

Modelling the growth of rearing cattle

HANNA UNTERAUER, NORBERT BRUNNER, MANFRED KÜHLEITNER*

Department of Integrative Biology and Biodiversity Research (DIBB), University of Natural Resources and Life Sciences (BOKU), Vienna, Austria

*Corresponding author: manfred.kuehleitner@boku.ac.at

Citation: Unterauer H., Brunner N., Kühleitner M. (2021): Modelling the growth of rearing cattle. Czech J. Anim. Sci., 66: 441–449.

Abstract: Scientific growth literature often uses the models of Brody, Gompertz, Verhulst, and von Bertalanffy. The versatile five-parameter Bertalanffy-Pütter (BP) model generalizes them. Using the least-squares method, we fitted the BP model to mass-at-age data of 161 calves, cows, bulls, and oxen of cattle breeds that are common in Austria and Southern Germany. We used three measures to assess the goodness of fit: *R*-squared, normalized root-mean squared error, and the Akaike information criterion together with a correction for sample size. Although the BP model improved the fit of the linear growth model considerably in terms of *R*-squared, the better fit did not in general justify the use of its additional parameters, because most of the data had a non-sigmoidal character. In terms of the Akaike criterion, we could identify only a small core of data (15%) where sigmoidal models were indispensable.

Keywords: Akaike information criterion; *Bos taurus*; Bertalanffy-Pütter differential equation; simulated annealing

According to [FAO \(2021\)](#), domestic cattle (this paper focuses on *Bos taurus*) are “the most common and widespread species of large ruminant livestock and are raised primarily to produce milk, meat and hides and to provide draft power”. In comparison with other livestock, the reproduction rate is low, and calves need much maternal care, whence the rearing of cattle is costly and there is an interest in growth modelling to improve selection and increase the efficiency of production ([Arango and Van Vleck 2002](#); [Mota et al. 2013](#); [Goldberg and Ravagnolo 2015](#)). Commonly used models, aside from simple linear or exponential growth, include Brody’s model and the sigmoidal models (with S-shaped growth curves) of Gompertz, Richards, Verhulst, and von Bertalanffy ([Nogales et al. 2017](#)). This paper studies the Bertalanffy-Pütter (BP) model ([Pütter 1920](#); [Ohnishi et al. 2014](#)), as it generalizes and unifies these models. The main advantage of this model over the mentioned simpler models is the added flexibility with respect to the shape of the growth curves ([Brunner et al. 2021](#)).

The location of the inflection point is a good example. For the Verhulst model of logistic growth the mass at the inflection point is always 50% of the asymptotic (adult) mass, regardless of the data. For the BP model the ratio may attain any value between 0% and 100% and there are also curves without inflection point. Its growth curves, mass $m(t)$ at time t , are solutions of the following differential equation:

$$m'(t) = p \times m(t)^a - q \times m(t)^b \quad (1)$$

The parameters of [Equation \(1\)](#) are the non-negative exponent pair $a < b$, the constants p and q , and the initial value, i.e. $m(t_0) = c > 0$, where t_0 is the first considered point of time (e.g. $t_0 = 0$ for natal mass). These five parameters are determined by fitting the model to mass-at-age data. The above-mentioned cited models are special cases: when the exponent pair (a, b) is preset, this defines a unique model BP(a, b) of a certain shape that uses only three parameters (p, q, c) .

BP(0, 1) is the Brody model, BP(1, 2) the Verhulst model of logistic growth, and BP(2/3, 1) the von Bertalanffy model. The Gompertz model is the limit case BP(1, 1) with a different differential equation (Marusic and Bajzer 1993). The Richards model is the BP model with $a = 1$ and the free parameters $b > 1$, c , p , and q .

The general BP model has been successfully used to describe the growth of chickens (Kuhleitner et al. 2019), dinosaurs (Brunner et al. 2019), fish (Renner-Martin et al. 2018), or goats and sheep (Brunner and Kuhleitner 2020). Here we asked if the BP model could provide additional insight into the growth of cattle, whereby we aimed at recommendations about growth modelling for practitioners: we compared linear and nonlinear models and asked which type of model might be most suitable for modelling the biological growth of cattle. Using size-at-age data from 161 male and female beef and dairy cattle from eight different breeds reared in Austria and Germany, for each animal we identified its best-fit parameters for the BP model by means of the least-squares method. A visual inspection of the growth data displayed a rather linear shape. However, as was pointed out by Nogales et al. (2017), traditional nonlinear models (Brody, Richards) achieved excellent fits to the biological growth curves of cattle. We therefore used the Akaike information criterion to decide if the improved accuracy could justify the added complexity of the model.

