

Comparison of two nonlinear functions describing the growth of Popielno White and New Zealand White rabbits

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SUMMARY

The objective of this study was to assess the possibility of using two nonlinear models, i.e. the von Bertalanffy and Gompertz functions, for fitting growth curves of Popielno White and New Zealand White rabbits. The study was conducted using 37 Popielno White (21 male and 16 female) and 55 New Zealand White (28 male and 27 female) rabbits. The nonlinear regression procedure (NLIN) in SAS 9.4 software was used to model the rabbits' growth curves from birth to 12 weeks of age. To see how rabbit growth might progress in subsequent weeks, we extrapolated the weights of the rabbits up to the age of 30 weeks. Six criteria were used to compare models: mean error, mean squared error, mean absolute error, quotient between the error sum of squares and observed sum of squares, corrected Akaike information criterion, and Bayesian information criterion. The shape of all curves was sigmoid, and both models fitted well to the data from birth to 12 weeks of age, i.e. during the interpolation process. A problem with the fit occurred later, during the extrapolation process, i.e. when the models were used to predict the animals' course of growth in subsequent weeks. When body weight was extrapolated in later weeks of life, the fitting of the von Bertalanffy model was slightly worse, and asymptotic body weight was overestimated. To predict the further course of rabbit growth in practice, the Gompertz function would be a better choice. The Gompertz model could also be a helpful tool for breeders to describe the growth process of rabbits and to select a more economically profitable breed.

KEY WORDS: body gain, body weight, growth curves, rabbits



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INTRODUCTION

According to the literature, the most important factors affecting the economic efficiency of rabbit breeding include litter size and a set of characteristics describing the course of their growth. The course of animal growth can be defined in different ways, but generally it is described by measuring body weight on successive days, weeks or months of age. On this basis, daily weight gains, growth rate and feed consumption per unit of weight gain can be determined (Blasco et al., 2018). Among the large variety of existing breeds of rabbits, medium-sized breeds are frequently used in commercial production due to their high prolificacy, fast weight growth, high dressing percentage and high meat quality (Tůmová et al., 2014; Wang et al., 2016; Blasco et al., 2018). The New Zealand White rabbit is one of the most economically exploited and suitable breeds for production of meat and skins (Santos et al., 2018).

Mathematical models, i.e. growth curves, have been widely applied to describe the weight–age relationship in many species of animals, such as cattle, sheep or pigs (Lupi et al., 2015; Teleken et al., 2017; Fernandes et al., 2019). Growth curves can be used not only to model the course of animal growth over time, but also to calculate and predict many interesting, biologically interpretable parameters, such as mature weight, rate of maturation, or rate of gain. Knowledge of such parameters may be useful for determining daily feed requirements or evaluating the influence of environmental conditions on weight gain. The growth functions can also be used to predict the optimum slaughter age (Goonewardene et al., 1981; Teleken et al., 2017).

There are a number of growth functions available in the literature (Blasco and Gómez, 1993; France et al., 1996; Gbangboche et al., 2008). In mathematical terms, growth models can be grouped into three main categories: those with diminishing returns, e.g. the Brody model, those with a sigmoidal shape and a fixed inflection point, e.g. the Gompertz, logistic and von Bertalanffy models, and those with a flexible inflection point, such as the Richards model. The Brody model does not have an inflection point. The von Bertalanffy, Gompertz and logistic functions have an inflection point at about 30%, 37% and 50% of mature weight, respectively; this point is interpreted as the time of maximum growth rate, after which growth slows down. The Richards function summarizes all the above-mentioned growth models in one function with a variable inflection point specified by the shape parameter, but as a four-parameter model it is more demanding than the others mentioned above, and fitting it to the data can be difficult (Teleken et al., 2017). The choice of the most appropriate model for a given animal species requires a preliminary comparison of the growth functions.

The use of growth models among rabbit breeders is rare (Ptak et al., 1994; Setiaji et al., 2013; Santos et al., 2018). Hence our intention was to draw breeders' attention to the use of growth curves as a helpful tool for controlling and optimizing rabbit production. The objective of this study was to assess the potential use of two nonlinear models, the von Bertalanffy and Gompertz functions, for fitting growth curves of Popielno White and New Zealand White rabbits. Due to differences in the body weights of females and males, the sex of the rabbits was additionally taken into account in the research.

