

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 related to the use of the Brody model for sheep and goats, respectively, followed by the Verhulst model (about 5500 and 3500 hits), the Gompertz model (ca. 4000 and 2000 hits), and the von Bertalanffy model (ca. 2500 and 1500 hits).

The Bertalanffy-Pütter (BP) model (Pütter, 1920) generalizes all

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

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 with 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 $n_D = 50$ data-points (median $n_D = 12$) 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_{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 $n_D = n_T$). 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_{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_{max} of 2 years or more). For some data numerous ages were reported (e.g. G01: $n_T = 252$). 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 thinnhorn 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 crossbreeds) 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 (Teleken, Galvão & Weber, 2017; Waheed, Khan & Sarwar, 2010), G11-G22 *Boer* from Mexico (Garcia-Muñiz, Ramirez-Valverde, Núñez-Domínguez & Hidalgo, 2019), G23 *Repartida* from Brazil (Pires et al., 2017), G24 *Saanen* from Turkey (Kor, Baspinar, Karaca & Keskin, 2006), and G25-G29 unspecified breeds from Tunisia and Turkey (Mabrouk et al., 2010; Tatar, Tekel, Özkan, Baritci & Dellal, 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-Severiano et al., 2010), S08 *Daglic* from Turkey (Akbas, Taskin, & Demirören, 1999), S09 *Deccani* from India (Bangar, Lawar, Nimase & Nimbalkar, 2018), S10 *Dorper* from Brazil (Malhado, Carneiro, Affonso, Souza & Sarmiento, 2009), S11-S12 *Hemisin* from Turkey (Kopuzlu, Sezgin, Esenbuga & 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; Teleken et al., 2017), S18-S34 different varieties and crossbreeds of colored and white *Karaman* from Turkey (Aytekin, Zulkadir, Keskin & Boztepe, 2010; Bilgin et al., 2004; Daskiran, Koncagul & Bingol, 2010; Gökda, Ulker, Karakuş, & Firat, 2006; Keskin, Dağ, Sariyel & Gökmen, 2009; Kucuk & Eyduran, 2009; Kum, Karakuş & Ozdemir, 2010), S35 *Kivircik* from Turkey (Abbas et al., 1999), S36 *Kordi* from Iran (Mohammadi, Mokhtari, Saghi & 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, Niar & Ababou, 2015), S41-S42 *Romney* from New Zealand (Hancock, Oliver, McLean, Jaquiere & Bloomfield, 2011), S43-S45 *Santa Ines* from Brazil (Santos et al., 2014; Sarmiento et al., 2006; Silva et al., 2012), S46-S47 *Scottish Blackface* from the UK (Friggens, Shanks, Kyriazakis, Oldham & McClelland, 1997), S48-S49 *Segurena* from Spain Lupi, Nogales, León, Barba Capote and Delgado, (2015), S50-S51 *Shetland* from the UK (Friggens et al., 1997), S52 *Sonadi* 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 (Sieklicki et al., 2016), S57-S59 *Thalli* from Pakistan (Iqbal, Waheed, Huma & Faraz, 2019; Teleken et al., 2017; Waheed et al., 2016), S60-S61 *Tsigai* and S62 *Valachian* from the Slovak Republik (Makovicky et al., 2017), S63-S64 *Welsh Mountain* from the UK (Friggens 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, Flook & Wishart, 1970) and W02-W05 *Thinnhorn* from Canada and the USA (Bunnell & Olson, 1976; Heimer, 1972; Nichols & Bunnell, 1999).

