Multiphasic growth models for cattle

H. Nešetřilová

Czech University of Agriculture, Prague, Czech Republic

ABSTRACT: There are several ways of generalizing classical growth models to describe the complex nature of animal growth. One possibility is to construct a model based on a sum of several classical growth functions. In this paper, such multiphasic growth models for breeding bulls of the Czech Pied cattle based on the sum of two logistic functions are studied. The logistic function was chosen as a base for the models due to the relatively low degree of nonlinearity for the growth data. The paper describes three steps of constructing such a multiphasic growth model: in the first step a model with four unknown parameters is considered, in the second step the number of model parameters which are to be estimated is increased to five and in the third step a general model with six parameters is used. In each step, statistical properties of the considered model are checked. The residual variability of the best fitting model is on average approx. 8 times lower than the residual variability of classical Gompertz model which is often used by breeders to model cattle growth.

Keywords: multiphasic growth models; nonlinear regression; degree of nonlinearity; cattle growth; breeding bulls

Interest in the modelling of animal growth is caused, besides interest in studying the biological phenomena themselves, by important economic implications growth has for animal breeders. A fitting model gives an opportunity to summarize important growth characteristics (such as growth rate, earliness, daily gain, food conversion, mature body size and weight, length of the time interval between birth and maturity) into just a few model parameters. These parameters can be used as a base of selection (e.g. Beltran, 1992; Mignon-Grasteau et al., 2000). Statistical analysis can also identify relations between growth curve parameters and important production and reproduction traits (e.g. de Torre et al., 1992; Menchaca et al., 1996; Hyánková et al., 2001). Frequently used are also allometric models (e.g. Zeger et al., 1987; Koops and Grossman, 1991b).

Classical growth models[1] assume that the postnatal growth rate monotonically increases until certain age when it reaches maximum and then it monotonically decreases and (asymptotically) reaches zero. The corresponding growth curve is a smooth monotonic sigmoidal curve with one inflection point (which corresponds to the maximum growth rate age) and an asymptote. The growth model often describes a relation between live weight of an animal y and its age t. Then the asymptote of the growth curve is usually interpreted as the final weight of an adult animal.

Observed growth data may reveal in some cases that the real growth is a more complex process than the above-mentioned classical model assumes. The growth data on Czech Pied breeding bulls in Figure 1 indicate that a multiphasic growth model with two classical phases could fit the data better than the classical one. Multiphasic growth models were proposed by Koops (1986) and since that time multiphasic growth was examined in several species (chicken – Koops and Grossman, 1988; mouse – Koops et al., 1987; Kurnianto et al., 1999; Koops and Grossman, 1991a,b; pig – Koops and Grossman, 1991c; Japanese quail – Knížetová et al., 1995; allometric relations in rabbits, fish and chicken – Koops and Grossman, 1993); for related papers see also Hyánek and Hyánková, 1995; Nešetřilová, 1998).

[1]See Zeger and Harlow (1987) for an overview of growth models.

METHOD

For the purpose of the study, data on body weight of 101 breeding bulls of the Czech Pied cattle were collected. Body weight was recorded from approx. 30 days up to (max.) 1 400 days of age. The weighing interval was approx. 30 days, nevertheless it differed individually.

The observed growth data (Figure 1) suggest that a suitable multiphasic growth model could be constructed either as a sum of two classical growth functions or as a change point model. In this paper, the first approach was considered and the mean body weight of *individual* bulls was modelled as a sum of two growth functions (corresponding to two "classical" growth phases). As possible candidates for the construction of such a multiphasic model were considered the following functions (which are used as the "classical" growth models):

Logistic

$$y = \frac{\alpha}{1 + \exp(\beta - \gamma t)} \qquad (1)$$

Gompertz

$$y = \alpha \exp(-\exp(\beta - \gamma t)) \qquad (2)$$

Richards

$$y = \alpha\,(1 + \exp(\beta - \gamma t))^{-1/\delta} \qquad (3)$$

Morgan – Mercer – Flodin

$$y = \frac{\beta\gamma + \alpha t^{\delta}}{\gamma + t^{\delta}} \qquad (4)$$

Weibull type

$$y = \alpha - \beta \exp(-\gamma t^{\delta}) \qquad (5)$$

Among those models, Gompertz and Richards functions have often been used for cattle growth modelling.