MATERIAL AND METHODS

Data

Our data were provided by cattle farms, industrial keepers, agricultural colleges, and animal research institutes from Austria and Germany. As two sources asked for commercial confidentiality, we pseudonymized the data.

Our data identified the breed, the sex and age class (nine female and eight male calves, 81 cows, 50 bulls, and 13 oxen), the feeding regime and the type of husbandry. The data could be grouped into three classes. 21 data were about beef cattle, namely Aberdeen Angus (two cows, six bulls) and Wagyu (13 oxen). 44 data were about traditional alpine breeds used both for milk and meat production. Of them, Fleckvieh (Simmental cross-

breeds) is the most common breed in Austria (ZAR 2014). We had data about one cow of Braunvieh (Brown Swiss), 18 bulls of Fleckvieh, nine female calves, eight male calves, two cows, and six bulls of Murbodner. The latter is a rare breed from the Eastern Alps and it is genetically related to Fleckvieh (Kidd and Pirchner 1971). Its conservation is supported under the Austrian gene protection program. The largest group was composed of 96 head of Holstein cattle (20 bulls, 76 cows), a specialized dairy breed that can be found across the world. Our data distinguish several varieties: 76 cows of Holstein-Schwarzbunt, and 6–7 bulls each of Holstein-Friesian, Austria varieties (AT), and New Zealand varieties (NZ). The beef breeds were grazing on pastures during summer, the 13 oxen all the year round (except during very harsh weather conditions), and they received additional feed (concentrates). The others were kept in play pens with occasional outdoor visits. Their feeding was based on silage with added concentrates, except for Murbodner (no added concentrates). In view of commercial confidentiality and ongoing experiments, we were asked not to disclose further details of the feed composition (each keeper used their own recipes optimized for the breed) or to aim at comparing the impact of different feed compositions.

The mass-at-age data were in the form kg at day, whereby birth was at day zero. We considered only data with five data points or more, as we fitted a five-parameter model to the data. However, eight or more data points were needed for the model comparison (see below). In the median calves were most often weighed (22 and 18.5 data points for females and males), followed by cows (15), oxen (11) and bulls (8). The timespan of the data differed, depending also on commercial practices. Animals that were needed for breeding could survive for several years; others were sold or slaughtered early. For 66 animals weighing started in the first week of their lives, amongst them all calves. For the oxen, weighing started late (in the median at day 880), as they were purchased from breeders for fattening. For cows and bulls, in the median weighing started at days 20 and 142.5, respectively. In the median the measurements ended at day 722 for cows, at day 509.5 for bulls, at day 1 107 for oxen and at days 365 and 215 for female and male calves, respectively. The maximum age was 2 585 days. For beef breeds the maximum

weights were 1 426 kg for Aberdeen Angus bulls (median maximal mass 522 kg), 1 175 kg (522 kg) for Aberdeen Angus cows, and 938 kg (822 kg) for Wagyu oxen. For traditional breeds, the maximal weights for Murbodner were 615 kg (472.5 kg) for bulls, 677 kg (613.5 kg) for cows, 432 kg (348 kg) for male calves and 470 kg (382 kg) for female calves. Further, we observed 748 kg for one cow of Braunvieh and 750 kg (677.5 kg) for Fleckvieh bulls. For Holstein cattle, the maximal weight was 830 kg (656.5 kg) for Schwarzbunt cows, 596 kg (579 kg) for AT bulls, 672 kg (639 kg) for Friesian bulls, and 609 kg (571 kg) for NZ bulls.

To eliminate from our data systematic effects which can affect the growing ability of individuals (other than sex, breed, feeding regime etc.), we considered only data that resembled biological growth, whence we disregarded sources that applied compensatory growth. Compensatory growth utilized the ability of animals to undergo enhanced growth after a period of restricted feeding (Mullins et al. 2020), whence the resulting growth curves systematically differed from the traditional model curves, as they added a phase of accelerated growth, where the traditional models (and the BP model) assumed a slowing down of growth. As to the sample size, the number of 161 individuals at first may appear small. However, our computations to identify the best-fitting BP model (using Mathematica software v12.3.1; Wolfram Research, Inc., Champaign, IL, USA) required about a week of central processing unit time per individual (based on standard commercial PCs), whence there were resource limitations. However, the sample size was large enough for our goal of comparing different models for the biological growth of cattle in general. Of course, when grouping the animals into 13 classes stratified by sex and breed, the resulting sample sizes were too small to identify possible influences of sex and breed on the pattern of growth. Further, for our data animals of the same sex and breed were grown under similar conditions, whence we did not aim at recommendations about husbandry or diet.