BP-models

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

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

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	t_0	t_{max}	unit	min	max	n_D	n_T	No	Sex	t_0	t_{max}	unit	min	max	n_D	n_T
G01	F	1.3	899.1	D	3.1	39.8	252	252	S33	FM	0	6	M	4.7	37.8	7	7
G02	FM	0.2	184.8	D	1.9	17	25	25	S34	FM	0	6	M	4.1	37.7	7	7
G03	FM	0	150	D	2.4	17	11	11	S35	M	0	420	D	3.7	69.1	14	14
G04	FM	0	150	D	1.9	13.6	11	11	S36	FM	0	360	D	4	41.6	13	13
G05	F	0	12	M	2.8	16.4	13	13	S37	FM	6	30	M	37.8	68.3	7	7
G06	M	0	12	M	2.9	22.7	13	13	S38	FM	0	680.5	D	2.5	34.1	26	26
G07	FM	0	12	M	3	19.1	13	13	S39	FM	0	90	D	3	14.5	13	13
G08	FM	0	12	M	2.7	20	13	13	S40	FM	0	90	D	3.2	16.4	13	13
G09	F	0	360	D	2.7	20.8	13	13	S41	F	0	360	M	6.6	45.1	18	18
G10	M	0	360	D	2.7	22.2	13	13	S42	F	0	360	M	5.3	45.4	18	18
G11	F	1	387	D	3.5	54	42	31	S43	FM	0	336	D	3.4	27	7	7
G12	F	1	375	D	3	49.5	31	18	S44	FM	0	168.4	D	3.5	22.3	7	7
G13	F	1	371	D	3.9	51	7	5	S45	FM	61.2	790.3	D	36.3	118.2	21	21
G14	F	1	380	D	3.5	55	24	16	S46	F	8	48	W	16.1	67.2	12	12
G15	F	1	1944	D	2.2	79.2	156	35	S47	M	8	44	W	18.2	74.1	11	11
G16	F	1	1574	D	1.5	80.2	201	62	S48	F	0	80	D	3.5	20.2	6	6
G17	F	1	385	D	3.2	66	65	44	S49	M	0	80	D	3.5	22	6	6
G18	F	1	733	D	2.3	67	166	83	S50	F	8	48	W	15.7	43.5	12	12
G19	F	1	571	D	2	58	685	155	S51	M	8	48	W	17.8	61	12	12
G20	F	1	454	D	2	60	720	186	S52	FM	0	12	M	3.3	23.2	13	13
G21	F	1	198	D	1.2	54	271	74	S53	F	0.1	117.2	D	4.1	26	78	78
G22	F	1	1944	D	1.2	80.2	2068	296	S54	M	0	117.2	D	4	28.9	86	86
G23	FM	0	270	D	5.2	15.4	10	10	S55	FM	1.4	150.8	D	0.8	62.8	7	7
G24	F	14.7	500.6	D	5.6	46.5	32	32	S56	M	0	120	D	4	32.6	9	9
G25	F	0	12	M	3.3	28.1	13	13	S57	F	1	720	D	3.5	38.8	10	10
G26	M	0	12	M	3.1	35	13	13	S58	M	1	720	D	3.7	48.5	10	10
G27	FM	0	150	D	2.3	13.7	6	6	S59	FM	0	365	D	3.1	28.9	13	13
G28	FM	0	150	D	2.5	15	6	6	S60	FM	0	270	D	4.9	38.7	15	15
G29	FM	0	150	D	2.4	10	6	6	S61	FM	0	270	D	4.9	38.7	15	15
S01	F	0	36	M	4.4	49.3	9	9	S62	FM	0	63	D	4.8	22.4	10	10
S02	F	1	720	D	3.6	39.2	10	10	S63	F	8	48	W	16.8	56.8	12	12
S03	M	1	720	D	3.6	47	10	10	S64	M	8	48	W	17.8	66.6	12	12
S04	FM	1	720	D	3.6	43.5	10	10	S65	F	0	180	D	1.9	16.8	7	7
S05	FM	1	720	D	3.4	42.5	10	10	S66	M	0	180	D	1.9	17.8	7	7
S06	FM	0	360	D	3.6	36	8	8	S67	FM	0	180	D	2.2	17.9	7	7
S07	M	28	168.6	D	6.9	40.5	11	11	S68	FM	0	180	D	1.6	16.7	7	7
S08	M	0	420	D	6.3	60.4	14	14	S69	F	0	119.3	D	1.8	7.2	18	18
S09	M	0	18	M	3.3	30.9	18	18	S70	M	0	119.2	D	1.9	7.7	18	18
S10	FM	0	210	D	3.4	27.5	8	8	S71	FM	0	118.9	D	1.9	7.7	18	18
S11	F	0	36	M	4	61	8	8	S72	FM	0	118.9	D	1.8	7.1	18	18
S12	M	0	36	M	4	75	8	8	S73	FM	0	105	D	1.7	7.6	7	7
S13	F	0	120	D	4.7	36.9	9	9	S74	FM	0	105	D	1.8	8.4	7	7
S14	F	0	210	D	4.6	43.2	8	8	S75	FM	0	105	D	1.4	6.6	7	7
S15	F	0	60	M	3.6	45	7	7	S76	FM	0	105	D	1.6	7.2	7	7
S16	F	0	720	D	4.7	77.9	17	17	S77	FM	1	20	W	5.1	15.7	20	20
S17	M	45	720	D	18.3	96.5	16	16	S78	F	0	344	D	4.3	58.7	8	8
S18	F	0	36	M	4.1	52.8	9	9	S79	M	0	344	D	4.7	61.2	8	8
S19	FM	0	180	D	4.7	33.6	7	7	S80	F	0	344	D	3.5	50.6	8	8
S20	FM	0	6	M	4.1	36	7	7	S81	M	0	344	D	3.7	52.9	8	8
S21	F	1	198	D	4.3	39.9	16	16	S82	M	0	730	D	3.6	45.7	15	15
S22	M	1	198	D	4.7	45.4	16	16	S83	F	0	730	D	3.5	37.9	15	15
S23	FM	1	198	D	4.6	43.1	16	16	S84	FM	0	730	D	3.6	41.9	15	15
S24	FM	1	198	D	3.8	40.6	16	16	S85	FM	0	730	D	3	40.2	15	15
S25	F	0	180	D	4.6	33.5	7	7	S86	FM	0	365	D	3.5	33.7	13	13
S26	FM	0	180	D	4.3	30.4	7	7	S87	FM	0	730	D	3.5	41.7	15	15
S27	F	0	480	D	4.4	51.1	17	17	S88	FM	0	730	D	3.5	41.2	15	15
S28	M	0	480	D	4.5	65.7	17	17	W01	FM	1	7	Y	76	237.3	7	7
S29	F	1	8	M	13.8	37.9	8	8	W02	F	0.1	13.6	Y	3	54.9	15	15
S30	F	1	8	M	17.6	44.3	8	8	W03	M	0.1	11	Y	4.7	82.9	10	10
S31	F	1	44	M	16.2	79.2	18	18	W04	FM	0	11	Y	8.2	82.4	9	9
S32	FM	0	6	M	4.7	39.5	7	7	W05	FM	1	9	Y	28.5	49.5	9	9