Nešetřilová (2001) compared statistical properties of functions (1) to (5) in classical models of growth data on the Czech Pied breeding bulls. Based on this study, two functions were considered for the construction of the multiphasic model, logistic and Gompertz. Especially the logistic function seemed to be a reasonable choice because of the low degree of nonlinearity. In this paper, the growth model based on the sum of two logistic functions is considered. For the model based on the sum of two Gompertz functions see Nešetřilová (2004).

The growth model which is a sum of two logistic functions has, in general, six parameters which have to be estimated from data. As the number of parameters was considered too high and as there were some indications that parameter β could be the same for both growth phases, the growth model was constructed in three steps.

In the first step the assumption was made that $\beta_1 = \beta_2$ (= β) and moreover its value was set fixed for each animal. (This step was considered as preparatory and its purpose was to help set initial values for estimates in the second step.) This growth model referred to as LOGISTIC 4 had four parameters which were estimated from the observed data,

$$y = \frac{\alpha_1}{1 + \exp(\beta_{\text{fix}} - \gamma_1 t)} + \frac{\alpha_2}{1 + \exp(\beta_{\text{fix}} - \gamma_2 t)} \qquad \text{(LOGISTIC 4)}$$

where: β_{fix} = the fixed numerical constant[2]
$\alpha_1, \alpha_2, \gamma_1, \gamma_2$ = model parameters

In the second step, β was considered to be an unknown parameter and thus the corresponding model LOGISTIC 5 had five parameters α_1, α_2, β, γ_1, γ_2

$$y = \frac{\alpha_1}{1 + \exp(\beta - \gamma_1 t)} + \frac{\alpha_2}{1 + \exp(\beta - \gamma_2 t)} \qquad \text{(LOGISTIC 5)}$$

The most general model was LOGISTIC 6 with six parameters α_1, α_2, β_1, β_2, γ_1, γ_2

$$y = \frac{\alpha_1}{1 + \exp(\beta_1 - \gamma_1 t)} + \frac{\alpha_2}{1 + \exp(\beta_2 - \gamma_2 t)} \qquad \text{(LOGISTIC 6)}$$

In these models α_1 (α_2) represents the asymptote of the first (second) growth phase, γ_1 (γ_2) growth rate in the first (second) growth phase and $\alpha_1 + \alpha_2$ is the asymptote of the resulting growth curve ($\lim_{t\to\infty} y(t) = \alpha_1 + \alpha_2$). Parameters β ($\beta_1$, β_2) have no straightforward biological interpretation.

Considered models are nonlinear regression models, thus their properties can be studied only in combination with data sets for which they are used. This is caused by the fact that the regression

[2]Choice of β was based on the fact that

$$\beta = \ln\left(\frac{\alpha_1 + \alpha_2}{y(0)} - 1\right)$$

where: $y(0)$ = the birth body weight

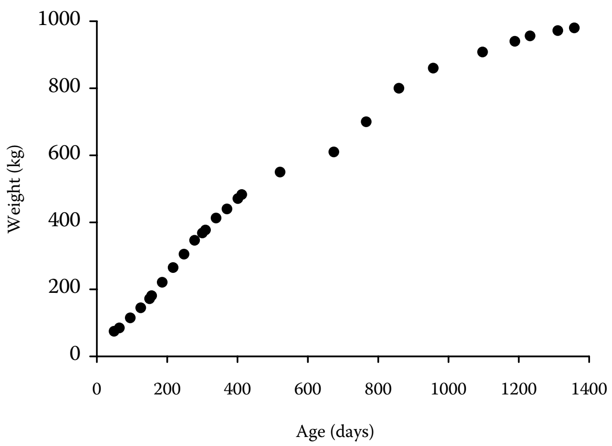

Figure 1. Data on the growth of Czech Pied cattle breeding bulls (example of individual growth)

response surface can have *different* properties for different data sets (see Ratkowsky, 1983).

