The growth of domestic goats and sheep: A meta study with Bertalanffy-Pütter models

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**ABSTRACT**

Growth literature often uses the Brody, Gompertz, Verhulst, and von Bertalanffy models. Is there a rationale for the preference of these classical named models? The versatile five-parameter Bertalanffy-Pütter (BP) model generalizes these models. We revisited peer-reviewed publications from the years 1970–2019 that fitted growth models to together 122 mass-at-age data of sheep and goats from 19 countries and studied the best-fit BP-models using the least-squares method. None of the named models was ever best-fitting. However, for 70% of the data a single non-sigmoidal model had an acceptable fit (normalized root mean squared error < 5% and F-ratio test > 5% in comparison to the best-fit): the Brody model. The inherently non-sigmoidal character was further underlined, as there were only 39% of the data, where the best-fitting BP-model had a discernible inflection point. For these data, conclusions of biological interest could be drawn from the sigmoidal best-fit BP-models: the maximal weight gain per day was about 55% higher than the natal weight gain per day.

**Introduction**

Domestic sheep (*Ovis aries*) and goats (*Capra aegagrus hircus*) are raised primarily for fibers (wool, hair), milk, meat, and hides. Since their domestication ca. 11,000 years ago (Alberto et al., 2018; Pereira & Amorim, 2010) they have been amongst the most important species in livestock, with a global head count of 1.1 billion sheep and 0.95 billion goats in 2010 (FAO, 2020; Gilbert et al., 2018). Different breeds are adapted to multiple environments, whence they are raised in a wide range of production systems.

In view of the economic importance of sheep and goats, there are multiple studies in animal science to characterize their growth patterns. These studies fitted common models to size-at-age data, such as simple linear or exponential growth, but also the negative exponential growth model, the Brody model, and models with sigmoidal (S-shaped) growth curves were considered. Examples for the latter are the models of von Bertalanffy, Gompertz, Richards, or Verhulst (logistic growth). A search in Google Scholar identified approximately 22,500 and 15,500 papers as possible. Where an informal check revealed possible differences, we tested for such differences. We used non-parametric tests: the Mann-Whitney test checked for equal location parameters and the Conover test for equal standard deviations. In case that these differences were not statistically significant, we pooled the data (i.e. we collected them across different species). A priori, for these models (it uses two additional parameters). Moreover, its parameters have a biological interpretation (Bertalanffy, 1957). Therefore, in this paper we revisit data from literature, seek the best fitting BP-models and ask, if in comparison to the best-fit models certain simple three-parameter model may be particularly suitable for the modeling the growth of small ruminants: Why was the Brody model so dominant in growth studies?

**Materials and methods**

**Materials**

We collected the data in spreadsheets, using Excel of Microsoft. To retrieve data from published graphics we used DigitizeIt software. We used Mathematica of Wolfram Research for computer algebra, including optimization (explained below) and statistical analysis.

For the statistical analysis, we aimed at keeping the samples as large as possible. Where an informal check revealed possible differences, e.g. between species, we first tested for such differences. We used non-parametric tests: the Mann-Whitney test checked for equal location parameters and the Conover test for equal standard deviations. In case that these differences were not statistically significant, we pooled the data (i.e. we collected them across different species). A priori, for

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*Abbreviations: BP model, Bertalanffy-Pütter model; SSE, sum of squared errors; NRMSE, normalized root mean squared error

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several biological parameters, such as breeds, we did not expect to find significant differences for the goodness of fit. (As the number of breeds was high, such tests would require a low P-value and therefore large samples to avoid errors of type-I; c.f. Miller, 1981). We then tested if the pooled data could be described by a common probability distribution. We used the Anderson-Darling test for distribution assumptions (Evans, Drew & Leemis, 2017), whereby we considered the normal, the lognormal and the Laplace distribution. Subsequently, we used the tested distribution to draw further inferences.

**Mass-at-age data**

We searched Science Direct, Google Scholar, Research Gate and Web of Science for peer-reviewed publications since 1970 with mass-at-age data about the growth of sheep and goats. We searched primarily for papers that fitted size-at-age data to certain named growth models, as we hoped to add information to that papers by identifying the best-fit BP-model. We used the keywords goat, sheep, growth model in combination by Brody, von Bertalanffy, Gompertz, and Verhulst. We thereby identified 53 publications (57% from 2010 to 2019) that in most cases studied these data with the aim of optimizing breeds and husbandry practices.

In these papers and their supporting information (if available) we searched for mass-at-age data in tables or graphics. Where a paper referred to an accessible primary source, we searched it, too. We did not consider papers that published best-fit model parameters without providing the data or an accessible primary source. In the average (Table 1), data were comprised of \( n_{p} = 50 \) data-points (median \( n_{p} = 12 \)) and they covered \( n_{t} = 5 \) to 296 points of time (mean \( n_{t} = 22 \), median \( n_{t} = 12 \)). We discarded papers that provided only data with \( n_{t} < 5 \) points of time, as then the optimization of five parameters would result in overfitting. For 16 data, the data-points were retrieved from graphics. (In Table 1 the first and/or last points of time, \( t_{0} \) and \( t_{\text{max}} \), were not integers.) One source provided individual growth data (datasets G11 to G22). For the other sources, the data were averages of size-at-age data (with \( n_{p} = n_{t} \)). Most average data did not inform about the spread (standard deviation) or about how many animals were weighed at each point of time.