Note: t_0 , t_{max} first/last age, using the units D/W/M/Y: day/week/month/year; min, max: minimal/maximal mass (kg); n_D , n_T : number of data points and of points of time.

An additional parameter is 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).

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 $BP(2/3, 1)$; 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 (1832) model is the limit case $BP(1, 1)$ with a different differential equation, where b converges to $a = 1$ from above (Marusic & Bajzer, 1993). The Richards (1959) model is a four parameter BP-model with $a = 1$ and the free parameters $b > 1$,

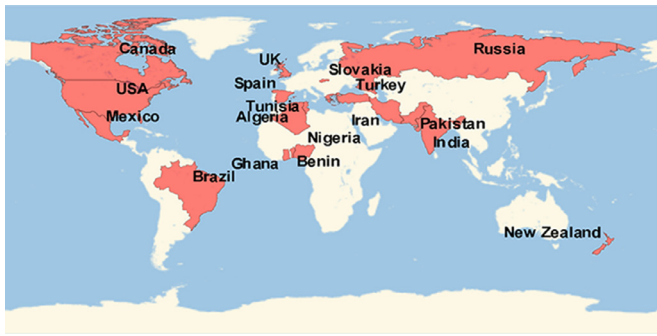


Fig. 1. World map; countries with data in red (plot using Mathematica 12.1).

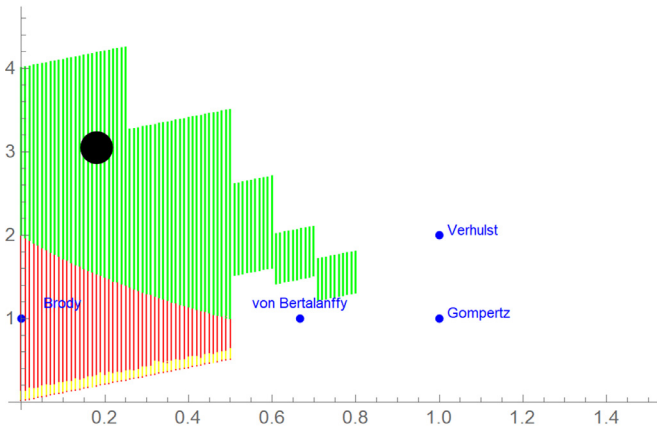


Fig. 2. Exponent-pairs of selected named models (blue dots), of the best-fit model (big black dot), of models with acceptable F-ratios (P-value above 5%) in green, of models with acceptable $NRMSE < 5\%$ (red), and remaining grid-points (yellow), based on G05. .

c , p and q . $BP(1, 2)$ is the [Verhulst \(1838\)](#) model of logistic growth. The West model $BP(3/4, 1)$ is the most recent of these named models ([West, Brown & Enquist, 2001](#)).