Two criterions were used to evaluate the goodness-of-fit of a growth model. The first criterion was residual variability measured by residual variance s^2

$$s^2 = \frac{S}{n-p}$$

where: $S = S(\hat{\vartheta})$ = the residual sum of squares of the parameter vector estimate, $\hat{\vartheta} = (\hat{\alpha}_1, \hat{\alpha}_2, \hat{\gamma}_1, \hat{\gamma}_2)$ and/or $\hat{\vartheta} = (\hat{\alpha}_1, \hat{\alpha}_2, \hat{\beta}_1, \hat{\gamma}_1, \hat{\gamma}_2)$ or $\hat{\vartheta} = (\hat{\alpha}_1, \hat{\alpha}_2, \hat{\beta}_1, \hat{\beta}_2, \hat{\gamma}_1, \hat{\gamma}_2)$

n = denotes the number of observations

p = the number of model parameters; (s^2 was preferred to S due to the unequal number of observations on individual animals)

The second criterion was the degree of "nonlinearity" for a specific model/data combination because regression models with a low degree of nonlinear behaviour have preferable statistical properties[3] (see Ratkowsky, 1983).

Nonlinearity of a model can be separated into two components: *intrinsic* nonlinearity (associated with geometric properties of the solution locus, with its curvature) and *parameter-effects* nonlinearity (associated with parametrisation of the model)[4]. It is strongly recommended to use close-to-linear models which have both the low intrinsic nonlinearity and low parameter-effects nonlinearity (for details see Ratkowsky, 1983; Zvára, 1989).

RESULTS AND DISCUSSION

The model LOGISTIC 4 (fixed β) was considered only as a preparatory step for the subsequent construction of more complex models. It helped to set initial estimates of parameters of the more complex model LOGISTIC 5 (β estimated parameter). Convergence to the final estimates was fast, also due to the relatively low[5] degree of nonlinearity of logistic models for the bull data (Tables 4 and 5). Table 1 summarizes residual sums of squares S and residual variances s^2 for bulls[6] from the considered group with maximum number of weight determinations n. In the model LOGISTIC 6 (generally $\beta_1 \neq \beta_2$) residual variability, measured by the residual sum of squares S, further decreased. The decrease in residual variability was marked in some

[3]Nonlinear regression models differ from linear regression models in this way: when the assumption of independent and identically distributed normal random errors is made, the least-squares estimators of linear model parameters are generally unbiased, normally distributed and have minimum variance while in the case of nonlinear models the least-squares estimators have these properties only asymptotically. Thus, the estimators are generally biased and their properties (in case of a finite sample) are not known. The extent to which a nonlinear model differs from a linear one (bias, degree of nonnormality, increase of estimator variability) can vary greatly for different nonlinear model/data combinations. Thus it is not possible to give a general recommendation as to how large the sample size must be so that the properties of a model are close to its asymptotic behaviour. Further, magnitude of an estimator bias and increase of the estimator variability are related to the degree of the "nonlinearity" of its distribution. Besides the advantages mentioned above (close-to-asymptotic behaviour), predicted response values y will have only a small bias and computational complexity and problem of the initial estimates of the parameter vector will also decrease.

[4]Intrinsic nonlinearity has an impact on the extent of bias of y predictions while parameter-effects nonlinearity may negatively influence the convergence to the least-square estimates of the model parameters. Parameter-effects nonlinearity may sometimes be decreased by suitable reparametrization of a model while intrinsic nonlinearity does not depend on parametrization.

[5]Degree of nonlinearity is considered low if it is bellow $(F_{0.95}(p, n-p))^{-1/2}$ (Tables 4–6).

[6]All models were constructed for individual animals.