Data fitting

We aimed at finding parameters that minimized sum of squared errors (*SSE*), the sum of squared errors. If $m(t)$ is a solution of Equation (1), using certain exponents $a < b$ and parameters p, q, c , and

if (t_i, m_i) are n mass-at-age data, then *SSE* is defined by Equation (2):

$$SSE = \sum_{i=1}^n [m_i - m(t_i)]^2 \quad (2)$$

Previously data fitting was troublesome for the BP model (numerical instability), as variations in one parameter could be offset by suitable changes of the other parameters. As common optimization tools were not always able to find the five best-fit parameters for Equation (1), we used the following strategy: we defined a grid of exponent pairs (a, b) with step size 0.01 in both directions and for each grid-point exponent pair we minimized Equation (2) for three parameters. Thus, we identified the best fitting model parameters (p, q, c) for fixed exponent pairs (a, b) . To speed up the computations, we started with a small grid. If the search identified a best-fit exponent pair on the boundary of the grid, we added more grid-points and continued optimization, until we found a best-fit exponent pair surrounded by suboptimal grid-points. For each grid-point (a, b) , the optimization of p, q , and c was done using a custom-made variant of the simulated annealing method (Vidal 1993). We thereby used a strategy that assured positive parameters (p, q, c) and therefore bounded growth functions. The details and the Mathematica-code were outlined in other papers (Renner-Martin et al. 2018).

Our grid search explains why the computations were so time-consuming. As mentioned in the data section, this resulted in limitations for sample size. For the same reason, we did not identify any confidence intervals for the best-fit parameters. Moreover, we were not so much interested in this variability of model parameters for one animal.

Instead, we wanted to study the (larger) variability of derived model parameters across the different animals. In view of the unknown distribution and the (occasionally) small sample sizes for this purpose, we used Clopper-Pearson 95% exact confidence intervals. These intervals are known to be conservative (the confidence for the lower and upper bounds was higher than the nominal 97.5%).

Model comparison

To compare the goodness of fit across different data, we report the coefficient of determination,

R -squared (R^2) of Equation (3); it uses the notation of Equation (2). We used the threshold $R^2 \geq 99\%$ to define an excellent fit.

$$R^2 = 1 - \frac{SSE}{\sum_{i=1}^n [m_i - \text{mean}(m_1, m_2, \dots, m_n)]^2} \quad (3)$$

We also report a normalization $NRMSE$ (normalized root mean squared error) of the root mean squared error; Equation (4). We used the threshold $NRMSE \leq 5\%$ to define a good fit.

$$NRMSE = \frac{\sqrt{SSE/n}}{\max_{i \leq n}(m_i)} \quad (4)$$

Owing to certain limitations of R^2 and $NRMSE$ (Spiess and Neumeyer 2010) we used the Akaike information criterion for model selection. Thereby, as the size of our data varied widely (five to 70 data points), we used its version Akaike information criterion together with a correction for small sample sizes (AIC_c) of Equation (5). It combined a measure of the goodness of fit with a penalty for model parameters, whereby for small datasets the penalty was particularly high (Motulsky and Christopoulos 2003; Burnham and Anderson 2004). When comparing two models, the model with the lower AIC_c was selected as the more parsimonious one.

$$AIC_c = \begin{cases} n \times \ln\left(\frac{SSE}{n}\right) + 2 \times k + 2 \times k \times \\ \times \frac{k+1}{n-k-1} \text{ for } n > k+1 \\ \infty \text{ otherwise} \end{cases} \quad (5)$$

where:

n – the number of data points;

k – the number of optimized parameters of the model (including SSE).

When comparing m models (with AIC_{c1} , ..., AIC_{cm} , respectively), whereby AIC_{cmin} is the least of their AIC_c values, then Equation (6) computes the probability, \wp_i , that the i^{th} model would be “true”, when compared to the other models. We used the threshold $\wp_i < 5\%$ to refute a model as “false”. Models with $\wp_i \geq 5\%$ had an acceptable fit (relative to the other models).

$$\wp_i = \frac{\exp\left(-\frac{AIC_{ci} - AIC_{cmin}}{2}\right)}{\sum_{j=1}^m \exp\left(-\frac{AIC_{cj} - AIC_{cmin}}{2}\right)} \quad (6)$$

In addition to these general measures for model comparison, we used the parameters of the best-fit BP Equation (1) to compute certain parameters with an empirical meaning. This allowed to check if the parameter values would be reasonable. Some authors defined growth models directly from such empirically interpretable parameters (Tjorve and Tjorve 2017).