The literature sources for our data fitted each dataset in the median to four named BP-models. The most often used model, fitted to 89 of 122 data (73%), was the Gompertz model $BP(1, 1)$. Rank two, fitted to 81 data (66%) was achieved by logistic growth $BP(1, 2)$. Some authors (7 data) considered the special case of exponential growth ($q = 0$). Rank three, fitted to 75 data (61%), was achieved by the Brody model $BP(0, 1)$. For 18 data the sources considered its special case of linear growth ($q = 0$) and for 13 data the sources considered the special case (Mitscherlich model) of negative exponential growth (initial condition $m(0) = 0$). The von Bertalanffy model $BP(2/3, 1)$ was fitted to 69 data (57%) and the Richards model to 33 data (27%). For 33 data (also) models of other classes were considered and for 20 data (16%) the sources did not mention any growth model. The main reasons, why so many authors choose these models, were their wide use in literature and the relative ease of data-fitting for three-parameter models.

The named growth models have been used for multiple purposes: Applications range from biological models for the length or mass of different species of animals, of the growth of plants (the original motivation for the Richards model), to ecological models for the sizes of animal populations or the spread of epidemics and to economic models for the growth of the capital stock (Solow-Swan model; it equals the generalized Bertalanffy model). Even in the field of biotechnology, where traditionally a different model of bacterial growth has been used (model of [Monod, 1949](#)), for certain strains the BP-model turned out to be superior ([Brunner & Kühleitner, 2020](#)). [Pütter \(1920\)](#) and [Bertalanffy \(1949, 1957\)](#) proposed a biological argument, why BP-models would be suitable for the modeling of the growth of animals.

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, D. 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_{max} (unbounded growth for $q = 0$) and the mass at the inflection point m_{infl} (no inflection point for $a = 0$) are displayed in [Eq. \(2\)](#) below; the age t_{infl} at the inflection point is computed numerically.

$$m_{max} = \left(\frac{p}{q}\right)^{\frac{1}{b-a}} \text{ and } m_{infl} = \left(\frac{a}{b}\right)^{\frac{1}{b-a}} \cdot m_{max} \tag{2}$$

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_{infl} 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_{infl} below the minimal observed mass or below the initial value) or NA3 a too high mass (m_{infl} above the maximal observed mass), NA4 a too early inflection ($t_{infl} < t_0$) or NA5 a too late one ($t_{infl} > t_{max}$). 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_{max} , the ratio m_{infl}/m_{max} , the age t_{infl} at maximal growth (inflection point), and the slope m'_{infl} 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_{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_i, m_i) are n mass-at-age data (we use the number $n = n_D$ 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	SS_A	$DF_A = n - p_A$
Model B: best-fit BP-model	SS_B	$DF_2 = DF_B = n - p_B$
Difference	$SS_A - SS_B$	$DF_1 = DF_A - DF_B$
F-value	$F = \frac{\frac{SS_A - SS_B}{DF_A - DF_B}}{\frac{SS_B}{DF_B}}$	
P-value	$= 1 - \text{CumulativeFRatioDistributionFunction}(F, DF_1, DF_2)$	

Note: $n = n_D$ number of data points used for optimization, p_A and p_B number of model parameters.

Eq. (3):

$$SSE = \sum_{i=1}^n (m_i - m(t_i))^2 \tag{3}$$

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):

$$RMSE = \sqrt{SSE/n} \text{ and } NRMSE = \frac{RMSE}{\max_{i \leq n} m_i} \tag{4}$$

For this paper, an acceptable fit means *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, *NRMSE* was acceptable, too. In addition, there were models with acceptable *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 *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, c) 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 1/2 to 1 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_{min}, b_{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_{min}, q_{min} , and c_{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 infinite) and the inflection points (if observable within the timespan of the respective 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 *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 *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 *NRMSE* values and found that the Anderson-Darling test did not refute the hypothesis that the logarithms of *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

Table 3
Best fit parameters and goodness of fit.