Table 1 summarizes information about the data that mattered for data fitting. 65% of the data started with natal birth. However, owing to different research questions (e.g. comparing growth before or after weaning) and different methods of data collection (e.g. weighing lambs sold at the market) there were also data, where \( t_{0} \), the first point of time, was significantly larger for systematic reasons. The maximal age, \( t_{\text{max}} \), ranged from 2 month (lambs before weaning) to 30 years (wildlife, where the age was estimated). Thereby, 46% of data were for young animals only (kids and lambs of age at most 9 months) and 29% were long term observations (\( t_{\text{max}} \) of 2 years or more). For some data numerous ages were reported (e.g. G01: \( n_{p} = 252 \)). In part this was due to the weighing of smaller fractions of large samples at different days. For additional information, all data identified the species and the home countries of the animals, 87% specified the breed and 57% specified sex. Thereby, about half of the samples (62 of 122) were controlled for both breed and sex and half were not. Several data differentiated between single and twin birth (21% of the data). Other considerations were the climate (4%: desert, humid, sub-humid), whether birth was in spring or in autumn (3%), and in what year (11%). Further and more detailed information about the surveyed animals is provided in the references below.

Summarizing, we studied 122 data from 19 countries across the world (Fig. 1): 29 domestic goat data came from five countries (Brazil, Mexico, Pakistan, Turkey, and Tunisia). 88 domestic sheep data originated from 16 countries (Algeria, Benin, Brazil, Ghana, Greece, India, Iran, Mexico, New Zealand, Nigeria, Pakistan, Russia, Slovakia, Spain, Turkey, and United Kingdom). 5 wildlife data about bighorn and thinhorn sheep (Ovis canadensis and Ovis dalli) were from Canada and the United States.

As to the sources and the breeds of goats, G01-G02 were Anglo Nubian (and crossbreds) from Brazil (Arre et al., 2019; Cavalcante et al., 2013; Santos et al., 2018), G03-G08 colored and white Angora from Turkey (Cak et al., 2017; Özdemir et al., 2009), G09-G10 Beetal from Pakistan (Tekelen, Galvão & Weber, 2017; Waheed, Khan & Sarwar, 2010), G11-G22 Boer from Mexico (García-Muñiz, Ramírez-Valverde, Núñez-Domínguez & Hidalgo, 2019), G23 Repartida from Brazil (Pires et al., 2017), G24 Saamen from Turkey (Kor, Baspinar, Karaca & Keskin, 2006), and G25-G29 unspecified breeds from Tunisia and Turkey (Mabrouk et al., 2010; Tatar, Tekel, Özkan, Barucci & Della, 2009).

For the sheep, S01 were Awassi from Turkey (Bilgin et al., 2004), S02-S06 Baluchi from Pakistan and Turkey (Iqbal et al., 2019; Tariq et al., 2013), S07 Blackbelly from Mexico (Jimenez-Seviero et al., 2010), S08 Daglic from Turkey (Akbas, Taskin, & Demirörenc, 1999), S09 Deccani from India (Bangar, Lawar, Nimase & Nimbalkar, 2018), S10 Dorper from Brazil (Malhado, Carneiro, Affonso, Souza & Sarmento, 2009), S11-S12 Hemsin from Turkey (Kopuzlu, Sezgin, Ensengoga & Bilgin, 2014), S13-S14 Ile-de France from Brazil (Falcao et al., 2015; Moreira et al., 2016), S15 Karachai from Russia (Semyonov & Selkin, 1989), S16-S17 Karagouniko from Greece (Goliomytis, Orfanos, Panopoulou & Rogdakis, 2006; Tekelen et al., 2018), S18-S34 different varieties and crossbreds of colored and white Karaman from Turkey (Aytekin, Zulkadir, Keskin & Boztepe, 2010; Bilgin et al., 2004; Daskiran, Koncagul & Bingol, 2010; Gökda, Ulker, Karakus, & Firat, 2006; Keskin, Daş, Sarıyal & Göksen, 2009; Kucuk & Eyduran, 2009; Kum, Karakus & Özdemir, 2010), S35 Kivić from Turkey (Abbasi et al., 1999), S36 Kordi from Iran (Mohammadi, Mohktari, Saghie & Shahdadi, 2019), S37 Mehraban from Iran (Bathaei & Leroy, 1998), S38 Morada Nova from Brazil (Paz et al., 2018), S39-S40 Ouled Djellal from Algeria (Zidane, Niær & Abassou, 2015), S41-S42 Romney from New Zealand (Hancock, Oliver, Mclean, Jaquery & Bloomfield, 2011), S43-S45 Santa Ines from Brazil (Santos et al., 2014; Sarmento et al., 2006; Silva et al., 2012), S46-S47 Scottish Blackface from the UK (Friggsens, Shank, Kyriazakis, Oldham & McClelland, 1997), S48-S49 Segurena from Spain Lusitania, Alentejo, Leão, Barba Capote and Delgado, (2015), S50-S51 Shetland from the UK (Friggsens et al., 1997), S52 Sondu from India (Gautam, Kumar, Waiz & Nagda, 2018), S53-S54 Spanish Merino from Spain (López et al., 2018), S55 Suffolk from the UK (Lewis & Brotherstone, 2002), S56 Texel from Brazil (Sieklucki et al., 2016), S57-S59 Thalhi from Pakistan (Iqbal, Waheed, Huma & Faraz, 2019; Tekelen et al., 2017; Waheed et al., 2016), S60-S61 Tsigai and S62 Valachian from the Slovak Republic (Makovicky et al., 2017), S63-S64 Welsh Mountain from the UK (Friggsens et al., 1997), S65-S76 West African Dwarf from Benin and Ghana (Gbangboche et al., 2006 and 2008; London & Weninger, 2011), S77 Yankasa crossbred from Nigeria (Raji, Okoro & Aliyu, 2013), and S78-S88 unspecified breeds from New Zealand and Pakistan (Cruickshank & Thomson, 2008; Ullah, Amin & Abbas, 2013).

For the wildlife, W01 were Bighorn from Canada (Blood, Flok & Wishart, 1970) and W02-W05 Thinhorn from Canada and the USA (Bunnell & Olson, 1976; Heimer, 1972; Nichols & Bunnell, 1999).