MATERIAL AND METHODS

The experiment was conducted under standardized conditions at the Experimental Station of the Department of Genetics, Animal Breeding and Ethology, University of Agriculture in Krakow. There were 37 Popielno White (21 male and 16 female) and 55 New Zealand White (28 male and 27 female) rabbits used in the research. Until weaning, the rabbits were housed with their mothers in wooden cages placed in a heated hall equipped with a water trough installation (nipple drinkers), lighting installation (14L:10D), and forced ventilation system. From weaning (5 weeks of age) until the age of 12 weeks, the animals were kept in wire metal cages intended for commercial rearing of rabbits (2 rabbits per cage). They were fed *ad libitum* with a commercial pelleted complete feed with 16,4% crude protein; 9,22% crude fibre; 2,70% crude fat; 4,82% crude ash and 10,11 MJ/kg metabolizable energy. According to the feed manufacturer (FHP Barbara Sp. z o. o., Turza, Poland), the feed contained wheat (29,58%), corn (24,50%), bran (15%), sunflower meal (11%), dried alfalfa (10%), soybean meal (7%), mineral-vitamin premix (1,50%), calcium carbonate (0,80%) and dicalcium phosphate (0,62%). Water was available *ad libitum*. The rabbits were slaughtered at the age of 12 weeks as described by Blasco and Ouhayoun (1996).

The nonlinear regression procedure (NLIN) in SAS 9.4 software (SAS, 2014) was used to model the rabbits' growth curves from birth to the age of 12 weeks. To see how rabbit growth might progress in subsequent weeks, we extrapolated the weights of the rabbits up to 30 weeks of age. Two three-parameter functions commonly used to describe growth curves in meat production studies were fitted:

$$\begin{array}{ll} \text{Gompertz (1825) model:} & y(t) = a \cdot \exp(-b \cdot \exp(-k \cdot t)) \\ \text{von Bertalanffy (1957) model:} & y(t) = a \cdot (1 - b \cdot \exp(-k \cdot t))^3 \end{array}$$

where $y(t)$ is the weight (in grams) at age t (in weeks), and a , b , and k are fitted parameters. Parameter a designates the average weight at maturity, b is a time scaling factor, and k is the rate of maturation. The higher the value of k , the faster the animals mature (Ptak et al., 1994; Gbangboche et al., 2008).

In addition, for both models the values of the first derivative ($y'(t)$) were calculated for each week of age (t), using the following formulas:

$$\begin{array}{ll} \text{Gompertz model:} & y'(t) = a \cdot b \cdot k \cdot \exp(-k \cdot t) \cdot \exp(-b \cdot \exp(-k \cdot t)) \\ \text{von Bertalanffy model:} & y'(t) = 3 \cdot a \cdot b \cdot k \cdot \exp(-k \cdot t) \cdot (1 - b \cdot \exp(-k \cdot t))^2, \end{array}$$

where a , b , and k are parameters of the fitted models. These values represented the average growth rate in subsequent weeks.

The inflection point ($t_i, y(t_i)$), at which the growth rate reaches its maximum, provides an estimate of age and weight at puberty (Ptak et al., 1994). In mathematical terms, the inflection point is the point at which the function changes its convexity, and the t -coordinate of this point is obtained by equating the second derivative of the function to zero, i.e. $y''(t) = 0$. The inflection point was at $t = \ln(b/k)$ for the Gompertz model and at $t = \ln(3b/k)$ for the von Bertalanffy model. For both of these t -values, the third derivative was different from zero, confirming that the inflection point existed at the designated t -values. The weight at the inflection point amounted to

0,30 and 0,37 of asymptotic (mature) weight according to the von Bertalanffy and Gompertz models, respectively.

The errors (e_i) were calculated as the differences between the measured (y_i) and estimated (\hat{y}_i) weights. The following criteria of goodness of fit were used to compare the models:

1. Mean error (ME): $ME = \frac{\sum e_i}{n}$
2. Mean squared error (MSE): $MSE = \frac{\sum e_i^2}{n}$
3. Mean absolute error (MAE): $MAE = \frac{\sum |e_i|}{n}$
4. Quotient (Q) between the error sum of squares and observed sum of squares: $(Q = \frac{\sum e_i^2}{\sum y_i^2})$, with lower

values indicating closer similarity between the true (y_i) and estimated (\hat{y}_i) values

5. Corrected Akaike information criterion (AIC_c): $AIC_c = AIC + \frac{2K(K+1)}{N-K-1}$,

where $AIC = N \log \left(\frac{\sum e_i^2}{N} \right) + 2K$, N is the number of experimental points, and K is the number of parameters of the model. Correction of the Akaike information criterion (AIC) is needed when the number of observations (N) is relatively small (i.e. the ratio of N to K is less than 40), because in this case the AIC may be not sufficiently accurate (Teleken et al., 2017). The actual values of AIC_c have no meaning, but AIC_c makes it possible to rank the models and select the best one, i.e. the one with the lowest AIC_c.