No	a	b	c	p	q	NRMSE	No	a	b	c	p	Q	NRMSE
G01	0.01	0.02	3.46	7.48	7.22	9.0%	S33	0.45	4.75	4.8	2.17	0+	0.9%
G02	0.33	6.47	2.35	0.05	0+	1.7%	S34	1.19	2.3	4.31	0.48	0.01	1.8%
G03	0.82	1.16	2.32	0.09	0.03	1.6%	S35	0	0.01	3.85	4.18	3.88	0.5%
G04	1.11	1.35	1.87	0.07	0.03	1.9%	S36	0.22	0.4	3.61	0.61	0.31	3.2%
G05	0.18	3.05	2.79	2.07	0+	1.3%	S37	0.01	1.01	37.78	7.99	0.11	0.0%
G06	0.6	0.75	2.77	5.87	3.67	4.7%	S38	0	0.01	3.85	3.18	3.04	3.3%
G07	0.26	4.52	3	1.72	0+	3.0%	S39	0.01	0.08	3.09	0.12	0+	0.6%
G08	0.39	0.54	2.59	8.41	5.31	3.7%	S40	0.19	3.02	3.22	0.11	0+	0.5%
G09	0	3.01	2.86	0.07	0+	0.7%	S41	0	1.62	6.82	0.37	0+	1.1%
G10	0	3.07	2.94	0.08	0+	1.1%	S42	0.48	0.65	5.18	0.45	0.23	1.6%
G11	0	5.48	3.84	0.19	0+	3.3%	S43	0.36	0.63	3.34	0.24	0.1	0.2%
G12	0.94	1.24	3.7	0.06	0.02	2.2%	S44	0	4.38	3.6	0.16	0+	0.4%
G13	0.85	1.3	3.95	0.05	0.01	1.8%	S45	0.76	1.04	35.18	0.04	0.01	1.0%
G14	0.29	30.16	3.84	0.09	0+	3.5%	S46	0.01	0.24	14.38	4.01	1.17	1.6%
G15	0.54	0.55	2.87	2.78	2.66	4.7%	S47	0.45	0.67	16.81	1.81	0.65	1.2%
G16	0.69	0.79	2.33	0.24	0.16	5.6%	S48	0.51	4.11	3.56	0.07	0+	0.9%
G17	0	2.06	4.64	0.26	0+	7.6%	S49	0.58	33.14	3.67	0.06	0+	0.8%
G18	0.72	0.73	3.53	2.49	2.39	12.3%	S50	0.98	1.29	14.76	0.25	0.08	2.0%
G19	0.77	1.02	3.52	0.1	0.04	12.2%	S51	0.01	0.03	17.03	22.84	20.28	1.7%
G20	0	0.01	3.37	7.93	7.57	9.0%	S52	0.1	0.27	3.15	12.26	6.93	2.1%
G21	0.21	0.22	4.23	0.11	0+	9.9%	S53	1.53	1.97	4.46	0.02	0.01	6.3%
G22	0.24	0.42	3.23	0.4	0.19	8.8%	S54	1.27	1.61	4.03	0.06	0.02	7.2%
G23	0.02	0.03	5.16	3.51	3.39	2.3%	S55	0.5	1.93	0.66	0.16	0+	0.2%
G24	0	0.01	6.45	7.58	7.25	2.2%	S56	0.04	0.33	4.04	0.7	0.21	0.8%
G25	0	0.19	3.37	26.67	14	2.4%	S57	0.01	0.25	3.33	0.4	0.16	1.2%
G26	0.01	0.18	3.12	40.09	21.85	3.0%	S58	0.17	0.18	3.41	6.1	5.86	1.1%
G27	0	0.02	2.54	0.66	0.57	1.5%	S59	0.78	0.95	1.57	0.15	0.08	3.9%
G28	0.22	66.27	2.52	0.06	0+	0.5%	S60	0.95	0.96	4.91	2.17	2.09	2.0%
G29	0.53	95.21	2.55	0.02	0+	2.9%	S61	1.06	1.07	4.92	2.19	2.12	0.4%
S01	0.01	0.02	5.47	306.81	295.05	2.8%	S62	0.37	0.38	6.02	0.12	0.02	3.0%