**BP-models**

The growth function \( m(t) \) of the Bertalanffy-Püttter (BP) model describes mass, \( m \), at time, \( t \). It is a solution of the following differential equation (Püttter, 1920), which can be solved analytically, though in general not by means of elementary functions (Ohnishi, Yamakawa & Akamine, 2014).

\[
m'(t) = p \cdot m(t)^{q} - q \cdot m(t)^{q}
\]  

(1)

The parameters of Eq. (1) are determined from fitting the model to mass-at-age data. Four parameters are displayed in the equation, namely the non-negative exponent-pair \( a < b \) and the constants \( p \) and \( q \).
Table 1
Characteristics of the mass-at-age data.

| No  | Sex | t₀   | tmax | unit | min | max | n₀  | nᵢ  |
|-----|-----|------|------|------|-----|-----|-----|-----|
| G01 | F   | 1.3  | 899.1| D    | 3.1 | 39.8| 252  | 252 |
| G02 | FM  | 0.2 | 184.8| D    | 1.9 | 17  | 25   | 25  |
| G03 | FM  | 0   | 150  | D    | 2.4 | 17  | 11   | 11  |
| G04 | FM  | 0   | 150  | D    | 1.9 | 13.6| 11   | 11  |
| G05 | F   | 0   | 12   | M    | 2.8 | 16.4| 13   | 13  |
| G06 | M   | 0   | 12   | M    | 2.9 | 22.7| 13   | 13  |
| G07 | F   | 0   | 12   | M    | 3   | 19.1| 13   | 13  |
| G08 | FM  | 0   | 12   | M    | 2.7 | 20  | 13   | 13  |
| G09 | F   | 0   | 360  | D    | 2.7 | 20  | 13   | 13  |
| G10 | M   | 0   | 360  | D    | 2.7 | 22  | 13   | 13  |
| G11 | F   | 1   | 387  | D    | 3.5 | 54  | 42   | 31  |
| G12 | F   | 1   | 375  | D    | 3   | 49.5| 31   | 31  |
| G13 | F   | 1   | 371  | D    | 3.9 | 51  | 7    | 7   |
| G14 | F   | 1   | 380  | D    | 3.5 | 55  | 24   | 16  |
| G15 | F   | 1   | 1944 | D    | 2.2 | 79.2| 156  | 35  |
| G16 | F   | 1   | 1574 | D    | 1.5 | 80.2| 201  | 62  |
| G17 | F   | 1   | 385  | D    | 3.2 | 66  | 65   | 44  |
| G18 | F   | 1   | 733  | D    | 2.3 | 67  | 166  | 83  |
| G19 | F   | 1   | 571  | D    | 2   | 58  | 685  | 155 |
| G20 | F   | 1   | 454  | D    | 2   | 60  | 720  | 186 |
| G21 | F   | 1   | 198  | D    | 1.2 | 54  | 271  | 74  |
| G22 | F   | 1   | 1944 | D    | 1.2 | 80.2| 201  | 62  |
| G23 | FM  | 0   | 270  | D    | 5.2 | 15.4| 10   | 10  |
| G24 | F   | 1.47| 500.6| D    | 5.6 | 46.5| 32   | 32  |
| G25 | F   | 0   | 12   | M    | 3.3 | 28.1| 13   | 13  |
| G26 | M   | 0   | 12   | M    | 3.1 | 35  | 13   | 13  |
| G27 | FM  | 0   | 150  | D    | 2.3 | 13.7| 6    | 6   |
| G28 | FM  | 0   | 150  | D    | 2.5 | 15  | 6    | 6   |
| G29 | FM  | 0   | 150  | D    | 2.4 | 10  | 6    | 6   |
| G30 | F   | 0   | 36   | M    | 4.4 | 49.3| 9    | 9   |
| G31 | F   | 0   | 720  | D    | 3.6 | 39.2| 10   | 10  |
| G32 | M   | 1   | 720  | D    | 3.6 | 47  | 10   | 10  |
| G33 | FM  | 1   | 720  | D    | 3.6 | 43.5| 10   | 10  |
| G34 | FM  | 1   | 720  | D    | 3.6 | 42.5| 10   | 10  |
| G35 | FM  | 0   | 360  | D    | 3.6 | 36  | 8    | 8   |
| G36 | FM  | 0   | 360  | D    | 3.6 | 36  | 8    | 8   |
| G37 | M   | 28  | 168.6| D    | 6.9 | 40.5| 11   | 11  |
| G38 | M   | 0   | 420  | D    | 6.3 | 60.4| 14   | 14  |
| G39 | M   | 0   | 18   | M    | 3.3 | 30.9| 18   | 18  |
| G40 | F   | 0   | 120  | M    | 4.6 | 27.5| 8    | 8   |
| G41 | F   | 0   | 36   | M    | 4   | 61  | 8    | 8   |
| G42 | M   | 0   | 36   | M    | 4   | 75  | 8    | 8   |
| G43 | F   | 0   | 120  | D    | 4.7 | 36.9| 9    | 9   |
| G44 | F   | 0   | 210  | D    | 4.6 | 43.2| 8    | 8   |
| G45 | F   | 0   | 60   | M    | 3.6 | 45  | 7    | 7   |
| G46 | F   | 0   | 720  | D    | 4.7 | 77.9| 17   | 17  |
| G47 | M   | 45  | 720  | D    | 18.3| 96.5| 16   | 16  |
| G48 | F   | 0   | 36   | M    | 4.1 | 52.8| 9    | 9   |
| G49 | F   | 0   | 198  | D    | 4.3 | 39.9| 16   | 16  |
| G50 | M   | 1   | 198  | D    | 4.3 | 45.4| 16   | 16  |
| G51 | F   | 1   | 198  | D    | 4.6 | 43.1| 16   | 16  |
| G52 | F   | 1   | 198  | D    | 3.8 | 40.6| 16   | 16  |
| G53 | F   | 0   | 180  | D    | 4.6 | 33.5| 7    | 7   |
| G54 | F   | 0   | 180  | D    | 4.3 | 30.4| 7    | 7   |
| G55 | F   | 0   | 180  | D    | 4.4 | 51.1| 17   | 17  |
| G56 | M   | 0   | 480  | D    | 4.5 | 65.7| 17   | 17  |
| G57 | F   | 1   | 8    | M    | 13.8| 37.9| 8    | 8   |
| G58 | F   | 1   | 8    | M    | 17.6| 44.3| 8    | 8   |
| G59 | F   | 1   | 44   | M    | 16.2| 79.2| 18   | 18  |
| G60 | F   | 0   | 6    | M    | 4.7 | 39.5| 7    | 7   |