Equation (7) computes the asymptotic mass m_{\max} for the best-fit model parameters; its empirical interpretation is adult mass. Note that the growth curve was unbounded if $q = 0$. We compared the asymptotic mass with the maximal observed mass $\max(m_i)$, the maximum of the data m_i . We considered that the asymptotic mass was supported by the data if the ratio $m_{\max}/\max(m_i)$ was below 2. Otherwise, asymptotic mass was excessive.

$$m_{\max} = \left(\frac{p}{q}\right)^{\frac{1}{b-a}} \quad (7)$$

Mass growth of animals in general has a sigmoidal pattern, with fast initial growth that slows down later. The sigmoidal character of the growth curves is established by the computation of the inflection point. Equation (8) computes the mass m_{infl} at the inflection point. Note that for $a = 0$ there is no inflection point (we then set $m_{\text{infl}} = 0$). The data had a discernible inflection point (visible already directly from the data), if m_{infl} was between the least and the largest of the observed masses: $\min(m_i) < m_{\text{infl}} < \max(m_i)$.

$$m_{\text{infl}} = \left(\frac{a}{b}\right)^{\frac{1}{b-a}} \times m_{\max} \quad (8)$$

RESULTS

Best-fit parameters

Overall, the general BP model achieved an excellent fit to the data: R -squared ranged from 64.8% to 100%, whereby $R^2 > 99\%$ for 115 data (71% of 161 data). The worst fit was observed for cow No. 088. As a closer inspection of its growth data (Figure 2) revealed the reason for this poor fit, an outlier at day 700, probably a typo. (As there were only four exceptional data with $R^2 < 90\%$, we did not take any action.) Similarly, $NRMSE$ ranged from 0.3% to 10.2%, whereby $NRMSE < 5\%$ established a good fit for 155 data (96% of 161 data).

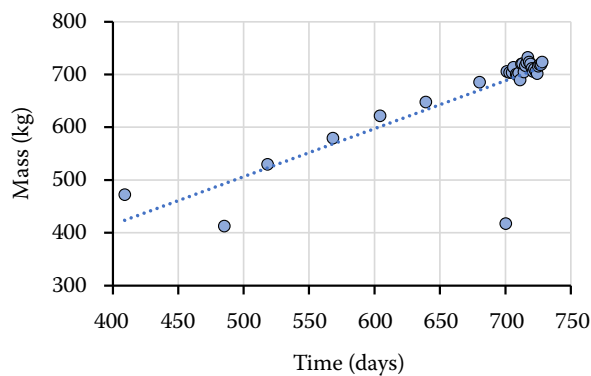


Figure 2. Plot of the growth data of cow No. F04 and its regression line (the most parsimonious model), where owing to an outlier linear growth and other models had their overall worst fit

As on a visual inspection the growth data appeared to be linear (also for Figure 2), we assessed the fit of linear growth. It was excellent for 70 (43%) of the 161 data, with $R^2 > 99$, whereby R^2 ranged from 64.4% (for cow No. 088) to (almost) 100%. Further, for the linear model, $NRMSE < 5\%$ for 142 (88%) of the data. This good fit of linear growth confirmed the rather linear character of the data.

Figure 3 plots the best-fit exponent pairs of the 161 data. We thereby identified for each animal the BP model with the best fit to its growth data, be-

cause we wanted to explore if there was a “typical” growth model for cattle: did the exponent pair cluster near some “typical” pair? As Figure 3 indicates, owing to the biological differences between individuals we could not discern such a pattern. (There was also a high variability of the exponent pairs for animals of the same sex and breed.) The exponent a ranged from 0 to 1.77 and exponent b varied between 0.01 and 48.28.

However, we identified a new model BP(0.2, 1.75) that came close to describing the “typical growth pattern” of cattle. To this end we asked if there was a three-parameter BP model that could be fitted well to most growth data. For each of the 161 animals, we thereby identified all exponent pairs (a , b) of our search grid, where the model BP(a , b) insofar had an acceptable fit, as in comparison with the best-fit BP model its probability to be true was 5% or higher: $\phi \geq 5\%$, using Equation (6) for $m = 2$ models. The exponent pair (0.2, 1.75) satisfied this condition for 131 of 161 growth data.