S02	0.12	0.42	3.48	0.26	0.08	1.6%	S63	0.77	0.99	15.72	0.56	0.22	1.5%
S03	0.05	0.06	3.3	6.93	6.65	1.6%	S64	0.01	0.17	16.5	5.66	2.48	1.7%
S04	0.09	0.23	3.4	0.54	0.31	1.4%	S65	0.87	1.1	1.82	0.09	0.04	1.8%
S05	0.12	0.13	3.15	4.62	4.43	1.9%	S66	0.75	0.99	1.78	0.11	0.05	1.8%
S06	0.29	0.47	3.53	0.32	0.16	0.8%	S67	0.95	0.96	2.09	1.54	1.5	1.5%
S07	0.45	1.21	6.78	0.11	0+	0.7%	S68	0.81	0.99	1.51	0.13	0.08	1.9%
S08	0.01	9.6	6.29	0.13	0	0.3%	S69	0.02	0.03	1.92	8.27	8.09	1.7%
S09	0.44	0.59	2.98	10.38	6.2	1.4%	S70	0	0.01	2.02	6.34	6.19	1.7%
S10	0	8.28	3.55	0.14	0+	0.7%	S71	0	0.01	1.99	7.38	7.22	1.7%
S11	0.04	0.05	4.68	371.67	356.51	2.9%	S72	0	0.01	1.92	6.44	6.3	1.7%
S12	0	0.43	4.42	11.58	1.73	3.7%	S73	0	0.01	1.71	5.77	5.63	1.1%
S13	0.86	1.16	4.69	0.12	0.04	1.3%	S74	0	0.01	1.81	5.7	5.54	0.6%
S14	0.02	2.46	4.68	0.27	0+	1.6%	S75	0.03	0.04	1.38	3.95	3.85	0.5%
S15	0.03	0.25	4.18	16.54	7.17	3.7%	S76	0	0.01	1.61	3.93	3.82	0.8%
S16	0	17.43	7.41	0.13	0+	5.6%	S77	0.01	0.02	5.56	33.39	32.12	0.2%
S17	0.01	29	18.32	0.15	0+	4.0%	S78	0.02	0.05	4.81	2.91	2.5	2.5%
S18	0.14	0.4	3.86	13.07	4.68	1.9%	S79	0	0.06	5.57	2	1.49	2.5%
S19	0.01	0.14	4.76	0.69	0.37	0.5%	S80	0	0.09	3.85	1.13	0.74	2.7%
S20	0.56	7.06	4.32	1.66	0+	1.6%	S81	0.04	0.09	4.76	2.01	1.6	2.8%
S21	0.64	7.77	4.59	0.04	0+	1.3%	S82	0.14	0.38	3.36	0.33	0.13	0.8%
S22	0.5	11.61	5.6	0.06	0+	1.3%	S83	0.07	0.49	3.36	0.24	0.05	1.1%
S23	0.4	11.21	5.51	0.07	0+	1.3%	S84	0.05	0.51	3.45	0.25	0.04	0.9%
S24	0.64	7.74	4.59	0.04	0+	1.3%	S85	0.02	0.84	3.02	0.15	0.01	1.1%
S25	0.12	9.23	4.84	0.14	0+	1.2%	S86	0.13	0.3	3.42	0.43	0.22	1.2%
S26	0	0.06	4.3	1.75	1.35	0.6%	S87	0.15	0.41	3.39	0.3	0.11	0.9%
S27	0	0.78	4.41	0.21	0.01	1.3%	S88	0.08	0.28	3.37	0.4	0.18	1.1%
S28	0.01	0.02	4.4	6.25	5.91	1.3%	W01	0.03	0.16	80.02	293.84	139.45	2.0%
S29	1.56	1.87	13.7	0.27	0.09	0.9%	W02	0.89	1.15	3.69	13.88	5.04	4.9%
S30	1.24	1.79	17.54	0.42	0.05	1.3%	W03	0	1.25	4.78	44.41	0.2	7.1%
S31	0	0.17	16.65	30.59	14.85	5.1%	W04	0	1.07	8.5	27.4	0.28	6.4%
S32	0.83	2.66	4.81	0.88	0+	0.9%	W05	0.03	0.38	28.94	53.02	13.73	3.7%