Note: t₀, tmax first/last age, using the units D/W/M/Y: day/week/month/year; min, max: minimal/maximal mass (kg); n₀, nᵢ: number of data points and of points of time.

An additional parameter is the initial value, i.e. m(t₀) = c > 0, where t₀ is the first considered point of time (e.g. t₀ = 0 for natal mass).

The BP-model generalizes several three-parameter models used in literature and therefore it allows for a unified presentation: Each exponent-pair (a, b) defines a unique model BP(a, b) that uses only three parameters (p, q, c). Fig. 2 plots the exponent-pairs of well-known special instances used in animal sciences and compares them with the exponent-pairs (yellow region) that this paper scanned in an initial search for the optimal model parameters. The von Bertalanffy (1949) model is BP(2, 1); the generalized Bertalanffy model is a four parameter BP-model with b = 1 and the free parameters a < 1, c, p and q. BP(0, 1) is the model of bounded exponential growth (monomolecular model) of Brody (1945). The Gompertz (1823) model is the limit case BP(1, 1) with a different differential equation, where b converges to a = 1 from above (Marusjc & Bajzer, 1993). The Richards (1959) model is a four parameter BP-model with a = 1 and the free parameters b > 1,
They explained growth in terms of the allocation of metabolic energy between growth and sustenance of an organism, whereby they perceived the parameters $a$, $b$ as “metabolic scaling exponents” (Pauly & Cheung, 2017). For vertebrates they argued in favor of $BP(0, 1)$ for length growth (VBGM in fishery science) and $BP(2/3, 1)$ for mass growth. A completely different biological explanation of growth (West et al., 2001) led to $BP(3/4, 1)$. This approach was later adapted to explain e.g. the growth of birds from bird-biology (West, Brown & Enquist, 2004) and the growth of forests from botanist principles (West, Enquist & Brown, 2009). However, also environmental factors matter for growth and when determining the best-fit models, different ambient conditions may result in different best-fit exponent-pairs.

We conclude that fundamentally different growth phenomena could be and have been described by the same models. The common basic assumptions for the considered phenomena are an increase of the data (e.g. no starvation) and the presence of at most one inflection point (i.e. modeling one growth phase). Any $BP$-model may be used to describe such phenomena, but some models will fit better than others. In this study we aim at finding the better fitting ones for the growth of goats and sheep.

**Alternative parametrization**

An advantage of using $BP$-models with variable exponent-pairs is the added flexibility for the location of the inflection point. For example, for the logistic growth model ($a = 1$, $b = 2$) the mass at the inflection point is always half of the asymptotic mass. For variable exponent-pairs different fractions between these masses are realized. The formulas for the asymptotic mass $m_{\text{max}}$ (unbounded growth for $q = 0$) and the mass at the inflection point $m_\text{inf}$ (no inflection point for $a = 0$) are displayed in Eq. (2) below; the age $t_\text{inf}$ at the inflection point is computed numerically.

\[
m_{\text{max}} = \left( \frac{a}{q} \right)^{\frac{1}{1-q}} \quad \text{and} \quad m_{\text{inf}} = \left( \frac{a}{b} \right)^{\frac{q}{1-q}} m_{\text{max}}
\]

(2)

Some authors (e.g. Knight, 1968) were concerned that computations of the asymptotic mass (mature body mass) or of the inflection point would be unreliable extrapolations, if these values exceeded the maximal observed mass substantially (Table 1: max) or if $t_\text{inf}$ was outside the timespan of data collection. In the results, we therefore did not report such inflection points. Instead, we informed NA1, if there was no inflection point ($a = 0$) or if it was not observable because there was NA2 a too low mass ($m_\text{inf}$ below the minimal observed mass or below the initial value) or NA3 a too high mass ($m_\text{inf}$ above the maximal observed mass), NA4 a too early inflection ($t_\text{inf} < t_0$) or NA5 a too late one ($t_\text{inf} > t_{\text{max}}$). Further, we did not report asymptotic weights above 1000 kg.

In literature there are alternative parametrizations, which use some or all of the parameters initial mass (natal mass), asymptotic mass $m_{\text{max}}$, the ratio $m_\text{inf}/m_{\text{max}}$, the age $t_\text{inf}$ at maximal growth (inflection point), and the slope $m_\text{inf}$ at the inflection point or natal slope $m_0'$ (Tjørve & Tjørve, 2017). We used the parametrization of Eq. (1), because for data-fitting we worked directly with the numerical solutions of the differential equation. Further, using the method of least squares, $BP$-models in general underestimate $m_{\text{max}}$, whence sufficiently long series of measurements are needed to identify the asymptotic mass, even if further growth is barely discernible. Such long-term measurements are rare.