6. Bayesian information criterion (BIC): $BIC = N \log \left(\frac{\sum e_i^2}{N} \right) + K \log(N)$, where N is the number of experimental points and K is the number of parameters of the model. The lower the BIC value, the better the model.

It is worth adding that the AIC and BIC criteria are not only measures of the goodness of fit of the model; the model complexity is included in calculations as well. Statistically, a good model should be as simple as possible, and a proper balance between underfitting and overfitting should be maintained (Portet, 2020).

RESULTS AND DISCUSSION

Table 1 shows the dataset characteristics, i.e. body weight in successive weeks of age in Popielno White and New Zealand White rabbits of both sexes. The mean body weight was generally higher for Popielno White rabbits than for New Zealand White rabbits, with greater standard deviations and wider ranges of values for Popielno Whites. After the age of 3 weeks, when pellets were introduced to the diet, body weight was similar for both sexes and breeds. In the last week of life, the body weight of Popielno White rabbits was slightly higher.

The growth curves of Popielno White and New Zealand White rabbits fitted by the Gompertz and von Bertalanffy models are shown in Figure 1. The shape of all curves was sigmoid, and both models showed good fit to the data from birth to the age of 12 weeks, i.e. during the interpolation process. A problem with the fit occurred later, during extrapolation, i.e. when the models were used to predict the course of the animals' growth in subsequent weeks. The Gompertz model better illustrated the further growth of rabbits, estimating an asymptotic value close to the average mature weight of Popielno White and New Zealand White rabbits (about 4 kg). The von Bertalanffy function significantly overestimated the real body weight, especially for New Zealand White males (reaching up to 5 kg at the age of 28 weeks).

Table 1

Descriptive statistics of body weights (in grams) of Popielno White and New Zealand White rabbits of both sexes

Age [weeks]		Popielno White		New Zealand White	
		Male	Female	Male	Female
Birth	Mean	68,21	74,03	64,98	62,15
	SD ¹⁾	9,24	10,68	17,83	14,22
	Min-Max	56,0-86,7	63,0-86,7	44,0-100,0	44,0-100,0
1	Mean	134,48	124,13	125,45	134,00
	SD	24,88	14,02	22,94	14,83
	Min-Max	70,0-168,7	104,3-138,7	78,3-155,8	108,3-155,8
2	Mean	249,54	224,98	220,34	228,94
	SD	52,17	48,84	33,82	33,16
	Min-Max	120,0-337,5	120,0-283,7	178,3-316,7	190,0-316,7
3	Mean	352,85	336,19	346,74	351,59
	SD	63,60	65,92	37,58	46,33
	Min-Max	240,0-440,0	220,0-420,0	280,0-440,0	255,0-470,0
4	Mean	566,43	559,53	479,82	488,72
	SD	121,04	140,63	64,45	64,84
	Min-Max	295,0-760,0	320,0-755,0	350,0-620,0	330,0-625,0
5	Mean	840,95	800,63	708,93	708,70
	SD	147,43	200,96	112,69	91,07
	Min-Max	560,0-1090,0	425,0-1090,0	410,0-885,0	495,0-910,0
6	Mean	1165,71	1034,38	945,86	927,96
	SD	211,96	306,94	134,52	141,61
	Min-Max	815,0-1685,0	620,0-1480,0	665,0-1240,0	620,0-1235,0
7	Mean	1439,52	1384,69	1073,57	1075,00
	SD	206,03	319,83	198,63	240,98
	Min-Max	1110,0-1830,0	840,0-1880,0	600,0-1440,0	525,0-1420,0
8	Mean	1718,52	1661,25	1278,30	1280,09
	SD	227,87	299,61	265,62	280,10
	Min-Max	1415,0-2200,0	1110,0-2110,0	685,0-1655,0	820,0-1740,0
9	Mean	2017,95	1898,91	1531,16	1459,91
	SD	240,02	314,61	324,59	315,76
	Min-Max	1675,0-2470,0	1400,0-2330,0	862,50-1240,0	800,0-1925,0
10	Mean	2290,71	2155,00	1726,88	1688,70
	SD	262,08	307,96	341,01	283,63
	Min-Max	1835,0-2720,0	1700,0-2560,0	1040,0-2255,0	1135,0-2150,0
11	Mean	2481,90	2347,81	2034,11	1920,00
	SD	263,95	264,53	309,20	331,81
	Min-Max	2105,0-2910,0	1950,0-2750,0	1335,0-2595,0	1250,0-2485,0
12	Mean	2751,67	2575,94	2316,79	2144,07
	SD	265,01	312,78	317,47	317,98
	Min-Max	2360,0-3235,0	2020,0-3020,0	1560,0-2925,0	1580,0-2790,0

