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1 Title: Comparison of different nonlinear functions and statistical models to describe beef  
2 cattle growth.

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9 Short title: Growth curves in beef cattle

10

11 Abstract.

12 The aim of this study was to describe the growth of Parda de Montaña females. Firstly, five  
13 non-linear functions (Richards, Brody, Von Bertalanffy, Gompertz and Logistic) were used to  
14 fit bodyweight (BW)-age data using the *nlme* procedure of R statistical software.

15 Comparisons were made among these functions for goodness of fit, standardized residuals  
16 and biological interpretability of the growth curve parameters. The Richards function showed  
17 the best goodness of fit. Both the Richards and Von Bertalanffy functions estimated more  
18 accurately BW at different time periods (at birth, during suckling, during rearing until the first  
19 mating and until the first calving) and underestimated or overestimated the BW to a greater or  
20 lesser extent, according to the standardized residuals. The Brody function had the best  
21 estimation of weight at maturity (599 kg) and the Richards function gave the closest  
22 estimation of birth weight (41 kg), average absolute growth rate (0.845 kg/day), age at  
23 puberty (56% of asymptotic BW; 365 days) and mature age (98% of asymptotic weight; 1260  
24 days). Different residual and random modeling structures were compared using the Richards  
25 function. The best goodness of fit was obtained in the model which included the constant plus  
26 power variance function and parameters  $A$ ,  $k$  and  $n$  as random effects. Finally, the predictive

27 ability of this model was checked. A strong correlation between the predicted and actual adult  
28 weight of cows with incomplete data ( $R=0.85$ ) was observed.

29

### 30 **Introduction.**

31 In animal science, growth is usually defined as an increase in tissue mass caused by  
32 hyperplasia early in life and hypertrophy later in life (Owens *et al.* 1995). The accurate  
33 knowledge of the growth curve is important due to its relation with the efficiency of  
34 production (Fitzhugh, 1976). The analysis of growth curves was initiated in the physical  
35 sciences, more fully developed in the biological sciences, and used in studies of the size and  
36 health of plants, animals and humans (McArdle, 2001).

37

38 Mathematical models can be used to describe animal growth using the bodyweights recorded  
39 throughout the animal's life. Since the publication of Brody (1945), several theories and  
40 sophisticated algorithms for analysis have been developed. Fitzhugh (1976) discussed and  
41 appraised different techniques for fitting and analyzing growth curves and their biological  
42 interpretation.

43

44 In beef cattle, different equations to model growth have been used and compared in Hereford  
45 (Brown *et al.* 1976), Angus (Beltran *et al.* 1992), Retinta (López de Torre *et al.* 1992),  
46 Belgian Blue (de Behr *et al.* 2001), Salers (Garcia *et al.*, 2008) and Nelore (Forni *et al.* 2009)  
47 females, among others. Neither the best equation to describe growth nor the way to model the  
48 residual variance are clear, they depend on the breed (Freetly *et al.* 2011) and sometimes on  
49 the structure of the data (Forni *et al.* (2009).

50

51 The aim of this study was to describe the growth of Parda de Montaña females from birth to  
52 adult age. Firstly, various nonlinear functions were compared to choose the best one to

53 describe the growth according to the goodness to fit. Then, different residual and random  
54 modeling structures were compared using the best function previously selected. Finally, the  
55 predictive ability of the best nonlinear mixed effects model was checked.

56

## 57 **Materials and methods.**

58 Data were collected in La Garcipollera Research Station (Spain, 42° 37' N; 0° 30' W; 945 m  
59 above sea level), in the mountain area of the southern Pyrenees (Spain), and in CITA research  
60 centre in Zaragoza (41° 43' N; 0° 48' W; 225 m above sea level), for 23 years, between 1987  
61 and 2010, from a Parda de Montaña cattle herd (60-100 adult cows over the study period).

62

63 Parda de Montaña (PM) is a suckler cattle breed widely spread throughout northern Spain that  
64 came from the ancient Brown Swiss and its crosses with local breeds. It had been used as a  
65 dual-purpose breed, milk-beef (Álvarez-Rodríguez *et al.* 2009), but in the last decades it has  
66 been selected basically for beef production and mothering abilities (weaning weight and  
67 calving ease).

68

69 The management of this herd of Parda de Montaña cattle consisted of housing during winter,  
70 grazing on high mountain pastures (1500-2200 m above sea level) during the summer and  
71 grazing on valley meadows and forest pastures (945-1500 m above sea level) during spring  
72 and autumn. Concerning the reproductive management, there are two calving seasons, spring  
73 (March to May) and autumn (September to November). Further details can be found in  
74 (Casasus *et al.* 2002). Cows remained in the herd until natural death occurred or they were  
75 culled for either sanitary reasons or reproductive failure.

76

77 The database was constructed with a total of 24174 bodyweights (BWs) registered from 1697  
78 females. They were weighed on the first week of life, at weaning, during rearing, at calving, at

79 the end of lactation, when they were turned-out to high mountain pastures and turned-into the  
80 farm facilities, and also at different frequencies in between these time points. Although all  
81 animals did not have the complete set of weights throughout their life, the data set had enough  
82 number of records on each age (Fig. 1). Within an age (in weeks), records outside the range of  
83 3 standard deviations from the observed bodyweight (BW) were considered as outliers and  
84 were not included in the analyses.