**Goodness of fit**

We aimed at finding parameters that minimized $SSE$, the sum of squared errors. If $m(t)$ is a solution of Eq. (1), using certain exponents $a < b$ and parameters $p$, $q$, $c$, and if $(t_q, m_q)$ are $n$ mass-at-age data (we use the number $n = n_0$ of data points of Table 1), then $SSE$ is defined by
Table 2
Model comparison using the F-ratio test.

| Model                          | SSE       | Degrees of freedom |
|--------------------------------|-----------|--------------------|
| Model A: simple model          | SSA       | DF_A = n-p_A       |
| Model B: best-fit BP-model     | SSB       | DF_B = n-p_B       |
| Difference                     | SSA - SSB | DF_F = DF_A + DF_B |
| F-value                        | \( F = \frac{SSE_{A} - SSE_{B}}{\text{SSA} + \text{SSB}} \) |                     |
| P-value                        | = 1 - \text{CumulativeFRatioDistributionFunction}(F, DF_A, DF_B) |                     |

Note: \( n \) is the number of data points used for optimization, \( p_A \) and \( p_B \) number of model parameters.

Eq. (3):

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

(3)

When assessing, whether the fit of a certain three-parameter BP-model A can be improved significantly by the best-fit five-parameter BP-model B we apply the F-ratio test using the scheme outlined in Table 2. A P-value below 5% indicates a significant improvement by the best-fit model, where the worse fit of model A could no longer be explained by random fluctuations owing to the higher degrees of freedom. We therefore accept the simpler model A if the P-value is higher than 5%.

To compare the goodness of fit across different data, we report a normalization NRMSE of the root mean squared error RMSE. NRMSE defines a dimensionless measure for the goodness of fit, namely RMSE as a fraction of the maximal observed mass, whereby Eq. (4) uses the notation of formula (3):

\[
\text{RMSE} = \sqrt{\text{SSE}/n} \quad \text{and} \quad \text{NRMSE} = \frac{\text{RMSE}}{\max m_i}
\]  

(4)

For this paper, an acceptable fit means \( \text{NRMSE} < 5\% \). Fig. 2 illustrates the two concepts of acceptability for G05. The exponent pair of the best-fit model is surrounded by the exponent-pairs of models with acceptable F-ratios (green area). For these models, \( \text{NRMSE} \) was acceptable, too. In addition, there were models with acceptable \( \text{NRMSE} \), whose F-ratio was not acceptable (red area). We used G05 for this illustration, as there were no exponent-pairs with an acceptable F-test and a too high \( \text{NRMSE} \). (For other data, this situation occurs, e.g. Brody model for G01.)

Data fitting

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. Standard optimization tools were not able to find all five best-fit parameters for model (1). In recent papers, this difficulty was overcome (e.g. Brunner, Kühleitner, Nowak, Renner-Martin & Scheicher, 2019; Renner-Martin, Brunner, Kühleitner, Nowak & Scheicher, 2019) and the BP-model achieved an excellent fit to the data, resulting in significant improvements over previous studies (e.g. Brunner et al., 2019; Renner-Martin et al., 2019).

We used the following strategy: We minimized (3) for three parameters, i.e. we identified the best fitting model parameters \( p, q \) for a fixed exponent-pairs \( a, b \) and repeated this for all exponent-pairs \( a, b \) on a grid with step size 0.01 in both directions (Fig. 1). 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 sub-optimal grid-points. We thereby searched grids with 12,686 to 189,523 grid-points (mean value 37,748). These computations took about \( \frac{1}{2} \) to 1\( \frac{1}{2} \) weeks CPU-time per dataset, whereby we used eight PCs for commercial use (Intel core i7 processors) in parallel.

Fig. 2 illustrates this search for G05, which resulted in a polygonal shape of the yellow region. The exponent-pairs of several named models remained outside the search grid.

For each grid-point \( (a, b) \), the optimization of \( p, q \), and \( c \) was done using a custom-made variant of the method of simulated annealing (Vidal, 1993). The details and the Mathematica-code were outlined in other papers (Brunner et al., 2019; Renner-Martin, Brunner, Kühleitner, Nowak & Scheicher, 2018 and 2019). Our strategy assured positive parameters \( p, q, c \) and therefore bounded growth functions.

The outcome was exported into a spreadsheet, whose columns listed the best-fit parameters \( a, b, c, p, q, \) and SSE for each grid-point. The best-fit exponent-pair \( (a_{\text{min}}, b_{\text{min}}) \) was identified with an accuracy of 0.01 (as we searched only grid points). Thereby we used the grid-point \( (0.67, 1) \) to represent the von Bertalanffy model and \( (1, 1.01) \) for the Gompertz model. The parameters of the best-fit model, \( p_{\text{min}}, q_{\text{min}}, c_{\text{min}} \) were in the same row, where the least value of SSE was attained. These parameters were optimized with a higher accuracy. For some data this resulted in extremely small values for \( q \): For S08, the optimal \( q \)-value was too small to be recorded properly by Excel; it changed it to \( q = 0 \).

Results and discussion

Best fit models

Our paper focuses on the question mentioned in the introduction: Why was the Brody model mentioned so often in growth studies about small ruminants? We thereby aimed at finding single models that in general would fit well to any data and found that the Brody model was amongst these models. As a yardstick for the assessment of the good fit we used the best-fit BP-models, whence we first analyzed these models.

The literature sources for our data considered unbounded models (e.g. linear and exponential growth), bounded non-sigmoidal growth functions (e.g. Brody model) and bounded sigmoidal models (e.g. logistic growth). Which of these growth patterns were supported by the present data when the best-fit BP model was used? Table 3 informs for each data about the parameters of the best fitting BP-growth curve, Table 4 lists the asymptotic mass (if not excessive or in data) to inform about the shape of the growth curve, and Fig. 3 plots the best-fit exponent-pairs \( (a, b) \) with different colors for goats, sheep, and wildlife. For our data, none of the above-mentioned named three-parameter models was optimal.