¹⁾ SD = standard deviation

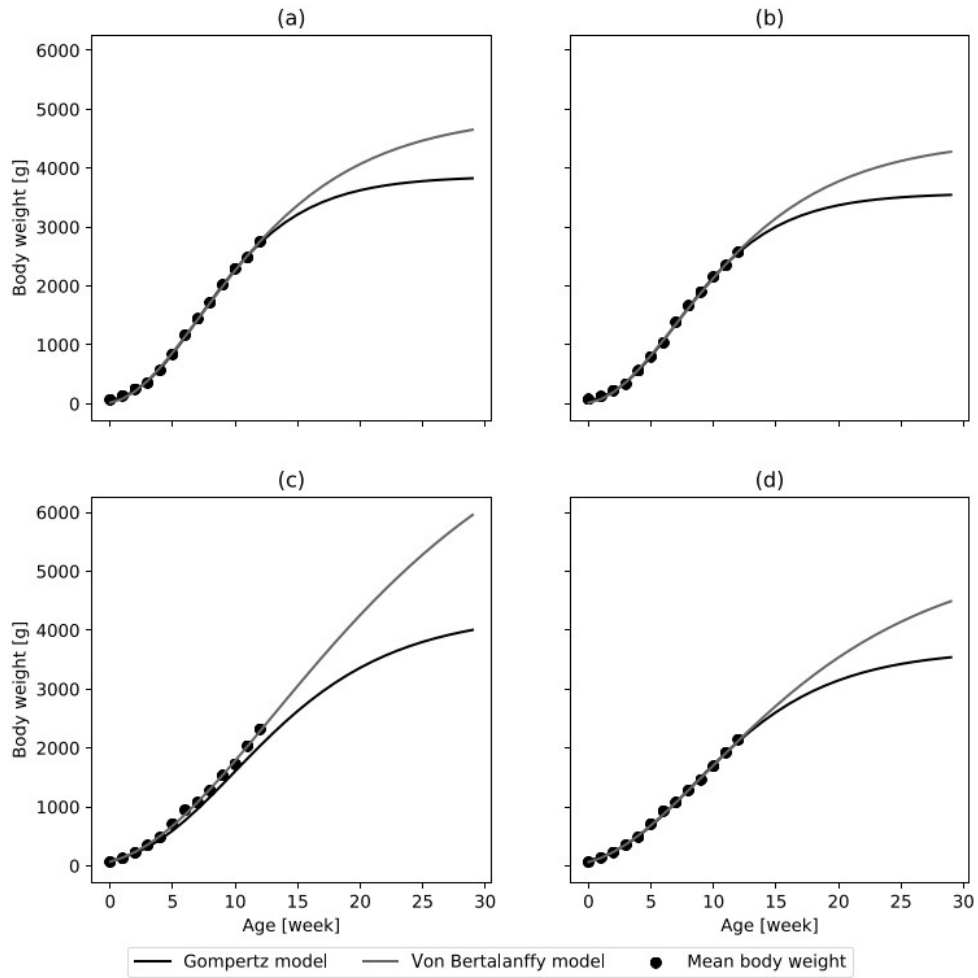


Fig. 1. Growth curves of male Popielno White (a), female Popielno White (b), male New Zealand White (c) and female New Zealand White (d) rabbits modelled using the Gompertz (black line) and von Bertalanffy (grey line) functions together with mean body weights (dots)