85 (Insert Fig. 1 here)

86 Five nonlinear functions frequently used for the description of growth curves in cattle were  
87 studied: Richards, Brody, Von Bertalanffy, Gompertz and Logistic as proposed by Fitzhugh  
88 (1976). These nonlinear functions are detailed in the Table 1. The functions were compared  
89 considering the goodness of fit and standardized residuals. Goodness of fit of the different  
90 models was evaluated using maximum likelihood of the model (the higher the better), Akaike  
91 information criterion (AIC) (the lower the better) and Bayesian information criterion (BIC)  
92 (the lower the better). A Likelihood Ratio Test (LRT) was performed to compare the model  
93 that had the best the goodness of fit with the remaining models. The models were fitted using  
94 the *nlme* procedure of the version 2.13.2 of R statistical software (Pinheiro & Bates 2000).

95 The model comparison was performed with *anova* procedure of R statistical software.

96 Standardized residuals of the different functions were obtained as the difference between  
97 estimated BW and actual BW divided by the standard deviation of the actual BW at the age of  
98 estimation.

99

100 The biological interpretation of the growth curve parameters (Table 1) is as follows:

101 -  $y_t$  = observed BW at age  $t$ .

102 -  $A$  = the asymptotic limit of the BW when age  $t$  approaches to infinity, interpreted as average  
103 size at maturity independent of short-term fluctuation of size in response to environmental  
104 effects such as the climate, the type and availability of feed, or due to the physiological status.

105 -  $b$  = integration constant, a time scale parameter.

106 -  $k$  = ratio of the relative intensity of growth that estimates the maturation rate of the curve. In  
107 order to obtain a proper convergence parameter  $k$  was scaled to obtain estimates of random  
108 parameters variances with similar magnitude.

109 -  $n$  = shape parameter determining the position of the inflection point (POI) of the curve.

110

111 Further parameters were obtained from the abovementioned ones: birth weight (calculated at  $t$   
112 = 0), BW ( $y^+$ ) and age ( $t^+$ ) at the point of inflection. Useful growth parameters can be derived  
113 from the method such as: average absolute maturing rate ( $v$ ) (kg/d) and average absolute  
114 growth rate ( $v^+$ ) (kg/d at POI), age at puberty (estimated at 56% of mature BW, according to  
115 Freetly *et al.* (2011),  $t^{56\%}$ ) and age to reach maturity (estimated at 98% of asymptotic BW,  
116 according to Johnson *et al.* (1990),  $t^{98\%}$ ).

117 (Insert Table 1 here)

118 The residual variance was included in the mixed models with no heteroscedasticity (constant  
119 residual variance; M1), using the power variance function (variance related with BW; M2) or  
120 the constant plus power variance function (equivalent to power variance function but with a  
121 constant value at low BW; M3). Mixed models were used to adjust the functions to data with  
122 parameters of the function defined as fixed effects (i.e. describing the population) and as  
123 random effects (i.e. describing the individual deviation from the mean value of the  
124 population). The function with best goodness of fit was selected for further statistical  
125 analyses. In the selected function, different random effects were also tested: all parameters  
126 ( $A$ ,  $k$ ,  $n$  and  $b$ ), parameters  $A$ ,  $k$  and  $n$ , parameters  $A$  and  $k$ , parameter  $A$  and  $n$  and only the  
127 parameters  $A$ . The models were compared considering the lack of solution (no convergence in  
128 the iterative procedure) and the goodness of fit, as described above. Growth curve parameters  
129 obtained for each model were compared using a t test.

130

131 Finally, a subset of our data was constructed including only cows with BWs available during  
132 their lifespan (complete dataset) to study the predictive ability of the best nonlinear mixed  
133 effects model. Using the best model, the “actual” adult deviation of each cow from the  
134 random effect  $A$  was estimated. The complete dataset was used to construct a second subset  
135 (reduced dataset). In the reduced dataset, half of the cows had BW over their whole lifespan  
136 and the other half only had BWs before 200 days of age, because BWs after this age were  
137 deleted. Then, the “predicted” adult deviation of all cows with reduced dataset was obtained  
138 using the best function adjustment and the “actual” and “predicted” adult weight of cows were  
139 compared.

140

#### 141 **Results and discussion.**

142 The Richards function had the best goodness to fit because it had the maximum likelihood  
143 and the lowest AIC and BIC values (Table 2) and so, the other functions were compared with  
144 it. High LRT values were obtained for all comparisons showing that the Richards function  
145 had a better adjustment than the others ( $P < 0.001$ ). The Von Bertalanffy function had a good  
146 adjustment whereas the Logistic function had the worst adjustment. The Richards and Brody  
147 functions were selected among others because they had the best goodness to fit according to  
148 the sum of squared deviations (Brown *et al.* 1976; DeNise and Brinks 1985; Doren *et al.*  
149 1989). These two equations were chosen by Beltran *et al.* (1992) to describe the growth of  
150 Angus cattle because of their goodness of fit and because the parameter estimates can be  
151 interpreted easily. The Brody function represented more accurately Nelore cattle growth  
152 whereas the Logistic function was the least accurate according to AIC and BIC (Forni *et al.*  
153 2009).