Table 1. Residual sum of squares S, residual variance s^2 and number of observations n for individual growth curves in models LOGISTIC4 – LOGISTIC 6

Model		LOGISTIC 4		LOGISTIC 5		LOGISTIC 6	
Bull No.	n	S	s^2	S	s^2	S	s^2
1	28	2 768.67	115.36	1 910.87	83.08	1 901.29	86.42
2	26	3 699.60	168.16	3 032.28	144.39	1 535.16	76.76
3	32	4 791.18	171.11	4 469.94	165.55	2 388.79	91.88
4	32	6 563.31	234.40	3 742.67	138.62	3 382.83	130.11
5	32	13 199.93	471.43	4 910.81	181.88	4 863.76	187.07
6	26	3 215.13	146.14	3 192.24	152.01	3 186.29	159.31
7	25	3 766.67	179.37	1 570.39	78.52	1 262.94	66.47
8	27	2 380.48	103.50	2 330.78	105.94	2 272.14	108.20

Table 2. Parameter estimates and their asymptotic standard errors of the model LOGISTIC 4 (fixed β)

Bull No.	Parameter α_1		Parameter α_2		Fixed β	Parameter γ_1		Parameter γ_2	
	estimate	ASE*	estimate	ASE*		estimate	ASE*	estimate	ASE*
1	384.553	11.364	705.665	37.776	3.055	0.01221	0.00033	0.00306	0.00016
2	332.079	12.860	692.543	13.711	3.106	0.01600	0.00056	0.00432	0.00012
3	314.477	16.502	623.625	17.342	2.944	0.01367	0.00057	0.00403	0.00017
4	303.255	13.538	789.670	14.210	3.066	0.01630	0.00069	0.00445	0.00011
5	341.826	18.803	642.274	20.814	3.229	0.01617	0.00082	0.00441	0.00018
6	296.640	14.454	699.899	13.956	2.944	0.01405	0.00058	0.00390	0.00011
7	309.308	9.008	735.177	38.382	3.001	0.01751	0.00068	0.00327	0.00016
8	392.951	13.367	570.090	13.750	2.890	0.01280	0.00034	0.00374	0.00014

*asymptotic standard error

Table 3. Parameter estimates and their asymptotic standard errors of the model LOGISTIC 5 (estimate β)

Bull No.	Parameter α_1		Parameter α_2		Parameter β		Parameter γ_1		Parameter γ_2	
	estimate	ASE*	estimate	ASE*	estimate	ASE*	estimate	ASE*	estimate	ASE*
1	373.184	11.876	709.692	31.572	2.883	0.052	0.01142	0.00038	0.00296	0.00014
2	323.963	14.857	709.412	16.066	2.906	0.087	0.01455	0.00085	0.00406	0.00016
3	306.640	18.801	637.842	20.572	2.815	0.089	0.01292	0.00082	0.00386	0.00022
4	280.949	15.934	829.902	15.917	2.724	0.069	0.01357	0.00081	0.00340	0.00013
5	328.209	20.965	703.299	20.256	2.624	0.075	0.01169	0.00074	0.00349	0.00018
6	294.427	16.227	703.920	17.680	2.905	0.102	0.01379	0.00090	0.00386	0.00017
7	287.769	8.864	792.407	34.367	2.672	0.057	0.01497	0.00063	0.00287	0.00013
8	394.642	13.011	566.179	14.649	2.943	0.078	0.01309	0.00057	0.00380	0.00017

*asymptotic standard error

Table 4. Parameter estimates and their asymptotic standard errors of the model LOGISTIC 6 (estimate β_1, β_2)

Bull No.	Parameter α_1		Parameter α_2		Parameter β_1		Parameter β_2		Parameter γ_1		Parameter γ_2	
	estimate	ASE*	estimate	ASE*	estimate	ASE*	estimate	ASE*	estimate	ASE*	estimate	ASE*
1	359.427	43.535	727.281	61.182	3.007	0.405	2.786	0.289	0.01187	0.00150	0.00289	0.00025
2	512.659	22.580	464.241	27.524	2.282	0.063	6.045	0.667	0.01052	0.00053	0.00742	0.00073
3	519.405	21.022	333.524	27.491	2.260	0.064	7.391	1.016	0.00925	0.00045	0.00900	0.00116
4	410.134	87.437	674.653	104.229	2.106	0.182	3.658	0.790	0.01044	0.00150	0.00490	0.00078
5	362.272	146.301	664.209	173.302	2.409	0.767	2.832	0.979	0.01080	0.00328	0.00365	0.00082
6	270.232	85.803	733.347	100.113	3.170	1.077	2.733	0.541	0.01488	0.00460	0.00370	0.00048
7	391.295	43.320	598.022	86.514	1.970	0.146	3.807	0.705	0.01134	0.00110	0.00404	0.00076
8	336.156	43.392	638.969	48.038	3.503	0.534	2.476	0.254	0.01514	0.00211	0.00339	0.00024