Model selection

The general BP model always had a better fit (in terms of SSE) than linear growth: for our 161 data, SSE of the BP model in the median was 45% lower

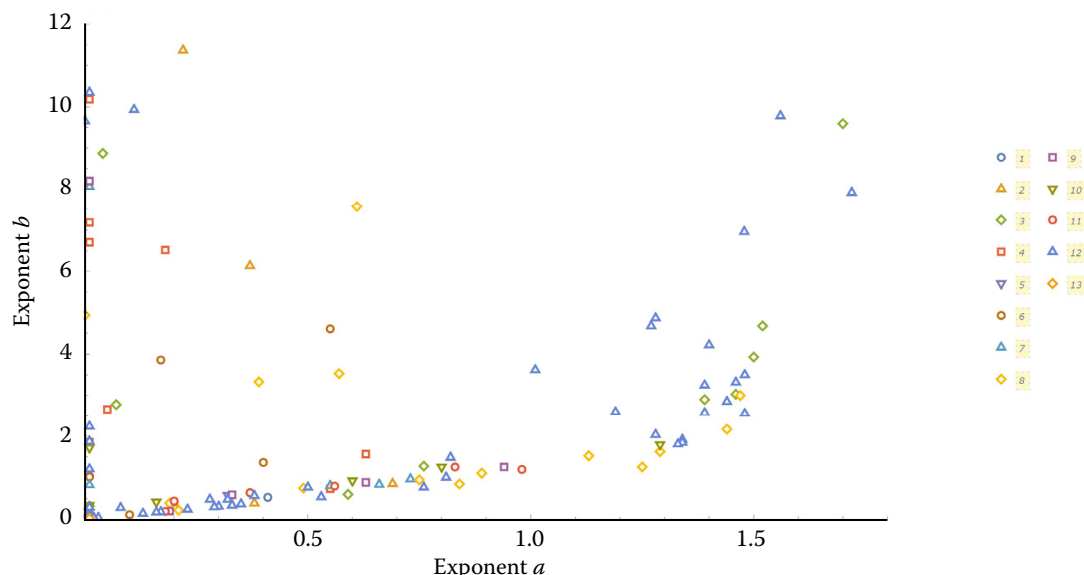


Figure 3. Best-fit exponent pairs to illustrate the lack of a pattern

Colour code: 1 = two Aberdeen Angus cows; 2 = six Aberdeen Angus bulls; 3 = 13 Wagyu oxen; 4 = nine female Murbodner calves; 5 = two Murbodner cows; 6 = eight male Murbodner calves; 7 = six Murbodner bulls; 8 = 18 Fleckvieh bulls; 9 = six Holstein bulls, New Zealand varieties; 10 = seven Holstein bulls, Austria varieties; 11 = seven Holstein Friesian bulls; 12 = 76 Holstein-Schwarzbunt cows; 13 = one Braunvieh cow

than SSE of linear growth. However, when we used the Akaike information criterion for model comparison, then there were only 38 (24%) of the 161 data, where the BP model was more parsimonious (meaning: AIC_c of the five-parameter BP model was smaller than AIC_c of linear growth). The reason was the high penalty for additional parameters: for the linear model, $k = 3$ in Equation (5) of AIC_c (counting the two linear parameters and SSE), while for the five-parameter BP model $k = 6$ (counting a , b , c , p , q , and SSE). This penalty was particularly high for data with few data points: it follows from Equation (5) that a model with five parameters ($k = 6$) fitted to seven or fewer data points would never be parsimonious. (This consideration applied to 16 of our data.)

In order to explore if there were any viable non-linear alternatives to linear growth with fewer than five parameters, we compared six promising models: linear growth ($k = 3$) and the general five-parameter BP model ($k = 6$), plus the four-parameter Richards model ($k = 5$), its three-parameter special case of logistic growth ($k = 4$), the non-sigmoidal growth model of Brody ($k = 4$), and in addition a new three-parameter model BP(0.2, 1.75) that was explained previously. We confined the model comparison to a set of 114 data. For, as was noted above, the consideration of the five-parameter BP model was meaningful only for the 145 data with eight or more data points. Further, as our search for the best-fit model stopped, as soon as the best-fit exponent pair was identified, for several data (where the best-fit exponents a or b were small) we did not further evaluate the fit of other common models, such as logistic growth. This was an issue for 31 of the 145 data

with eight or more data points. Therefore, for the following comparison we removed these data.

Figure 4 summarizes the results of this comparison. Linear growth (two parameters) was selected as the most parsimonious model for 49 (43%) of the 114 data and Richards model (four parameters) was selected for three (3%) of the data. As could be seen from the non-overlapping 95% confidence intervals, these rates were significantly higher and lower, respectively, than the rates of 13–17% for the selection of one of the three-parameter models (Brody, logistic growth, and the new model). The general BP model (five parameters) was selected for 9% of the data (no significant difference from the other models, except for linear growth).