154 (Insert Table 2 here)

155 The observed BW and mean predicted curve obtained with the different functions are shown  
156 in Fig. 2. The accuracy of the prediction varied over the different time periods: at birth, during

157 suckling (until 140 to 170 days old, depending on the calving season), during rearing from  
158 weaning until the first mating (until 600 to 660 days old), then from the first mating until the  
159 first calving (910 to 1000 days old) and finally during maturity. According to the standardized  
160 residuals (Fig. 3), the Richards and Von Bertalanffy functions estimated more accurately the  
161 BW at all ages. Similarly, Brown *et al.* (1976) reported that the Richards function gave a  
162 generally unbiased fit at all ages and Von Bertalanffy function fit reasonably well over all  
163 ages, although it usually overestimated BWs at ages prior to 6 months in Hereford and Jersey  
164 cattle.

165 (Insert Fig. 2 here)

166 Concerning the remaining functions studied in the current analysis, the Logistic and  
167 Gompertz functions tended to overestimate birth weights. The Brody function overestimated  
168 the BW during the suckling period whereas the Gompertz and Logistic underestimated it.  
169 From 360 days to the first mating, the behaviour of these three functions was inverse, the  
170 Logistic and Gompertz functions overestimated the BW and the Brody function  
171 underestimated it. During maturity, all functions underestimated or overestimated the BW to a  
172 greater or lesser extent, alternatively. The results agree partially with those reported by Brown  
173 *et al.* (1976). They reported that the Brody, Gompertz and Logistic functions over- and  
174 underestimated BW in different periods but not in the same way as these functions in the  
175 current analysis. In the abovementioned study, the Gompertz function consistently  
176 overestimated early BWs, the Brody function tended to either over or underestimate BWs prior  
177 to 6 months but fitted the observed data well for BWs after 6 months whereas the Logistic  
178 function tended to overestimate early BWs and underestimate the mature BW. In Nelore  
179 cattle, the Brody function provided more accurate estimates of birth weights whereas the  
180 Logistic function overestimated the birth weights (Forni *et al.* 2009). The differences between  
181 studies could be related to the different maturing rate of the breeds studied, and to the effect  
182 of the feeding management on the shape of the growth curve.



183 (Insert Fig. 3 here)

184 Within the function that better fitted the data, Forni *et al.* (2009) found that the poor fitting  
185 until 48 months of age was explained by a wide relative variation of records in early life. In  
186 our analyses, the greater variability in fit was found after first calving (30-months-old). In this  
187 period, BW of cows could vary: i) due to the physiological state, a dry cow can be 10%  
188 lighter than the same cow being 9 months pregnant (INRA, 1978), and ii) as a response to  
189 grazing, in the management scenario where data were obtained, a cow could gain 12% of BW  
190 in the summer grazing period (Casasus *et al.* 2002).

191

192 The parameters estimated from the different nonlinear functions are given in Table 3. The  
193 letters used to represent those parameters are the same in all functions but they do not have  
194 the same mathematical meaning and their comparison among functions is not possible, except  
195 for parameter A, which represents the asymptotic BW. According to the different models,  
196 mature BW ranged from 489 to 599 kg, for the Logistic and Brody functions, respectively.  
197 Bodyweight of multiparous Parda de Montaña cows at calving was 574 and 599 kg in the  
198 spring and autumn calving seasons, respectively (Casasus *et al.* 2002). Parameter A estimated  
199 with the Brody function was the closest to the abovementioned values, followed by the  
200 Richards function, which underestimated the adult BW. Conversely, better estimates of  
201 mature BW were obtained with the Richards function than with the Brody function in Angus  
202 cattle (Beltran *et al.* 1992) or with the Von Bertalanffy function than with the Brody function  
203 in Retinta cattle (López de Torre *et al.* 1992). The Von Bertalanffy function was also chosen  
204 to define the adult BW of different strains of Holstein-Friesian cattle (Berry *et al.* 2005). In  
205 the current analysis, the least accurate estimate was given by the Logistic function as it has  
206 been reported in Nelore (Forni *et al.* 2009) and in Holstein and Ayrshire cattle (Perotto *et al.*  
207 1992).

208 (Insert Table 3 here)

209

210 The mean predicted curve obtained by the Logistic function was below the observed values  
211 (Fig. 2) and had underestimated mature weight (Table 3). This function made biased estimates  
212 of the random effects for the cows depending on the structure of the available data (Fig. 4). It  
213 provided a biased estimation of the  $A$  random parameter depending on the number of records  
214 available per cow whereas the Richards function estimations were relatively unbiased. The  
215 Logistic function tended to underestimate  $A$  for animals with a low number of records (i.e.  
216 with actual data until weaning) and overestimate  $A$  for animals with a high number of records  
217 (i.e. with data from birth to mature age).

218 (Insert Fig. 4 here)

219 The calculated birth weight ranged between 38 kg in the Brody function to 59 kg in the  
220 Logistic function (Table 4). The birth weight of Parda de Montaña female calves was 40.2 to  
221 41.9 kg (Villalba *et al.* 2000; Casarus *et al.* 2002), which is close to the birth weight  
222 calculated with the Richards function.