Note: Parameters rounded to 2 decimals; 0+ is a small positive number.

best-fit model would not have an acceptable fit (i.e. $NRMSE \geq 5\%$). 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. $q = 7 \cdot 10^{-97}$ 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

Table 4
Asymptotic mass and inflection point based on the best-fit BP-model.

No	m_{max}	m_{infl}	t_{infl}	No	m_{max}	m_{infl}	t_{infl}	No	m_{max}	m_{infl}	t_{infl}	No	m_{max}	m_{infl}	t_{infl}
G01	36.3	NA2	NA2	S03	60.9	NA2	NA2	S33	38.3	22.1	2.7	S63	69.2	22.1	12.8
G02	17.8	11	106.4	S04	50.5	NA2	NA2	S34	38.4	21.2	2.9	S64	176.4	NA2	NA2
G03	18.9	6.8	38.1	S05	57.8	NA2	NA2	S35	exc	NA1	NA1	S65	20	7.2	59.8
G04	15.2	6.7	59.1	S06	45.3	NA2	NA2	S36	44.3	NA2	NA2	S66	21.3	6.7	48.1
G05	16.4	6.1	1.3	S07	69.8	19	77.9	S37	70.2	NA2	NA2	S67	21.4	7.5	56.2
G06	23.1	5.2	0.8	S08	exc	NA3	NA3	S38	71.2	NA1	NA1	S68	19.6	6.4	51.5
G07	18.3	9.4	2.4	S09	31	4.4	0.3	S39	exc	NA3	NA3	S69	8.2	NA2	NA2
G08	21.5	NA2	NA2	S10	28.4	NA1	NA1	S40	24.7	9.3	41.1	S70	10.8	NA1	NA1
G09	23.3	NA1	NA1	S11	64.4	NA2	NA2	S41	45.6	NA1	NA1	S71	9.9	NA1	NA1
G10	23.9	NA1	NA1	S12	83	NA1	NA1	S42	45	7.6	7.8	S72	9.3	NA1	NA1
G11	51.6	NA1	NA1	S13	43.7	16.1	38.8	S43	29.1	NA4	NA4	S73	13	NA1	NA1
G12	49.1	19.5	87	S14	46.8	6.5	6.6	S44	23.2	NA1	NA1	S74	16.3	NA1	NA1
G13	52.9	20.6	93.6	S15	44.7	NA2	NA2	S45	126.2	41.2	91.3	S75	14.1	NA2	NA2
G14	51.7	44.2	201.5	S16	69.6	NA1	NA1	S46	207.7	NA2	NA2	S76	17.7	NA1	NA1
G15	70.9	NA4	NA4	S17	92.5	70.3	375.8	S47	104.6	NA2	NA2	S77	49.5	NA2	NA2
G16	69.3	17.9	82.8	S18	51.9	NA2	NA2	S48	24.7	13.9	51.2	S78	166	NA2	NA2
G17	59.9	NA1	NA1	S19	134.4	NA2	NA2	S49	22	19.4	64.6	S79	130.7	NA1	NA1
G18	54.9	13.8	50.5	S20	35.3	23.9	3	S50	46.6	19.2	12.1	S80	108.9	NA1	NA1
G19	51.7	16.8	72.5	S21	40.7	28.7	125.5	S51	381	NA2	NA2	S81	99.6	NA2	NA2
G20	106.4	NA1	NA1	S22	45.2	34	123.1	S52	28.7	NA2	NA2	S82	51.1	NA2	NA2
G21	exc	NA3	NA3	S23	43.2	31.8	120.7	S53	22.8	12.9	40.5	S83	40.6	NA2	NA2
G22	69.9	NA2	NA2	S24	40.7	28.7	125.4	S54	25.3	12.6	35.8	S84	45.7	NA2	NA2
G23	30.7	NA2	NA2	S25	34.1	21.2	88.7	S55	70	27.2	63.2	S85	44.7	NA2	NA2
G24	78	NA1	NA1	S26	74.6	NA1	NA1	S56	66.7	NA2	NA2	S86	47.7	NA2	NA2
G25	29.7	NA1	NA1	S27	72.7	NA1	NA1	S57	44.4	NA2	NA2	S87	45.5	NA2	NA2
G26	35.6	NA2	NA2	S28	266.8	NA2	NA2	S58	56.6	NA2	NA2	S88	47.3	NA2	NA2
G27	exc	NA1	NA1	S29	39.2	21.8	2.6	S59	28.4	8.9	58.5	W01	309	NA2	NA2
G28	15	13.8	127.4	S30	45.4	23.3	1.9	S60	38.3	13.4	34.9	W02	49.1	18.3	0.6
G29	10	9.4	127.4	S31	70.1	NA1	NA1	S61	27.6	10.8	24.8	W03	75.3	NA1	NA1
S01	49.8	NA2	NA2	S32	42.4	22.4	3	S62	exc	NA3	NA3	W04	73.4	NA1	NA1
S02	43.4	NA2	NA2	W05	47.5	NA2	NA2								

Note: mass in kg, t_{infl} in the units of Table 1, exc = excessive asymptotic mass, NA = no/not observable inflection point.

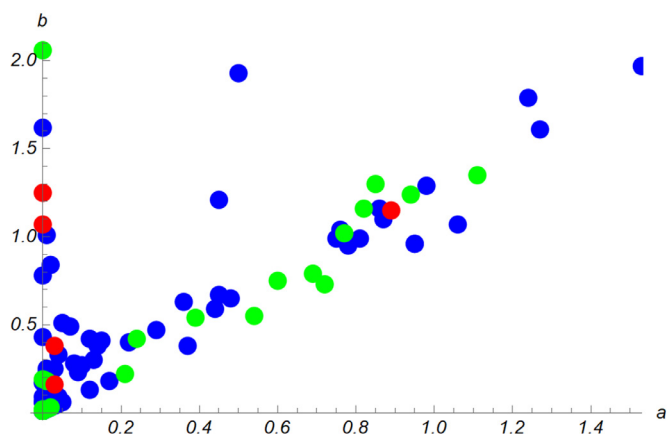


Fig. 3. Best-fit exponent-pairs for goats (green), sheep (blue) and wildlife (red) in the region $0 \leq a \leq 1.5$, $0 \leq b \leq 2$.