Table 3 reports the goodness of fit of it in terms of \( \text{NRMSE} \). It ranged from 0.01% to 12.3%, whereby the medians differed between the species: 4.9% for wildlife, 3% for goat and 1.3% for sheep. The differences in \( \text{NRMSE} \) between sheep and goat respectively sheep and wildlife were statistically significant (Mann-Whitney test, \( P \)-values below 0.0015), but not the difference between goats and wildlife (\( P \)-value 0.33). We nevertheless pooled the \( \text{NRMSE} \) values and found that the Anderson-Darling test did not refute the hypothesis that the logarithms of \( \text{NRMSE} \) were Laplace distributed (\( P \)-value 0.524, maximum likelihood parameters: mean value \( -4.139 \) and shape parameter 0.682).

Under this hypothesis, we could expect that for 9.3% of all data the
best-fit model would not have an acceptable fit (i.e., NRMSE ≥ 5%). The present sample met this expectation approximately: The best-fit model was not acceptable for 14 (11% of 122) data, namely 8 (28% of 29) goats, 4 (5% of 88) sheep, and 2 (40% of 5) wildlife.

While unbounded growth is unrealistic, the initial phase of growth often displays an exponential growth pattern, whence data that cover only this initial phase may result in an unbounded growth model. For the BP-model, unbounded growth is characterized by the parameter q = 0. Although our optimization strategy was designed to ensure positive parameters, q-values close to zero were obtained for 32 data (26% of 122 data with 0+ in Table 3). Some of these values were extremely small, e.g. q = 7.10−10 for G28. However, in view of the asymptotic mass (Table 4), these low parameter values did not always indicate unbounded growth. For instance, for G28 the asymptotic mass was 15 kg. (This was also the maximal mass observed for these data). There were only six data with excessive asymptotic mass (above 1000 kg), namely G21, G27, S08, S35, S39, and S62. Thus, as excessive (or unbounded) growth was observed for only 5% of 122 data, we
conclude that unbounded growth was rather exceptional.

Mass growth in general has a sigmoidal (S-shaped) pattern, with fast initial growth that slows down later. However, growth data may not always display this pattern, e.g. if only data close to the termination of growth have been collected. For the present data, we distinguished between properly non-sigmoidal models, characterized by the parameter \( a = 0 \) (NA1 in Table 4) and rather non-sigmoidal growth curves, where the inflection point (it demonstrates the sigmoidal character) could not be discerned from the data (with reasons NA2-NA5 in Table 4). For the present data, the best-fit parameter \( a = 0 \) was observed in 28 cases (23% of 122 data) and for another 46 data (38%) the inflection point could not be discerned from a plot of the data (NA2-NA5). Thus, in total 74 of the data (61%) had a best-fit growth curve of a rather non-sigmoidal character, of them 16 (55% of 29) for goats, 54 (61% of 88) for sheep and four (80% of 5) for wildlife. We conclude that for the present data growth curves of a rather non-sigmoidal character were prevalent for all species.

Data with discernible inflection points

For 48 (39% of 122) data there was an inflection point and it was discernible from the data (14 goats, 33 sheep, 1 wildlife). There was no significant difference in the goodness of fit (NRMSE) for data with rather non-sigmoidal growth curves and data with discernible inflection points (medians 1.7% and 1.6%, respectively, P-value for the Mann-Whitney test for location 0.848, and for the Conover test for variance 0.178).

For the sigmoidal growth curves the inflection point (Table 4) provides additional biologically relevant information, as at this point growth is fastest. As our data were comprised of different species and within the species of different breeds with different typical sizes, our analysis considered the quotient \( \frac{m_{\text{inf}}}{m_{\text{max}}} \) of mass at the inflection point over asymptotic mass to eliminate size dependency: In view of Eq. (2) this quotient depends on the best-fit exponent-pair, only. This allowed us to pool the data (i.e. the data of all species were considered). For, the Anderson-Darling test did not refute the hypothesis of a normal distribution of the logarithms of these quotients (P-value 0.1, maximum likelihood parameters: mean value – 0.82 for the logarithms, standard deviation 0.46). Thus, in the median the mass at the inflection point was about 43.9% of the asymptotic mass, compared to 29.6% of the von Bertalanffy model, 36.8% of the Gompertz model and 50% of logistic growth. (All of these fractions were in the 90% confidence interval between 20.6% and 93.9%).

For the time variable, we considered the quotient \( \frac{t_{\text{inf}}}{t_{\text{max}}} \) of the age at the inflection point over the time of the last measurement and pooled the data again. For the 48 considered data, this quotient was in the interval between 0 and 1, as we had removed all other data as rather...
non-sigmoidal. The hypothesis of a normal distribution of these quotients was not refuted (Anderson-Darling test, P-value 0.17) and the maximum likelihood parameters were mean value 0.347 with standard deviation 0.224 for these quotients. (Under this distribution, only 0.1% of quotients were expected to be larger than 1 but still 6% could be smaller than 0.)

Another question of biological interest asks: By how much did the speed of growth increase from \( t = 0 \) (birth) to \( t = t_{\text{off}} \) (maximal growth)? To this end we evaluated the quotient \( m_{\text{off}}/m_0 \) for mass (maximal mass gain per day). Similarly, for the speed of growth increase from \( t = 0 \) (birth) to \( t = t_{\text{max}} \) (maximum mass), the estimate \( c \) for \( m(t) \) was substituted. As for this evaluation we considered only data with \( t_0 < 1 \), \( c \) estimated natal mass \( m_0 \). Further, we considered only data, where the best-fitting growth curve had an acceptable fit: NRMSE < 5%. This reduced the count of the considered data to 28 (8 goats, 19 sheep and 1 wildlife). We expect that in average this quotient will be different for different species. However, for the present data we could not confirm a significant difference, as there were too few representatives left for each species, and we pooled the data. The Anderson-Darling test indicated a good fit of the logarithms of the quotients to a normal distribution (P-value 0.533). The maximum-likelihood parameters were 0.439 for the mean value and 0.308 for the standard deviation. (We expect the standard deviation will be lower if the computation is based on studies with larger samples controlled for e.g. sex, breed, and nutrition.) The corresponding lognormal distribution resulted in mean value 1.63 and median 1.55 for the quotients. Thus, for 50% of data we can expect that the estimated natal speed of growth increases by up to 55% and for 50% of data the increase will be even higher.