223

224 All the functions, but the Brody function, are designed to include a point of inflection (POI)  
225 when growth rate changes from an increasing to a decreasing function of age. The Von  
226 Bertalanffy, Gompertz and Logistic functions have a fixed POI at some proportion of the  
227 mature size ( $8/27$ ,  $e^{-1}$ , and  $0.5$ , respectively) and so  $BW (y^+)$  and age at the  $POI (t^+)$  only  
228 depend on estimated mature  $BW$ . Consequently, these parameters (Table 4) had relatively low  
229 coefficients of variation (2.0 to 2.5%). Only the Richards function allows for a variable POI  
230 derived from the parameter  $n$  but the scarcity of observations in the segment of the curve  
231 around the inflection point may lead to inappropriate conclusions, because the curve shape  
232 seems to be the aspect of growth that is most sensitive to environmental factors (López *et al.*  
233 2000). In the current analysis, there were enough data at all ages, however, and the estimated  
234 Richards function had the POI at 21% of mature size and showed the lowest  $y^+$  and  $t^+$  values

235 with a coefficient of variation of approximately 7%. Other authors describe the growth in only  
236 one phase (Beltran *et al.* 1992) because  $n$  values obtained were not within the range that  
237 allows the calculation of the POI.

238

239 The parameters  $v$  and  $v^+$  calculated with the Logistic function (Table 4) were biologically  
240 unlikely when they were compared with growth rates reported in previous studies. Growth  
241 rates at 120, 150 and 180 days in Parda de Montaña females were 0.831, 0.828 and 0.826  
242 kg/day (Villalba *et al.* 2000), respectively, which is close to  $v^+$  value calculated with the  
243 Richards function. Casarus *et al.* (1995) reported weight gains of 0.830 kg/day in grazing 15-  
244 month-old heifers. Variation of the growth parameters calculated with the Richards function  
245 were lower, approximately 2.5%, than the variation of these parameters calculated with the  
246 Gompertz and Von Bertalanffy functions, approximately 5.0%. With the Brody function, only  
247 parameter  $v$  could be calculated and it was similar to the one estimated with the Richards  
248 function.

249

250 Within *Bos taurus*, the relative range in proportion of mature BW at puberty (56-58%) is  
251 highly conserved, suggesting that proportion of mature BW is a more robust predictor of age  
252 at puberty across breeds than absolute weight or age (Freetly *et al.* 2011). Using this  
253 proportion, the age at puberty estimated with the different nonlinear functions ( $t^{56\%}$  in Table  
254 4) varied between 280 and 420 days calculated with the Logistic and Brody functions,  
255 respectively. Revilla *et al.* (1992) reported that Parda de Montaña heifers reached puberty at  
256 378 days and 329 kg, being both close to those calculated with the Richards function (Table  
257 4). Different studies reported that Brown Swiss reached puberty at 344 days and 297 kg  
258 (Gregory *et al.* 1978), 349 days and 281 kg (Laster *et al.* 1979) and 317 days and 305 kg  
259 (Ferrell, 1982). The difference in POI observed between Parda de Montaña and Brown Swiss  
260 (despite their common origin) could be explained because breeds that have been selected for

261 milk production (Brown Swiss) reach puberty at a younger age and at a lighter weight,  
262 relative to mature weight, than breeds selected solely for beef production (Ferrell, 1982), as  
263 Parda de Montaña in the last decades.

264

265 Johnson *et al.* (1990) referring to previous studies of Brody and Taylor, considered animals to  
266 be fully mature when they had attained 98% of their asymptotic weight ( $t^{98\%}$  in Table 4).

267 Large differences were observed between the functions, clearly the Logistic and Gompertz  
268 functions had considerably underestimated age at maturity (2.0 and 2.5-years-old,

269 respectively) and the Brody overestimated it (5.7-years-old). As the Richards function has

270 been the most accurate and has shown the best fit, the estimation of the adult age could be

271 done using this function, so the age to reach maturity of Parda de Montaña cows could be set

272 at about 4.0-years-old.

273 (Insert Table 4 here)

274 The following analyses compared different types of modeling random and residual effects

275 using the Richards function because it was chosen as the best function according to its better

276 goodness of fit and the behavior of residuals. The best model was the M3 because it had the

277 maximum likelihood and the lowest AIC and BIC values (Table 5). M3 model included a

278 heterogeneous constant plus power variance based in two parameters, one for BW close to 0

279 and the second one as a power of the absolute value of BW. High LTR values were obtained

280 for all comparisons indicating that model M3 had a better adjustment than the other models ( $P$

281  $< 0.001$ ), especially in comparison with the model with homogeneous (M1) variance which

282 was the worst option. Pinheiro and Bates (2000) considered that the model M3 was better than

283 the model with only power variance (M2) because it generally gives a more realistic output

284 when the variance covariate was close or equal to 0.

285 (Insert Table 5 here)

286 Regarding the inclusion of random effects, the model did not converge in the iterative  
287 procedure when all parameters were included ( $A$ ,  $k$ ,  $n$  and  $b$ ). A possible reason could be that  
288 there was a strong correlation among these parameters in our fittings (either in random but  
289 also in the fixed component  $R > 0.9$ ) as described in other studies (Fang and Bailey 2001;  
290 Giraldo *et al.* 2002). Some studies even used a modified Richards function with only three  
291 parameters (Nahashon *et al.* 2006). In our analyses, the model which included the parameters  
292  $A$ ,  $k$  and  $n$  as random effects, showed the maximum likelihood, but the estimated standard  
293 deviation for the  $k$  random effect was very low and the correlation between  $k$  and  $n$  random  
294 effects was close to 1. This suggests that one of these parameters can be treated as a fixed  
295 effect. Pinheiro and Bates (2000) stated that creating a better-fitting model for the fixed  
296 effects, by including their dependence on covariates, reduced the need for random-effects  
297 terms. In these cases, the between-group parameter variation is mostly explained by the  
298 covariates included in the model. Accordingly, in our analyses the models M4 and M5 (with  
299 only one of the two random effects, either  $n$  or  $k$ ) showed lower AIC and BIC than model M3  
300 and so they can be considered more parsimonious because they included fewer random  
301 effects.

