the structure of the available data (Fig. 4). It provided a biased estimate of the *A* random parameter depending on the number of records available per cow whereas the Richards and B-spline function estimations were relatively unbiased. The Logistic function tended to underestimate *A* for animals with less than four records (i.e. with actual data until weaning) and overestimate *A* for animals with more than 30 records (i.e. with data from birth to mature age).

Fig. 4. Average estimates for the adult weight (*A*) random effect in the Logistic (—◇—), Richards (—▲—), and B-spline (—) functions relative to the number of available bodyweight records.



The growth traits calculated from the non-linear models are presented in Table 3. All the non-linear functions, except the Brody function, are designed to include a point of inflection (POI) when growth rate changes from increasing to decreasing as a function of age. The Von Bertalanffy, Gompertz and Logistic functions have a fixed POI at given proportions of mature size ($8/27$, e^{-1} , and 0.5 , respectively), and so $BW(y^+)$ and age (t^+) at the POI is only dependent on estimated mature BW. Only the Richards function allows for a variable POI derived from the *M* parameter. Nevertheless, Beltran *et al.* (1992) described growth in only one phase because *M* values obtained were not within a range that allows for the calculation of the POI. The problem in estimation of the POI was attributed to the scarcity of observations in the segment of the curve around the POI, because the shape of the curve seems to be the aspect of growth that is most sensitive to environmental influences (López *et al.* 2000). In the present analysis, there was enough data at all ages, however, and the Richards function had a POI at 21% of mature size and showed the lowest y^+ and t^+ values.

Table 3. Growth traits derived from five non-linear models fitted to data from Parda de Montaña females

y^+ : BW and age; t^+ : age, at the point of inflection; v : average absolute maturing rate; v^+ : average absolute growth rate at point of inflection; $t^{56\%}$: age at puberty; and $t^{98\%}$: time to reach maturity

Function	Richards	Brody	Von Bertalanffy	Gompertz	Logistic
Parameter					
Birthweight (kg)	41	38	44	46	59
y^+ (kg)	121	–	162	191	244
t^+ (day)	98	–	152	189	249
v (kg/day)	0.555	0.541	0.578	0.612	0.652
v^+ (kg/day)	0.845	–	0.857	0.900	0.979
$t^{56\%}$ (day)	365	420	330	305	280
$t^{98\%}$ (day)	1530	2120	1260	1020	740

The parameters, v (average absolute maturing rate), and v^+ (average absolute growth rate) calculated with the Logistic function (Table 3) are considered biologically unlikely. Growth rates in Parda de Montaña female calves have been reported as 0.831, 0.828 and 0.826 kg/day at 4, 5, and 6 months, respectively (Villalba *et al.* 2000), and 0.830 kg/day in 15-month-old heifers (Casasús *et al.* 1995), which are close to the v^+ value calculated with the Richards function.

Using the Brody function, only the v parameter could be calculated and it was similar to that estimated with the Richards function.

In *Bos taurus* cattle, the relative range as a proportion of mature BW at puberty (56–58%) is highly conserved, suggesting that the proportion of mature BW is a more robust predictor of age at puberty across breeds than absolute weight or age (Freetly *et al.* 2011). Using this proportion, the age at puberty estimated with the different non-linear functions ($t^{65\%}$ in Table 3) varied between 280 and 420 days with the Logistic function predicting the lowest and the Brody function the highest, respectively. Revilla *et al.* (1992) using data from blood progesterone reported that Parda de Montaña heifers reached puberty at 378 days and 329 kg, both being close to those calculated with the Richards function (Table 3). Different studies reported that Brown Swiss reached puberty at 344 days and 297 kg (Gregory *et al.* 1979), 349 days and 281 kg (Laster *et al.* 1979) and 317 days and 305 kg (Ferrell 1982). The difference in puberty onset observed between Parda de Montaña and Brown Swiss, despite their common origin, could be explained because breeds that have been selected for milk production (for example, Brown Swiss) tend to reach puberty at a younger age and at a lighter weight, relative to mature BW, than breeds selected solely for beef production (Ferrell 1982).