The growth curve parameters for each model, breed, and sex within breed are presented in Table 2. The asymptotic weight (a-parameter) is interpreted as the average weight at maturity. The lowest value of the a-parameter, close to the rabbits' actual mature body weight (3,5-5,0 kg), was achieved by the Gompertz function for each breed and sex. For Popielno Whites, the a-parameter estimated by the von Bertalanffy model was also close to the actual mature body weight (4,5-5,0 kg), but for New Zealand White rabbits this function overestimated the mature body weight, especially for males (8,5 kg). In all cases the Gompertz model showed higher values of the b-parameter (time scaling factor) and k-parameter (maturation rate) than the von Bertalanffy model.

Coordinates of the inflection point, i.e. the moment at which animals achieve the highest growth rate, are presented in Table 2. The inflection point corresponds to two parameters: age at the point of inflection (t_i) and weight at the point of inflection (y_i). The highest growth rate occurred at about 8 weeks of age for Popielno White rabbits and slightly later for New Zealand White rabbits, between 9 and 14 weeks of age. Later the animals' growth gradually slowed down. The Gompertz function modelled the highest growth rate slightly earlier (from less than 8 to about 11 weeks) than the von Bertalanffy function (from more than 8 to about 14 weeks). This analysis showed that the body weight achieved at the point of inflection generally varied from 1,3 kg to about 1,6 kg and was very similar for all groups of rabbits. The only exception was the body weight of New Zealand White males when the von Bertalanffy function was used (2,5 kg). The values of the k-parameter and t_i -coordinate of the inflection point indicated that Popielno White is a faster and earlier maturing breed than New Zealand White.

Table 2

Estimated growth curve parameters (a, b, k) of the Gompertz and von Bertalanffy models and coordinates of the inflection point (t_i, y_i) for Popielno White and New Zealand White rabbits

Breed	Model ¹⁾	Sex	Parameter			Inflection point ²⁾	
			a	b	k	t_i	y_i
Popielno White	Gompertz	Male	3865,3	5,36	0,21	7,97	1421,96
		Female	3576,5	5,42	0,22	7,86	1315,72
	von Bertalanffy	Male	4928,9	0,96	0,13	8,11	1460,41
		Female	4504,9	0,97	0,13	8,22	1334,79
New Zealand White	Gompertz	Male	4294,9	4,54	0,14	10,89	1580,01
		Female	3671,1	4,41	0,16	9,29	1350,52
	von Bertalanffy	Male	8513,7	0,86	0,07	13,92	2522,58
		Female	5389,4	0,85	0,09	10,49	1596,86

¹⁾ Gompertz: $y(t) = a \cdot \exp(-b \cdot \exp(-k \cdot t))$, von Bertalanffy: $y(t) = a \cdot (1 - b \cdot \exp(-k \cdot t))^3$

²⁾ t_i – age at point of inflection, y_i – weight at point of inflection

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Table 3 summarizes the values of different goodness of fit criteria obtained for the two models. According to all six criteria, i.e. ME, MSE, MAE, Q, AIC_c and BIC, both models provided similar fit to weight–age data. The Gompertz function showed better fit to the weight–age data of Popielno White rabbits, as the values of most criteria were lower for this breed. Interestingly, the same model, i.e. the Gompertz function, less accurately modelled the growth course of New Zealand White males. This was confirmed by the higher values for all the criteria used (Table 3). The AIC_c and BIC values gave the same ranking for both models, indicating that the Gompertz model was better for Popielno White females, while for New Zealand White females the von Bertalanffy model was better fitted to the data (Table 3).

Table 3

Goodness of fit parameters of the Gompertz and von Bertalanffy models for Popielno White and New Zealand White rabbits

Breed	Model ¹⁾	Sex	Goodness of fit parameters ²⁾					
			ME	MSE	MAE	Q	AIC _c	BIC
Popielno White	Gompertz	Male	2,20	497,59	19,84	0,00016	43,73	38,40
		Female	2,86	453,98	17,85	0,00022	42,83	37,51
	von Bertalanffy	Male	4,94	1086,33	29,30	0,00001	48,13	42,81
		Female	62,83	5591,66	63,68	0,00266	57,54	52,22
New Zealand White	Gompertz	Male	100,17	17533,14	104,73	0,01173	64,25	58,92
		Female	-2,13	726,69	21,06	0,00053	45,97	40,65
	von Bertalanffy	Male	-1,91	970,27	23,00	0,00065	47,91	42,58
		Female	0,02	448,95	14,76	0,00033	43,56	38,24