302

303 The estimated fixed parameters and their standard errors using the different models with the  
304 Richards function are shown in Table 6. All the estimated parameters of the model M1 were  
305 different from those obtained with the models that included the heterogeneity of residuals ( $P <$   
306  $0.05$ ). In the simplified model (M1),  $A$  was overestimated while  $k$  was underestimated  
307 compared to those of the models that had better adjustment to the observed data (M2-M6).  
308 Within models that include constant plus power variance structure, the exclusion of some  
309 random effect in models M4 and M6 led to significant differences ( $P < 0.05$ ) for  $b$ ,  $k$ , and  $n$   
310 fixed parameter estimates.

311 (Insert Table 6 here)

312 Concerning the predictive ability of the mixed models using M3 with the Richards function,  
313 there was a strong correlation between the “predicted” and “actual” adult BW of cows  
314 included in the reduced dataset ( $R=0.85$ ; Fig. 5). It even predicted reasonably well the mature  
315 BW of cows with only three weights before weaning. Bullock *et al.* (1993) reported a low  
316 phenotypic correlation between mature and birth or weaning BW (0.33 and 0.32 respectively),  
317 but a medium to high genetic correlation (0.64 and 0.80 for birth and weaning BW,  
318 respectively). The inclusion of random effects in the nonlinear models (even when genetic  
319 relationships between animals were not included) allowed an approximation to the mature  
320 BW based on two sources of information, first the actual data at young ages and second the  
321 pattern of growth obtained from animals with data within all ages. This implies that in  
322 experiments of characterization of growth curves and mature BW an optimal protocol can be  
323 designed to avoid the control of all the cows at all ages.

324 (Insert Fig. 5 here)

### 325 **Conclusion.**

326 The Richards function is the best function to describe growth of Parda de Montaña females.  
327 The use of nonlinear mixed models allowed the description not only of the mean curve but  
328 also the individual curve from birth to maturity for each female even when dataset of an  
329 animal was not complete. Obtaining the function parameters with biological meaning for each  
330 individual will be very useful to discuss the efficiency at an animal level.

331

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441

442 Table 1. Nonlinear functions applied to describe the growth curves.

443  $y_t$  = observed BW at age  $t$ ;  $A$  = the asymptotic limit of the BW when age  $t$  approaches to  
 444 infinity;  $b$  = integration constant;  $k$  = ratio of the relative intensity of growth;  $n$  = shape  
 445 parameter determining the position of the inflection point (POI) of the curve.

Name	Functions
Richards	$y_t = A (1 \pm be^{-kt})^{-1/n}$
Brody	$y_t = A (1 - be^{-kt})$
Von Bertalanffy	$y_t = A (1 - be^{-kt})^3$
Gompertz	$y_t = A \exp(-be^{-kt})$
Logistic	$y_t = A (1 + be^{-kt})^{-1}$

446

447 Table 2. Maximum likelihood, Akaike information criterion (AIC) and Bayesian information  
 448 criterion (BIC) of the different nonlinear functions and comparison with Richards function  
 449 using *anova* and Likelihood Ratio test (LRT). P-value and LRT calculated calculated with  
 450 respect to the best (Richards) function.

Functions	Richards	Brody	Von Bertalanffy	Gompertz	Logistic
Criteria					
Likelihood	-113682	-115415	-114429	-116324	-120344
AIC	227398	230854	228883	232670	240713
BIC	227536	230951	228980	232759	240810
P-value		<0.0001	<0.0001	<0.0001	<0.0001
LRT		3466	1495	5284	13325

451

452 Table 3. Statistics of the growth curve estimated parameters.

453  $A$  = the asymptotic limit of the BW when age  $t$  approaches to infinity;  $b$  = integration  
 454 constant;  $k$  = ratio of the relative intensity of growth;  $n$  = shape parameter determining the  
 455 position of the inflection point (POI) of the curve.

Functions	Richards		Brody		Von Bertalanffy		Gompertz		Logistic	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Parameter										
A	568	2.5	599	2.1	546	2.2	520	2.3	489	2.8
b	-0.798	0.0041	0.936	0.0003	0.569	0.0005	2.427	0.0033	7.349	0.0329
k (x1000)	2.713	0.0209	1.805	0.0069	3.531	0.0262	4.704	0.0379	8.011	0.0780
n	-0.611	0.0075								

456

457 Table 4. Statistics of biologically traits inferred from the growth curves.

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

Functions	Richards	Brody	Von Bertalanffy	Gompertz	Logistic
Parameter					
Birth weight (kg)	41	38	44	46	59
$y^+$ (kg)	121		162	191	244
$t^+$ (days)	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
$t^{56\%}$ (days)	365	420	330	305	280
$t^{95\%}$ (days)	1260	1620	1000	820	620

460

461

462 Table 5. Maximum likelihood, Akaike information criterion (AIC) and Bayesian information  
 463 criterion (BIC) of different random effect components and different variance structure  
 464 included in the Richards function model. P-value and LRT calculated calculated with respect  
 465 to the best (M3) function.