Johnson *et al.* (1990), when referring to previous studies by Brody (1945) and Taylor (1965), considered animals to be fully mature when they had attained 98% of their asymptotic weight ($t^{98\%}$ in Table 3). In the present study, large differences were observed in this parameter among functions, with the Logistic and Gompertz functions considerably underestimating age at maturity (2.0 and 2.8 years, respectively), whereas it was overestimated with the Brody function (5.8 years). As the Richards function was the most accurate and showed the best fit, the estimation of age at maturity could be considered around 4.2 years.

Predictive ability of the models

The description of the mean growth curve (linear or non-linear) of a population is not enough if decisions need to be taken at the individual cow level. The environmental and animal effects that modify the mean growth curve could be included using random regression models, which are widely used in animal genetics (Schaeffer and Jamrozik 2008). Random regression models allow the prediction of individual values for each parameter, in non-linear models, or coefficient, in linear models, as a deviation from the population mean. The predicted parameters or coefficients and the correlation between them could be used to estimate the BW of a heifer (i.e. just before mating) based on the mean curve of the population, the environmental effects and the animals actual birthweight.

The Richards function was selected to compare its predictive ability with the B-spline function because it provided the best fit among the non-linear models. Different residual variance structures were considered during this testing, which provided the models with different goodness of fit (Table 4). The heterogeneous constant plus power variance model based on two parameters: one for BW close to 0 and the second as a power of the absolute value of BW, was the best method to model residual effects using the Richards function according to AIC and BIC. The heterogeneous power variance model had similar but slightly higher values of AIC and BIC than the aforementioned model. Pinheiro and Bates (2000) considered that the former was better than the latter because it generally gave a more realistic output when the variance covariate was close or equal to 0. Therefore, the Richards function with random parameters A , k and M and a constant plus power residual variance was used to study its predictive ability when estimating mature BW.

Table 4. The log-likelihood, Akaike information criterion (AIC) and Bayesian information criterion (BIC) of different residual variance structures included in the Richards function

Variance structure	Criteria		
	–2 log-likelihood	AIC	BIC
Constant	183 333	183 379	183 560
Power	173 390	173 438	173 626
Constant plus Power	173 194	173 244	173 440

Target BW at first breeding has been the gold standard measure for determining breeding readiness of heifers (Patterson *et al.* 1992). The target BW, as a percentage of mature BW, is generally calculated using the average mature BW for the herd or breed. In the present data, the random parameter for mature BW was quite variable. The standard deviation of the mature BW parameter (A) in the Richards function was 63 kg and for the B-spline coefficient was 56 kg at 3000 days of age. This animal variation in mature BW could be explained by genetic and environmental causes. The assumption that all cows have the same (breed average) mature weight leads to deviations from the actual maturity index of heifers and may explain in part the diverse results found in evaluation of effects of the reduction of BW at first conception (Patterson *et al.* 1992; Martin *et al.* 2008). Recently, Stockton *et al.* (2013) proposed the use of measurable physical characteristics to forecast beef heifer mature BW and maturity. These authors focussed the forecast on environmental effects (nutritional and dam age) common to a group of heifers, and they obtained a better prediction of maturity index compared with the use of the average breed value. The use of this group prediction of mature weight, calculating maturity index, also demonstrated economic implications at the farm level.

When BW data throughout an animal's lifespan is available, the prediction of mature BW could be improved using the estimated environmental effects (in this study birth season and age of dam) obtained in the described models (non-linear Richards or B-spline) to correct the breed average mature BW. In the present study, the estimated mature BW was obtained from a model with fixed effects (from A parameter in Richards function, and B-spline coefficient at 3000 days, respectively). Moreover, if individual BW data is available from birth to the time point when decisions about maturity must be taken (i.e. from birth to 700 days to decide whether or not a heifer has achieved the maturity threshold to be bred) random animal mature deviation could be predicted. This mature deviation is estimated according to the correlation between random coefficients from the growth curve obtained using all data from the population combined with partial data (i.e. birth to 700 days) from the heifer. Thus, in the present analyses, the estimated fixed effects and the predicted random deviations obtained from the TEST_HF subset were used to calculate the predicted mature animal weight of the HF animals (cows with only weights to 700 days at TEST_HF subset but with actual mature BW available in the global subset) using the Richards and B-spline functions. The accuracy of predicting adult weight of both

functions is presented in Table 5.