¹⁾ Gompertz: $y(t) = a \cdot \exp(-b \cdot \exp(-k \cdot t))$, von Bertalanffy: $y(t) = a \cdot (1 - b \cdot \exp(-k \cdot t))^3$

²⁾ ME = mean error, MSE = mean squared error, MAE = mean absolute error, Q = quotient between the error sum of squares and observed sum of squares, AIC_c = corrected Akaike information criterion, BIC = Bayesian information criterion

The growth rate in successive weeks of the rabbits' life was calculated using the first derivative of the Gompertz and von Bertalanffy functions. Figure 2 illustrates changes in the rabbits' growth rate with age. The von Bertalanffy model highly overestimated the growth rate of New Zealand White males and females, compared to Gompertz model, especially during the extrapolation period, i.e. after 12 weeks of age. The phase of increasing growth rate in both breeds and sexes was similarly designated by both functions.

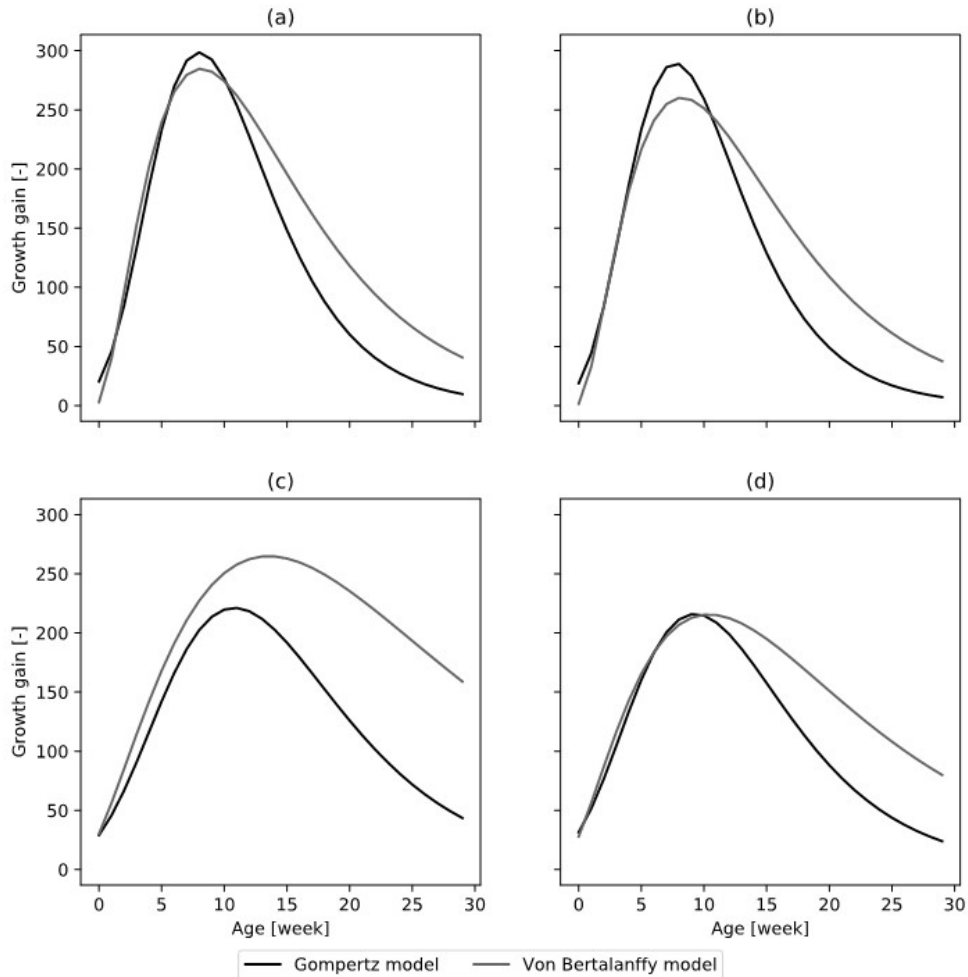


Fig. 2. Growth rate in successive weeks of age of male Popielno White (a), female Popielno White (b), male New Zealand White (c) and female New Zealand White (d) rabbits modelled using the Gompertz (black line) and von Bertalanffy (grey line) functions.