Models <sup>A</sup>	M1	M2	M3	M4	M5	M6
Variance structure	Constant	Power		Constant plus Power		
Random parameters		A k n		A k	A n	A
Criteria						
Likelihood	-119131	-113752	-113682	-114659	-113752	-114659
AIC	238292	227536	227398	229347	227531	229343
BIC	238413	227665	227536	229460	227636	229440
P-value	<0.001	<0.001		<0.001	<0.001	<0.001
LRT	10898	139		1955	140	1955

466 <sup>A</sup> The Model with the four parameters (A, k, n and b) included as random did not converge.

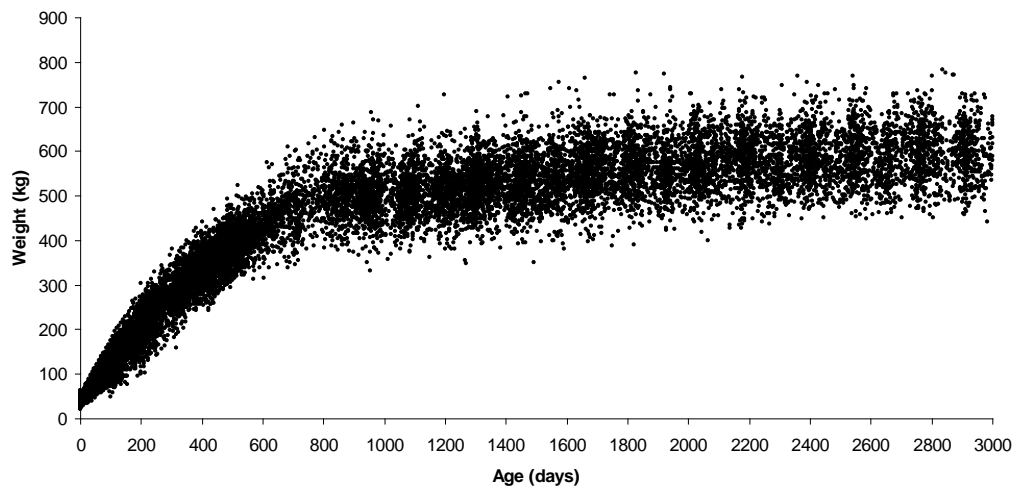
467

468 Table 6 Statistics of models including different random effect components and different  
 469 variance structure in the model.

470 A = the asymptotic limit of the BW when age *t* approaches to infinity; *b* = integration  
 471 constant; *k* = ratio of the relative intensity of growth; *n* = shape parameter determining the  
 472 position of the inflection point (POI) of the curve.

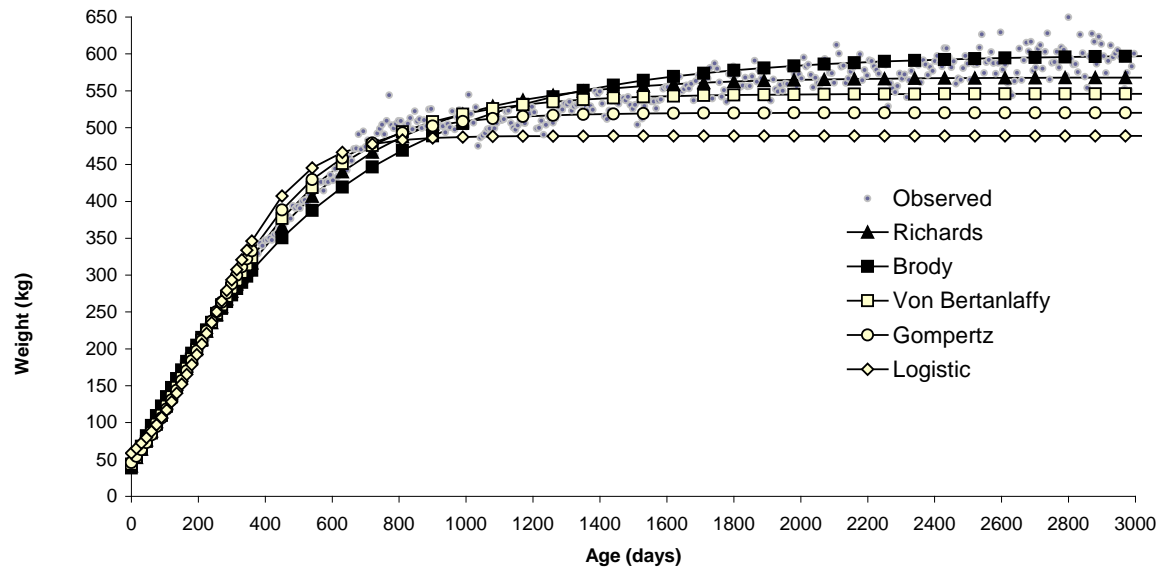
Models	M1		M2		M3		M4		M5		M6	
Variance structure	Constant		Power				Constant plus Power					
Random parameters			A k n				A k		A n		A	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Parameter												
A	590	2.7	569	2.5	568	2.5	577	2.1	569	2.5	577	2.1
b	-0.914	0.0040	-0.801	0.0040	-0.798	0.0041	-0.846	0.0032	-0.800	0.0040	-0.846	0.0032
k (x1000)	2.087	0.0290	2.692	0.0210	2.713	0.0209	2.437	0.0186	2.693	0.0210	2.437	0.0186
n	-0.895	0.0127	-0.615	0.0075	-0.611	0.0075	-0.707	0.0072	-0.614	0.0075	-0.707	0.0072