Further, linear growth insofar most often had an acceptable fit, as in comparison with the other five models its probability to be true was 5% or higher for 70 (61%) of 114 data: $\phi \geq 5\%$, assuming Equation (6) for $m = 6$ models. While this rate was not significantly different from the rates of 46–56% for an acceptable fit of the considered three-parameter models, the rates of 20–21% for an acceptable fit of the Richards model and the general BP model were significantly lower than the other four rates.

These results confirmed the generally linear nature of the data. However, linear growth was not suitable for all data: while linear growth achieved an acceptable fit for 61% of the data, the general BP model achieved an acceptable fit for half of the remaining data, covering together 81% of the data. If one more model was considered (namely the new model), an acceptable fit to 92% of the data could be achieved. All models, except the Richards model,

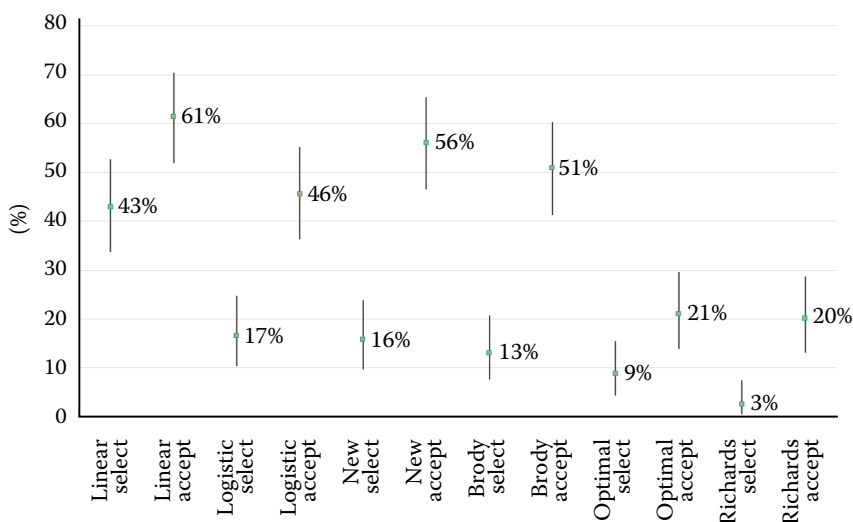


Figure 4. Comparison of six models using the Akaike information criterion (AIC_c), based on 114 selected data

The figure informs about the percentages (dots), how often a model was most parsimonious ("select") and how often its fit was acceptable ("accept"), and it plots the 95% Clopper-Pearson confidence intervals (lines)

were needed if a subset of models with an acceptable fit to all data was desired. For, there were 14 data where linear growth was the sole model (amongst the six considered ones) with an acceptable fit. Similarly, logistic growth was the sole acceptable model for six data, the general BP model for five data, the new model for three data, the Brody model for one datum and only the Richards model for none.

Genuinely sigmoidal data

As the apparent linear character of most data may have blurred the evaluation of the models, we repeated the model selection for certain data of a rather non-linear appearance. We identified 57 “genuinely sigmoidal” data (35% of 161 data), where asymptotic mass was not excessive and where the inflection point was discernible (both computations based on the best-fit BP model). Whereas for 115 data the best-fit growth curve was sigmoidal (exponent $a > 0$), the inflection point was discernible for only 60 data (37%). Further, the asymptotic mass for the best-fit model was excessive (not supported by the data) for 76 (47%) of 161 animals.

Amongst the above 114 data, where our optimization considered also logistic growth, 42 data (37%) were genuinely sigmoidal. Amongst these 42 data and six considered models, the new model was selected most often, for 12 (29%) of 42 data (95% confidence interval 16–45%), followed by linear growth (26%), logistic growth and the general BP model (17% each), the Richards model (7%) and the Brody model (5%). A different picture emerged when models were assessed by their acceptable fit: the new model performed best, with an acceptable fit to 24 (57%) of the 42 data (95% confidence interval: 41–72%), followed by logistic growth (48%), linear growth (45%), the Brody model (43%), the general BP model (33%) and Richards model (29%). Thus, even for these 42 genuinely sigmoidal data a model without inflection point (linear growth or Brody model) was selected as most parsimonious for 13 data. Further, for 25 data the linear model or the Brody model (or both) had an acceptable fit. Consequently, amongst 114 data we found 17 (15%) where only sigmoidal models had an acceptable fit (95% confidence interval: 9–23%). These data included representatives of all three types (beef, traditional, and dairy) of breeds. (The data were about four Aberdeen Angus bulls, one male

and two female Murbodner calves, two Murbodner bulls, three Fleckvieh bulls, two Holstein bulls, and three Holstein cows.)