Table 5. The correlation between predicted and actual adult weight ($r_{\text{act_pred}}$), slope of the regression of actual on predicted adult weight ($b_{\text{act_pred}}$) and mean absolute percentage error (MAPE) of adult weight predictions of Parda de Montaña females when using fixed and random values in the Richards and B-spline functions
*, slope statistically different from unity ($P < 0.05$). ***, correlation significant ($P < 0.001$). n.s., not significant

Prediction of adult bodyweight using	$r_{\text{act_pred}}$	$b_{\text{act_pred}}$	MAPE
B-spline function			
with fixed and random values	0.57***	1.15	5.70%
with fixed values	-0.02n.s.	-0.09*	7.40%
Richards function			
with fixed and random values	0.53***	0.43*	6.60%
with fixed values	0.18n.s.	0.75*	6.70%

Actual BW was correlated with predicted BW when using fixed and random effects in the Richards and B-spline functions but not with predicted BW when using fixed effects only (Table 5). Prediction accuracy using Richards function (including or not random effects) was low, with linear regression slopes between predicted and actual BW statistically different from unity ($P < 0.05$; Table 5). Predicted BW using fixed and random effects in B-splines showed more accuracy. Linear regression of actual BW on predicted BW using fixed and random effects in B-splines had a slope not statistically different from unity (Table 5). The MAPE calculated using the breed average adult BW was lower (~7%) than the value obtained by Stockton *et al.* (2013) (12%). These authors improved the estimation of adult BW by including the nutritional management of heifers and age of the dam (reducing the MAPE from 12% to 5%). In the present study, the fixed effects were less detailed and the MAPE obtained for the estimation of adult BW using fixed effects was similar to that obtained with the breed average value. Although, the inclusion of the animal effect reduced the MAPE using both the Richards and B-spline functions, the reduction was larger (down to 5.7%) for the B-spline function.

The use of BW from birth to maturity in a population (herd) modelled using B-splines resulted in a better estimation of adult BW in the HF animals (only using data until 700 days of age) than when non-linear models were considered. However, the accuracy of prediction could be further improved in two ways. First, the prediction could be optimised by including in the model all fixed effects that could explain the differential growth of animals as heifers, such as feeding and management during both lactation (Blanco *et al.* 2008) and rearing periods (Rodríguez-Sánchez *et al.* 2014). Second, the genetic relationship between cows in the model could be included (Meyer 2005b) to have a better estimation of adult BW of animals that only have heifer weights available using the adult BW of cows genetically related to them. In this sense, Bullock *et al.* (1993) reported that mature BW had low phenotypic correlations with birth and weaning BW (0.33 and 0.32, respectively), but medium to high genetic correlations (0.64 and 0.80, respectively).

In summary, the B-spline function had higher goodness of fit than the non-linear functions when describing the growth of Parda de Montaña females. The use of B-splines and non-linear mixed models allowed for a description of the mean growth curve to be developed and also individual animal growth curves from birth to maturity for each female even when an animal's dataset was not complete. Predicted adult BW of heifers obtained with B-splines and population growth curves improved the estimation of mature weight compared with those estimated with breed average adult weight, which could be useful as a basis for management decisions and genetic evaluation purposes.

Acknowledgements

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The authors recognise the CITA farm staff working at La Garcipollera and Zaragoza Research Stations for their technical support. This research was funded by INIA (RZP2009-005, RTA2010-057) and the European Regional Development Fund.

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