Finally, we explored the differences between data supporting either non-sigmoidal or sigmoidal models. As shown in Fig. 5, the best-fit exponent-pairs spread over a large region with a concentration of exponent-pairs close to the lines \( a = 0 \) and \( a = b \). Both lines were associated to growth curves of a rather non-sigmoidal character. Comparing data with rather non-sigmoidal growth curves and data with discernible inflection point, for the latter the best-fit exponent \( a \) was stochastically higher (median \( a = 0.645 \) and 0.75 for sigmoidal goats and sheep, respectively, compared to median \( a = 0 \) and 0.01 for rather non-sigmoidal growth curves, P-values below 0.0001 using the Mann-Whitney test). Further, for the latter the exponent-difference \( b - a \) was stochastically higher (median \( b - a = 0.395 \) and 0.55 for sigmoidal goats and sheep, respectively, compared to median \( b - a = 0.15 \) and 0.16 for rather non-sigmoidal growth curves, P-values below 0.013).

In addition, the sheep-data with rather non-sigmoidal growth curves differed significantly in the following aspects from the data with discernible inflection points: For the former, the study durations (difference \( t_{\text{max}} - t_0 \) in days) were stochastically higher, in the median 360 days compared to 180 days (P-value 0.0014, using the Mann-Whitney test), and also the average timespan between successive weight measurements (the quotient \( t_{\text{max}} - t_0 )/n \) was stochastically higher, in the median 30 days compared to 25.7 days (P-value 0.0004).
the transformation for the data-points of the dataset and plot them. Fig. 5 is the superimposition of these plots.

Amongst the other (sigmoidal) named models, the von Bertalanffy model performed best with 38% acceptable fits compared to 17–22% for logistic and Gompertz models. However, the exponent-pairs of these models were so remote from the best-fit exponent-pairs that for 35%–55% of the data they were not even included in the search grid.

We conclude that the non-sigmoidal Brody model achieved almost the best result that could be obtained by a single three-parameter model $BP(a, b)$. What was the reason for this good fit? We had only one source with growth data from a controlled study that provided mass-at-age of individual animals, which we collected in G11 to G22: The Brody model had an acceptable fit to only one of these 12 data, while its fit was acceptable for 85 of the 110 other data. Using a chi-squared test for contingency ($P$-value 0.7-10$^{-7}$), this indicated that the Brody model would rather not be suitable for large collections of individual data from controlled studies. We obtained another significant contingency ($P$-value 0.011) when we distinguished between stratified data, where females and males were collected separately, and pooled data: The Brody model had an acceptable fit for 43 of the 70 stratified data and for 43 of the 52 pooled data. We conclude that the growth curves of females and males may both be sigmoidal, but if the sigmoidal character is only slightly pronounced, it may be lost from averaging over female and male animals. The same reasoning about averaging may apply for other factors, too. We therefore conjecture that the reasons for the dominance of the Brody model were on the one hand the barely noticeable sigmoidal character of the growth curves and on the other the study design of our source papers. For, the sample sizes for these papers often did not allow an additional stratification (e.g. sex, season of birth, or order of birth for twins): In the median the size of the pooled data (FM) was $n_f = 10$ and $n_m = 13$ of the data stratified by sex (Mann-Whitney test: $P$-value 0.002).

Conclusion

Our research confirmed that the intuition of the authors of the source papers was right, who used the common three-parameter models of BP-type to identify the growth patterns for goats and sheep, namely the models of von Bertalanffy, Gompertz, and Verhulst with a sigmoidal growth curves and the non-sigmoidal Brody model. For the present data, most of which came from studies with small samples, and amongst the named models, the model of Brody was the most sensible choice for data-fitting, as this model achieved an acceptable fit to 70% of data (Fig. 5), which was close to the maximum number of data that could be fitted by a single three-parameter BP-model. This outcome may explain, why this model is mentioned so often in growth studies about sheep and goat. We may therefore recommend this model for small samples, particularly if the samples bring together different types of animals (e.g. females and males).

Using general BP-models confirmed the inherent non-sigmoidal character of our data: There were only 39% of data, where the best-fitting BP-model had a discernible inflection point. These genuinely sigmoidal best-fit models were of interest because from them biologically relevant conclusions could be drawn, e.g. a comparison of natal weight gain per day $m'_{n}$ with maximal weight gain $m^*_{n}$.

Declarations of Competing Interest

The authors declare no competing interests. There occurred no ethical issues, as the research was based on publications in peer-reviewed journals that checked that matter. On request, the authors provide additional information (e.g. Mathematica file for the optimisation).

References

Akbas, Y., Taskin, T., & Demiriren, E. (1999). Comparison of several models to fit the growth curves of Kissirk and Dagli male lambs. Turkish Journal of Veterinary and Animal Sciences, 23, 537-544.

Alberto, F. J., Boyer, F., Orozcoter-Wengel, P., Streeter, I., Servet, R., & Villeneuve-R, P. D. (2018). Convergent genetic signatures of domestication in sheep and goats. Nature Communications, 9. https://doi.org/10.1038/s41467-018-03206-y published online: Doi.

Arré, F., Campelom, J., Sarmento, J., Filho, L., & Cavalcante, D. (2019). A comparison of nonlinear models for describing weight-age data in angu-inobian does. Revista Coatinga, 32, 251-258.