*asymptotic standard error

animals but in others it was only so slight that the residual variance s^2, which penalizes the model for the number of parameters, increased. The comparison of models LOGISTIC 5 and LOGISTIC 6 indicates that for some animals the parameter β might be the same for both growth phases but for others it is not true.

Point estimates of model parameters and their precision (characterised by asymptotic standard errors) for models LOGISTIC 4–LOGISTIC 6 are given in Tables 2–4. As expected, the precision of estimation decreased with the number of parameters of the model but the drop was not fatal. This fact is related to the increase of nonlinearity (see below). The shape of growth curves LOGISTIC 5 and LOGISTIC 6 and their correspondence to data can be visually inspected in Figure 2.

The second criterion to evaluate the goodness-of-fit was a close-to-linear behaviour of a growth model. For its evaluation, measures of nonlinearity of considered model/data combinations in models LOGISTIC 4–LOGISTIC 6 were computed (Tables 5–7). Nonlinearity is usually classified as high if the maximum of the corresponding measure exceeds

$F_{0.95}(p, n-p))^{-1/2}$

where: n = the size of a data sample
p = the number of model parameters (see Zvára, 1989, p. 230)

A comparison of the level of nonlinearity in the models LOGISTIC 5 and LOGISTIC 6 is interesting in this respect. While in the model LOGISTIC 5 the intrinsic nonlinearity was low and the parameter-effects nonlinearity exceeded $F_{0.95}(p, n-p))^{-1/2}$ only

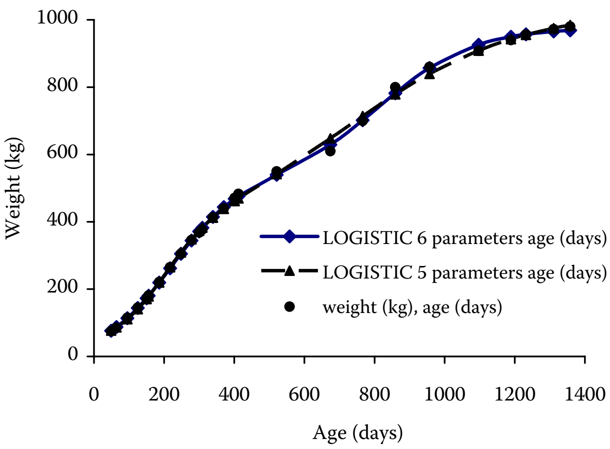

Figure 2. Individual growth modelled by LOGISTIC 5 and LOGISTIC 6

Table 5. Degree of nonlinearity of the multiphasic growth model LOGISTIC 4 (fixed β) for data on Czech Pied bulls

Bull No.	Average curvature		Maximum curvature		$(F_{0.95}(p, n-p))^{-1/2}$
	parameter effects	intrinsic	parameter effects	intrinsic	
1	0.7707	0.1211	2.1603	0.3218	0.6002
2	0.2067	0.0727	0.4300	0.1770	0.5958
3	0.4175	0.1037	1.0353	0.2729	0.6070
4	0.2113	0.0799	0.4894	0.2026	0.6070
5	0.3160	0.1077	0.6808	0.2673	0.6070
6	0.2667	0.0760	0.6378	0.1978	0.5958
7	0.5942	0.0972	1.6407	0.2359	0.5934
8	0.3167	0.0710	0.8092	0.1830	0.5980

Table 6. Degree of nonlinearity of the multiphasic growth model LOGISTIC 5 (estimate β) for data on Czech Pied bulls