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 m_{infl}/m_{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 t_{infl}/t_{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

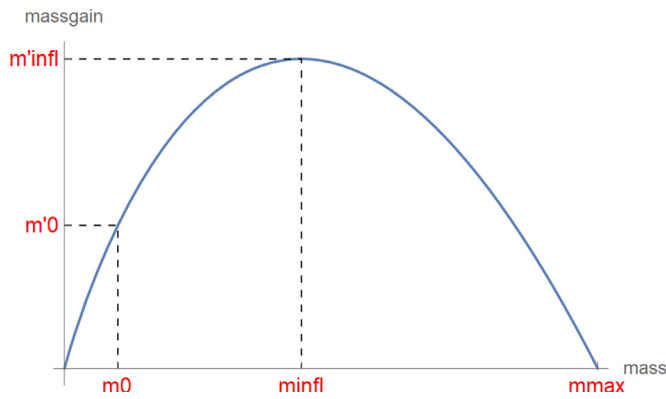


Fig. 4. Explanation of the quotient m'_{infl}/m'_0 .

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 $t = t_{infl}$ (maximal growth)? To this end we evaluated the quotient m'_{infl}/m'_0 (see Fig. 4): Thereby, m'_{infl} is the right-hand side of (1), when m_{infl} was substituted for mass (maximal mass gain per day). Similarly, for m'_0 the estimate c for $m(t_0)$ 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. 3, 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 $t_{max} - t_0$ 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

Table 5

Count of datasets with an acceptable fit to the indicated named models.

	Brody model	von Bertalanffy@@@model	Gompertz@@@model	Verhulst@@@ (logistic) model
not in grid	1	43	64	67
NRMS criterion				
acceptable	104	63	41	39
not acceptable	17	16	17	16
F-ratio test criterion				
acceptable	94	58	36	33
not acceptable	27	21	22	22
both criteria				
acceptable	86	47	27	21
not acceptable	35	32	31	34

Notes: The table counts, for how many data the model had the following outcome: not in grid indicates that this model was not in the search grid, as its exponent-pair was too remote from the best-fit exponent-pair; criterion $NRMSE$ means $NRMSE < 5\%$; F-ratio test criterion means an P-value $< 5\%$ for the comparison of this model with the best fit model; not acceptable means that one of these criteria was not satisfied (although the exponent-pair of the model was in the grid).

measurements (the quotient $(t_{max} - t_0)/n_T$) was stochastically higher, in the median 30 days compared to 25.7 days (P-value 0.0004).

Fit for named models

Next, we searched for models that achieved an acceptable fit to as much data as possible. We used two criteria, $NRMSE < 5\%$ (the plot showed a growth curve close to the data) and F-ratio test with P-value $> 5\%$ (the best-fit model did not achieve a statistically significant improvement of the fit): A model had an acceptable fit if both criteria were satisfied. We confined the search to $a < 1$ and $a < b < 3$ and identified six models with an acceptable fit to 90 (74% of 122) data: $BP(0.02, 1.1)$, $BP(0.02, 1.12)$, $BP(0.06, 0.99)$, $BP(0.06, 1.02)$, $BP(0.16, 0.77)$, and $BP(0.24, 0.71)$. Thus, for the present dataset, the count of 90 was the maximum number of data to which a single three-parameter model $BP(a, b)$ could have an acceptable fit in terms of both aspects $NRMSE$ and F-ratio test.

Table 5 compares this outcome with the fits for the models of von Bertalanffy, Brody, Gompertz, and Verhulst. For the Brody model $NRMSE$ was acceptable for 104 data (for the best-fit models: 108 data), the F-ratio was acceptable for 94 data and the fit was acceptable under both aspects for 86 data (70% of 122 data), which was close to the best performance for a single model. To illustrate the good fit, Fig. 5 plots the transformed dimensionless data-points. There were 82 datasets with an acceptable fit to the Brody model and asymptotic mass below 1000 kg. We used the best-fit parameters of this Brody model to define

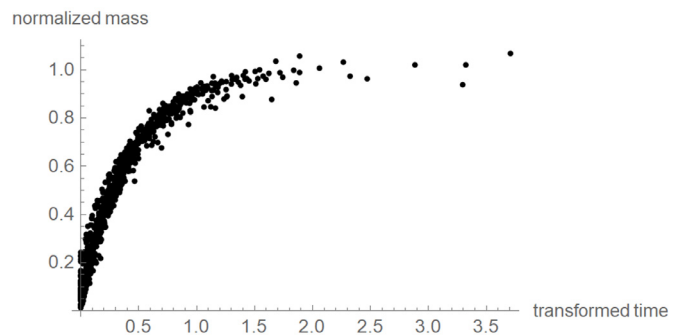


Fig. 5. Plot of data-points that were transformed using the Brody model with the best fit to the dataset. For each of 82 datasets with acceptable fit and asymptotic mass below 1000 kg, mass was divided by asymptotic mass and age was divided by the age, at which 90% of asymptotic mass was reached.

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 $0.7 \cdot 10^{-7}$), 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 $n_D = 10$ and $n_D = 13$ 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'_0 with maximal weight gain m'_{inf} .

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 optimization).

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