DISCUSSION AND CONCLUSION

Do size-at-age data support the hypothesis that the biological growth of cattle is sigmoidal? We studied this question on 161 data that we obtained from keepers with commercial or scientific interests. From an initial visual inspection, most data appeared to grow linearly in a first approximation. Indeed, for 43% of the data the fit by the linear regression line was excellent ($R^2 > 99\%$). The likely reason was restrictions in data collection (Renner-Martin et al. 2018). For instance, cattle breeders weighed their calves from birth, but they sold them before they reached their adult mass. Keepers who purchased the calves for fattening recorded the weight increases, but they were unaware of the previous life history. Thus, the data did not extend over the whole lifetime of the animals. Rather, they covered small periods of life, for which linear growth modelling was sufficient for most data. It follows that for a typical commercial cattle keeper linear growth modelling may suffice for most practical purposes. However, this also means that such data may be unsuitable to estimate the mature mass.

The general BP model improved the linear fit considerably; $R^2 > 99\%$ for 71% of the 161 data. Further, for 71% of the data the BP model with the best fit was sigmoidal, because there was an inflection point. However, only for 35% of the data this inflection point was discernible, and the asymptotic mass was not excessive (genuinely sigmoidal data). Further, in terms of parsimony the better fit by the BP model did not in general justify the use of its additional parameters. Most of the data had a non-sigmoidal characteristic insofar, as linear growth or the Brody model of bounded exponential growth achieved an acceptable fit to the data (5% probability to be true), when the general BP model, Richards model, Brody model, logistic growth, linear growth, and a new model were compared. We could identify only a small core of data (15%) where sigmoidal models were indispensable.

Amongst sigmoidal models, the Richards model is commonly used for modelling the biological growth of cattle (Nogales et al. 2017): a Google search identified 18 800 publications since 2011

with the key words cattle and Richards model. However, for our data the performance of the Richards model was surprisingly poor (Figure 4). A reason for the preference of Richards model over the simpler three-parameter models (e.g. logistic growth) is the more reliable estimation of the mature weight (asymptotic mass) due to the additional model parameter (Speidel 2011; Upperman 2021). However, this requires a high density of weight records. Our data suggest that in comparison with the Richards model, its simpler special case of logistic growth in general was good enough, when parsimony was considered: owing to the additional parameter, Richards model always achieved a better fit (smaller SSE) than logistic growth, but in general this improvement of AIC_c was offset by the penalty for the additional parameter. For 37 data, where logistic growth achieved an acceptable fit, the fit by Richards model was not acceptable in terms of AIC_c . (For only eight data, Richards model was acceptable, but logistic growth was not.) The main reason was the relatively small number of weight records, because the last term in Equation (5) was particularly high for individuals with few size-at-age data. However, datasets with large numbers of weighings of each individual are scarce for large animals, such as cattle. Further (Figure 3), the best-fit exponent pairs were in general remote from the line $a = 1$, which collects the exponent pairs of the Richards model.

For literature data about sheep and goats there was a similar observation about the difficulty to identify sigmoidal growth data (Brunner and Kuhleitner 2020). There the Brody model was outstanding. By contrast, the present data identified a certain sigmoidal model as outstanding in the following sense: owing to the variations of the growth pattern between the individual animals, we could not identify a “universal model” for the biological growth of cattle. However, we identified a new three-parameter model, BP(0.2, 1.75), that came close to being universal: amongst the above-mentioned six models it was the most parsimonious model for 29% of the genuinely sigmoidal data and its fit was acceptable for 57% of these data.

Acknowledgements

The paper originates from the master thesis of the first author (Unterauer 2021) under

the guidance of the second and third authors at University of Natural Resources and Life Sciences, Vienna. The authors appreciate the support by the Behringer and Wendler families, ELP Kalsdorf, HBLFA Raumberg-Gumpenstein, Hofgut Neumuhle, and Marbelution Genetics, who provided the size-at-age data for this paper.

Conflict of interest

The authors declare no conflict of interest.