Aytekin, İ., Zülkadir, U., Keskin, İ, & Boztepe, S. (2010). Fitting of Different Mathematical Models to the Growth Curves of Female Malay Sheep Weaned at Two Different Live Weights. Trends in Animal and Veterinary Sciences Journal, 1, 19-23.

Bangar, Y., Lawar, V., Nimase, R., & Nimbalkar, C. (2018). Comparison of Non-linear Growth Models to Describe the Growth Behaviour of Deccani Sheep. Agricultural Research, 7. https://doi.org/10.1017/s40003-018-0338-2 published online: Doi.

Bathaei, S. S., & Leroy, P. (1998). Genetic and phenotypic aspects of the growth curve characteristics in Mehraban Iranian fat-tailed sheep. Small Ruminant Research, 29, 261-269.

Bertalanffy, L. (1949). Problems of organic growth. Nature, 163, 156–158.

Bertalanffy, L.V. (1957). Quantitative laws in metabolism and growth. Quarterly Reviews in Biology, 32, 217-231.

Bilgin, O. C., Esenbuga, N., Maiti, M., & Kaoaglu, M. (2004). Growth curve characteristics in Awasu and Morkaraman sheep, part I: Comparison of nonlinear functions. Wool Technology and Sheep Breeding, 52, 1-7.

Blood, D. A., Flook, D. R., & Wishart, W. D. (1970). Weights and growth of Rocky Mountain Bighorn Sheep in Western Alberta. The Journal of Wildlife Management, 34, 451-455.

Brody, S. (1945). Bioenergetics and growth. New York, NY: Hafner Pub. Comp.

Brunner, N., & Kühleitner, M. (2020). Modeling the growth of Pseudomonas putida using the Bertalanffy-Putter model. Research Journal of Pharmaceutical, Biological and Chemical Sciences, 11, 173-179.

Brunner, N., Kühleitner, M., Nowak, W. G., Renner-Martin, K., & Scheicher, K. (2019). Comparing growth patterns of three species: Similarities and differences. Plos one, 14. https://doi.org/10.1371/journal.pone.0224168 published online.

Bunnell, F. A., & Onon, N. A. (1976). Weights and growth of Dall sheep in Kluane Lake Park Reserve. Yukon Territory. Canadian Field Naturalist, 90, 157-162.

Çak, B., Yılmaz, O., Keskin, S., Bayrıl, T., & Tarih, M. (2017). Determination of Appropriate Growth Models for Early Selection Possibilities in Goats. Pakistan Journal of Zoology, 49, 505–509.

Cavalcante, D. H., Campelo, J. E. G., Sousa, S. C., Sousa, G. G. T., Araújo, I. J. M., Araújo, A. C., et al. (2013). Modelos não paramétricos para ajustes de curva de crescimento emcaprinos Sem Raça De emcaprinos Sem Raça De. Ciências Agrárias Ambiental. Curitiba, 11, 283-289.

Cruickshank, G., & Thomson, B. (2008). Modelling management change on production efficiency and methane output within a sheep flock. Final report. sustainable land management and climate change. Wellington, New Zealand: Ministry of Agriculture and Forestry.

Daskiran, I., Koncagöll, S., & Bingol, M. (2004). Growth curve characteristics in Mehraban Iranian fat-tailed sheep. Review of Animal Breeding, 451–258.

Falcão, P. F., Pedrosa, V. B., Moreira, R. P., Sieklicki, M.d. F., Rocha, C. G., Santos, I. C., Ferreira, E. M., et al. (2015). Growth curves for Ile de France ram lambs raised in feedlot. RevistaBrasilieira deSaúde Produtor Animal (Salvador), 16, 377-386.

FAO. (2020). Livestock systems. Rome: Food and Agriculture Organization. published online: www.fao.org/livestock-systems last accessed 12.03.2020.

Friggens, N., Shanks, M., Kyriazakis, I., Oldham, J., & McClelland, T. (1997). The growth of Dall sheep in Kluane Lake Park Reserve. Yukon Territory. Canadian Field Naturalist, 90, 157-162.

Gautam, L., Kumar, V., Waiz, H., & Nagda, R. (2018). Estimation of growth curve parameters using non-linear growth curve models in Sonadi Sheep. International Journal of Livestock Research, 8, 113.

Gautam, L., Kumar, V., Waiz, H., & Nagda, R. (2018). Estimation of growth curve parameters using non-linear growth curve models in Sonadi Sheep. International Journal of Livestock Research, 8, 113.

Ghangboche, A., Ple, K., Romain, L., Salifou, S., Albuquerque, L., & Leroy, P. (2008). Comparison of non-linear growth models to describe the growth curve in West African Dwarf sheep. Animal: An International Journal of Animal Bioscience, 2, 1003–1012.

Ghangboche, A., Ousso, A., Karim, I., Senou, M., Adamou-Ndiaye, I., Ahissou, A., et al. (2006). Examination of non-genetic factors affecting the growth performance of Djallonke sheep in Soudanian zone at the Okpara breeding farm of Benin. Tropical Animal Health and Production, 38, 55-64.

Gilbert, M., Nicolas, G., Cinard, G., Van Boeckel, T. P., Vanwanmekele, S. O., Wint, G. R. W., et al. (2018). Data descriptor: global distribution data for cattle, buffaloes, horses, sheep, goats, pigs, chickens and ducks in 2010. Scientific Data, 5. https://doi.org/10.1038/sdata.2018.227 published online:DOI.

Gelioymitis, M., Orfíanos, S., Panopoulou, E., & Roudakis, E. (2006). Growth curves for body weight and kev raw components, and carcass composition of the Kabargoum sheep, from birth to 720 d of age. Small Ruminant Research, 66, 222-229.