473



474

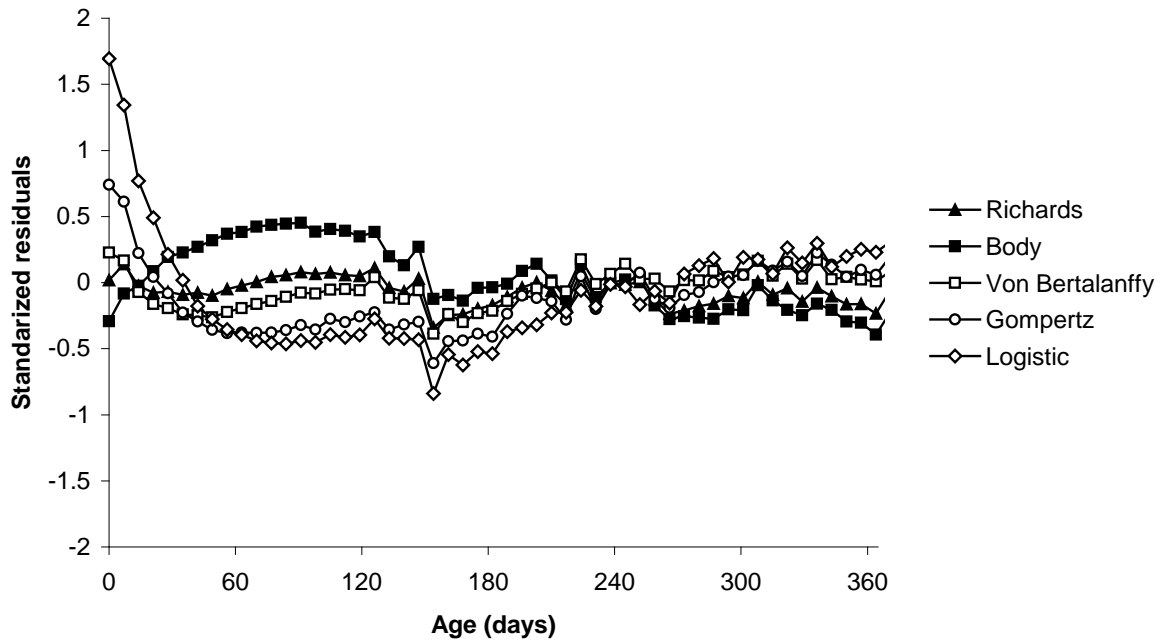
475 Fig. 1 Distribution of weight records on the data set.



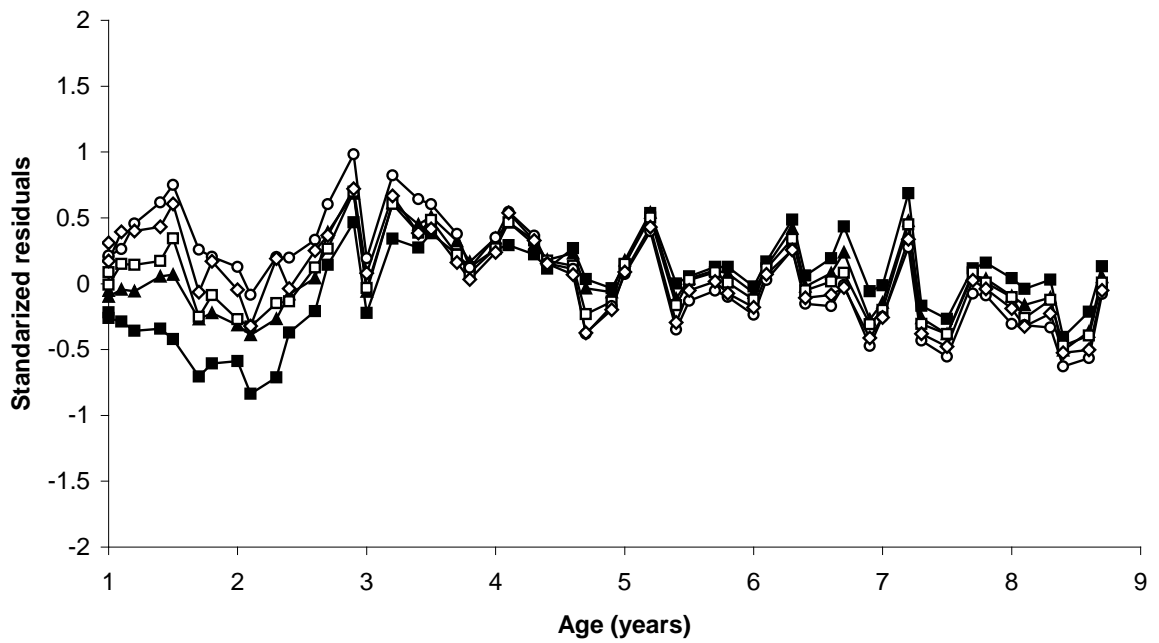
476

477 Fig. 2 Weekly average of the observed weights and estimated weights with the different  
 478 nonlinear functions tested.