REFERENCES

- Arango JA, Van Vleck LD. Size of beef cows: Early ideas, new developments. *Genet Mol Res.* 2002 Mar;1(1):51-63.
- Brunner N, Kuhleitner M. The growth of domestic goats and sheep: A meta study with Bertalanffy-Putter models. *Vet Anim Sci.* 2020 Dec;10: [10 p.].
- Brunner N, Kuhleitner M, Nowak WG, Renner-Martin K, Scheicher K. Comparing growth patterns of three species: Similarities and differences. *PLoS One.* 2019;14(10): 9 p.
- Brunner N, Kuhleitner M, Renner-Martin K. Bertalanffy-Putter models for avian growth. *PLoS One.* 2021 Apr 26;16(4): 18 p.
- Burnham KP, Anderson DR. Multi-model inference. *Understanding AIC and BIC in model selection. Sociol Methods Res.* 2004 Nov;33(2):261-304.
- FAO – Food and Agriculture Organization. Livestock Systems [Internet]. Rome (Italy): Food and Agriculture Organization of the United Nations. 2021 Feb [cited 2021 Feb 19]. Available from: www.fao.org/livestock-systems.
- Goldberg V, Ravagnolo O. Description of the growth curve for Angus pasture-fed cows under extensive systems. *J Anim Sci.* 2015 Sep 1;93(9):4285-90.
- Kidd KK, Pirchner F. Genetic relationships of Austrian cattle breeds. *Anim Blood Grps Biochem Genet.* 1971 Aug; 2(3):145-58.
- Kuhleitner M, Brunner N, Nowak WG, Renner-Martin K, Scheicher K. Best-fitting growth curves of the von Bertalanffy-Putter type. *Poult Sci.* 2019 Sep 1;98(9):3587-92.
- Marusic M, Bajzer Z. Generalized two-parameter equations of growth. *J Math Anal Appl.* 1993 Nov 15;179(2):446-62.
- Mota RR, Marques LFA, Lopes PS, da Silva LP, Hidalgo AM, Leite CDS, Torres RA. Random regression models in the evaluation of the growth curve of Simbrasil beef cattle. *Genet Mol Res.* 2013 May;12:528-6.
- Motulsky H, Christopoulos A. Fitting models to biological data using linear and nonlinear regression: A practical

- guide to curve fitting. New York: Oxford University Press; 2003. 351 p.
- Mullins Y, Keogh K, Kenny DA, Kelly A, O' Boyle P, Waters SM. Label-free quantitative proteomic analysis of *M. longissimus dorsi* from cattle during dietary restriction and subsequent compensatory growth. *Sci Rep*. 2020;10: 13 p.
- Nogales S, Calderón J, Lupi TM, Bressan MC, Delgado JV, Camacho ME. A comparison of the growth performance between cattle reared in conventional systems and in feral conditions. *Livest Sci*. 2017 Dec 1;206:154–60.
- Ohnishi S, Yamakawa T, Akamine T. On the analytical solution for the Putter-Bertalanffy growth equation. *J Theor Biol*. 2014 Feb 21;343:174–7.
- Putter A. Studien uber physiologische Ahnlichkeit. VI. Wachstumsahnlichkeiten. *Pflugers Arch Gesamte Physiol Menschen Tiere*. 1920 Dec;180(1):298–340. German.
- Renner-Martin K, Brunner N, Kuhleitner M, Nowak WG, Scheicher K. On the exponent in the Von Bertalanffy growth model. *PeerJ*. 2018 Jan 4;6: [26 p.].
- Speidel SE. Random regression models for the prediction of days to finish in beef cattle [dissertation]. [Colorado]: Colorado State University; 2011. 258 p.
- Spiess AN, Neumeyer N. An evaluation of R^2 as an inadequate measure for nonlinear models in pharmacological and biochemical research: A Monte Carlo approach. *BMC Pharmacol*. 2010 Jun 7;10(1): 12 p.
- Tjorve KMC, Tjorve E. A proposed family of unified models for sigmoidal growth. *Ecol Modell*. 2017 Sep 10;359:117–27.
- Unterauer H. Optimale Wachstumsmodelle vom Typ Bertalanffy-Putter fur Rinder [master's thesis]. [Vienna]: University of Natural Resources and Life Sciences; 2021. 81 p. German.
- Upperman LR. Estimation of breed effects and genetic parameters for age at slaughter and days to finish in a multi-breed beef cattle population [dissertation]. [Nebraska]: University of Nebraska; 2021. 105 p.
- Vidal RVV. Applied simulated annealing. Berlin: Springer-Verlag; 1993. 355 p. (Lecture notes in economics and mathematical systems; vol. 396).
- ZAR – Zentrale Arbeitsgemeinschaft Österreichischer Rinderzuchter. Rinderzucht in Österreich [Internet]. Wien: Zentrale Arbeitsgemeinschaft Österreichischer Rinderzuchter; 2014 [cited 2014 Apr 10]. Available from: <https://zar.at/Rinderzucht-in-Oesterreich.html>. German.

Received: June 5, 2021

Accepted: September 30, 2021

Published online: November 1, 2021