Bull No.	Average curvature		Maximum curvature		$(F_{0.95}(p, n-p))^{-1/2}$
	parameter effects	intrinsic	parameter effects	intrinsic	
1	0.6651	0.0394	2.2365	0.1176	0.6155
2	0.3010	0.0560	0.8620	0.1782	0.6103
3	0.5100	0.0736	1.5506	0.2394	0.6235
4	0.3032	0.0610	0.9401	0.2019	0.6235
5	0.4762	0.0730	1.3832	0.2367	0.6235
6	0.3243	0.0606	0.9540	0.1980	0.6103
7	0.5760	0.0420	1.9220	0.1332	0.6073
8	0.3298	0.0501	0.9899	0.1538	0.6130

Table 7. Degree of nonlinearity of the multiphasic growth model LOGISTIC 6 (estimate β_1, β_2) for data on Czech Pied bulls

Bull No.	Average curvature		Maximum curvature		$(F_{0.95}(p, n-p))^{-1/2}$
	parameter effects	intrinsic	parameter effects	intrinsic	
1	2.1110	0.0974	8.1116	0.3268	0.6263
2	0.5685	0.0672	2.1728	0.2275	0.6203
3	0.7522	0.0884	2.8429	0.3222	0.6356
4	4.2738	0.2219	17.1583	0.8468	0.6356
5	12.4479	0.8538	49.8223	3.4802	0.6356
6	4.9739	0.4821	19.6920	1.9430	0.6203
7	3.5960	0.1620	14.0853	0.6232	0.6169
8	1.6390	0.1107	6.3994	0.3028	0.6234

moderately, the intrinsic nonlinearity in the model LOGISTIC 6 was high and parameter-effects nonlinearity exceeded $F_{0.95}(p, n-p))^{-1/2}$ considerably in all cases. The apparent nonlinearity of the model LOGISTIC 6 was reflected by increased values of the asymptotic standard errors of the parameter

Table 8. Residual sum of squares of the classical Gompertz model and the multiphasic logistic model LOGISTIC 6 and their ratio

Bull No.	*n*	Residual sum of squares (Gompertz model) S_G	Residual sum of squares (model LOGISTIC 6) $S_{LOGISTIC\ 6}$	Ratio $S_G/S_{LOGISTIC\ 6}$
1	28	26 431.50	1 901.29	13.90
2	26	22 107.73	1 535.16	14.40
3	32	19 945.13	2 388.79	8.35
4	32	15 241.12	3 382.83	4.51
5	32	17 805.46	4 863.76	3.66
6	26	18 339.96	3 186.29	5.76
7	25	31 267.80	1 262.94	24.76
8	27	25 648.05	2 272.14	11.29
Sum		176 786.75	20 793.20	8.50

estimates (Table 4). Thus, the model LOGISTIC 5 had better statistical properties than the model LOGISTIC 6 but the question if it was acceptable for the observed data was open. To answer it, an asymptotic test for testing $H_0 : \beta_1 = \beta_2$ against $A : \beta_1 \neq \beta_2$ was performed (see Ratkowsky, 1983, p. 138). The test, based on the change in the residual sum of squares between models LOGISTIC 5 and LOGISTIC 6 for all considered animals, ended in rejection of the null hypothesis ($\alpha < 0.01$).

Thus the general model LOGISTIC 6 with six parameters $\alpha_1, \alpha_2, \beta_1, \beta_2, \gamma_1, \gamma_2$ should be considered as adequate for the modelling of bull growth. To document the improvement of using this model in comparison with the classical Gompertz model, the residual variability for both models is presented in Table 8. For the same growth data, the multiphasic growth model LOGISTIC 6 has on average more than 8 times lower residual sum of squares than the Gompertz model which is often used to model cattle growth.

Efforts to find a growth model which fits the observed data as close as possible are justified by the fact that parameters of the growth model can be used for estimation of breeding value of an animal and for subsequent selection. Considering the impact breeding bulls have on production and reproduction traits in cattle subpopulations, further research on more appropriate growth models is desirable.

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Corresponding Author

Doc. RNDr. Helena Nešetřilová, CSc., Czech University of Agriculture, Kamýcká 129, 165 21 Prague 6-Suchdol, Czech Republic
Tel. +420 224 382 253, fax + 420 220 920 321, e-mail: nesetrilova@pef.czu.cz