479



480



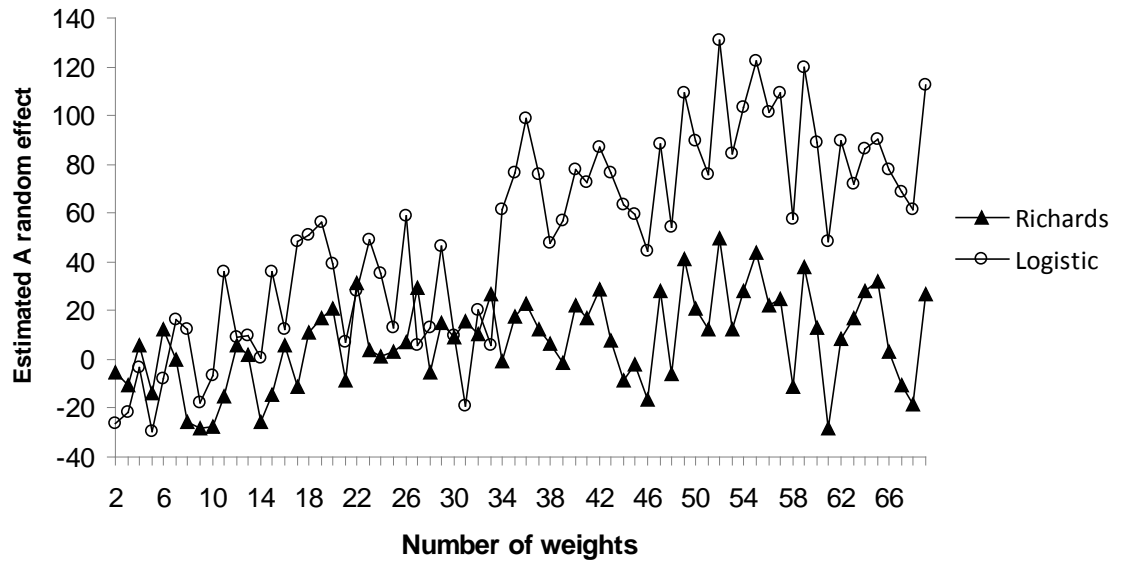
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482 Fig. 3 Standardized residuals of the different nonlinear functions during first year of age

483 (above) and after first year of age age (below).

484

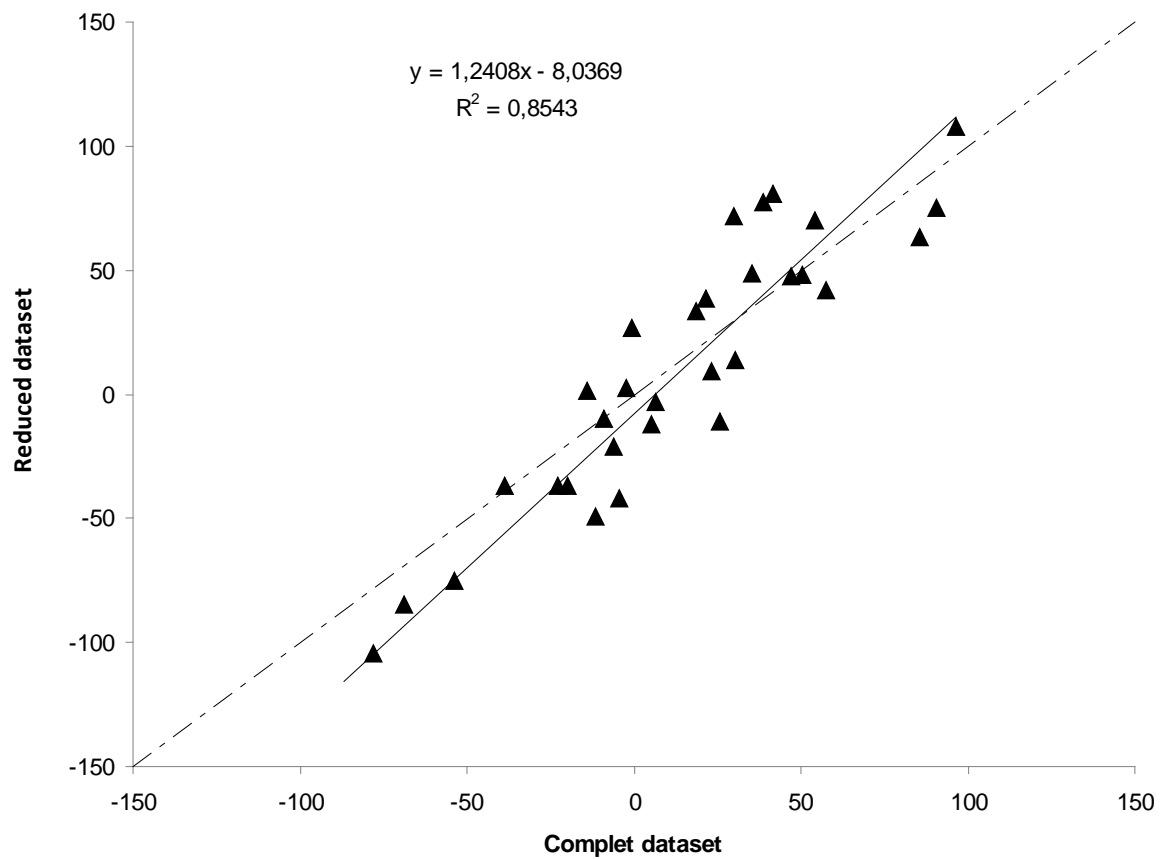




485

486 Fig. 4 Estimates of the A random effect in the Logistic and Richards functions depending on  
 487 number of available bodyweights.

488



490

491 Fig. 5 Estimates of the A random effect in the Richards functions obtained with all data

492 available (complete dataset) and using only data until 200 days of age (reduced dataset).