This study analysed and modelled the growth of Popielno White and New Zealand White rabbits using two nonlinear three-parameter functions: Gompertz and von Bertalanffy. Both models showed similar goodness of fit to the weight–age data of rabbits. Teleken et al. (2017) compared the goodness of fit of the most common growth curve models, i.e. Brody's, von Bertalanffy, Gompertz, Richards and logistic, to data on the body weight of many species, including cattle, sheep, goats, various species of birds, and two breeds of rabbit – New Zealand White and Californian. The authors showed that there was no single, universal function which would correctly reflect the different growth patterns of each of the species. The Gompertz function modelled the body weight of the Californian rabbits well, while the von Bertalanffy model properly mimicked the course of growth of the New Zealand White rabbits, which is not confirmed by the results of our study. The Gompertz function accurately modelled not only the growth of Californian rabbits, but also that of hens and guinea fowl, while the von Bertalanffy model also worked well in the case of Holstein-Friesian cattle (Teleken et al., 2017). The Gompertz model was also used by Setiaji et al. (2013) to compare the growth curves of the Flemish Giant, Rex and local Indonesian breed of rabbits. The authors weighed the rabbits every three days over a period of 63 days, obtaining more data than in our study. The Gompertz function fitted well to the data of each breed, suggesting that it can be useful for analysing rabbit growth (Setiaji et al., 2013). Ptak et al. (1994) compared three growth curve models, i.e. the von Bertalanffy, Gompertz and logistic models, fitted to the body weight of New Zealand White and Tan rabbits and their reciprocal crosses. The authors found that the von Bertalanffy curve modelled the course of growth much better than the other two functions, i.e. the Gompertz and logistic models. These two functions underestimated the asymptotic body weight of rabbits (a -parameter) and overestimated the maturity index (k -parameter), in contrast with our results. We found that the Gompertz model predicted the final body weight more precisely than the von Bertalanffy model, especially for the New Zealand Whites. A study by Blasco and Gomez (1993) confirmed that the Gompertz curve was suitable for describing rabbit growth. Santos et al. (2018) compared five curves (Richards, logistic, Brody, von Bertalanffy and Gompertz) to model the growth of New Zealand rabbits and concluded that the Gompertz function was the best fitted to the data from birth to 150 days of age. Fernandes et al. (2019) presented a few variants of the von Bertalanffy model and concluded that this curve, if modified, could be used successfully to describe the growth course of meat-producing mammals, including rabbits. In a study by Liao et al. (2021), five models of growth curves (logistic, Gompertz, Brody, von Bertalanffy and Richards) were fitted to data on the body weights of a crossbred population of Kangda5 and Californian rabbits, and the logistic model proved to be the best according to the Akaike (AIC) and Bayesian (BIC) information criteria. The Gompertz model was only slightly worse than the logistic model. The results of all of these studies indicate that the choice of the best model to illustrate changes in the growth of rabbits would be breed- or population-dependent.

Selection for growth rate has been a common practice in commercial rabbit meat production programmes. It helps to establish an economically acceptable age at slaughter and an optimal feeding regime, but can also lead to undesirable consequences, such as animals that are too large and difficult to handle (Blasco and Gomez, 1993). A growth rate calculated using estimated parameters of a growth curve, such as the Gompertz model, could be helpful in selection of rabbits, but unfavourable consequences should be examined before using this criterion in practice.

CONCLUSION

The results of this study showed that both models, Gompertz and von Bertalanffy, reflected the real data well up to 12 weeks of age, i.e. during the interpolation process. When body weight was extrapolated to subsequent weeks of life, we noted slightly worse fitting of the von Bertalanffy model than in the Gompertz model and overestimation of the asymptotic body weight of animals. At the point of inflection, i.e. the moment at which the animals' growth rate was highest, the body weight of all groups of rabbits showed similar variation when fitted by the Gompertz model, from 1,3 kg to about 1,6 kg. Moreover, the Gompertz function modelled the highest growth rate slightly earlier than the von Bertalanffy function. To predict the further course of rabbit growth in practice, the Gompertz function would be a better choice. It seems that the Gompertz model could be a helpful tool for breeders in selecting a more profitable breed.

To confirm the results of this study, a similar analysis should be conducted using a larger dataset, i.e. with more individuals and measurements over a longer period of time.

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