

A derivation and evaluation of the von Bertalanffy equation for describing growth in broilers over time

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ABSTRACT

Growth in broilers has been largely described in the literature by the Gompertz equation. In the present study, the von Bertalanffy equation is evaluated with regard to its ability to describe the relationship between body weight and age in chickens, and is compared with its limiting cases: the Gompertz and the Fabens equations. A total of 60 time course profiles with broilers (male and female) and with meat and egg strain pullets and hens taken from the literature were used in the analysis. A comparative analysis was carried out based on model behaviour, biologically meaningful parameter estimates and statistical performance. The results of this study based on residual sums of squares values confirm the initial assumption of the possible limitation of the Gompertz equation with its fixed point of inflexion at $1/e$ ($=0.368$) times the final weight. This was especially true for female data profiles. For these data profiles, the point of inflexion of the von Bertalanffy equation, which gave a better fit to the data than the Gompertz and Fabens equations, occurred at 0.296 to 0.357 of the final weights.

KEYWORDS: body weight, broilers, growth curve, Fabens, Gompertz, von Bertalanffy

INTRODUCTION

The Gompertz equation has been the function of choice for describing growth in broilers over time. Wilson (1977) suggested the Gompertz is applicable to avian species. Tzeng and Becker (1981) fitted non-linear and polynomial models to growth

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data on broiler chickens and observed that the Gompertz gave the best fit to live body weight and to carcass weight while the logistic and the von Bertalanffy equations described better the growth of the abdominal fat. However, the latter study was aimed primarily at relating growth in abdominal fat to total carcass fat. After studying how the Gompertz, von Bertalanffy, logistic and Richards fitted growth data, Ricklefs (1985) restricted his attention to the Gompertz model, stating that the fitted parameters are difficult to interpret with the Richards and that the growth of most galliforms, including poultry, conforms closely to the shape of the Gompertz curve. Wiseman and Lewis (1998) employed the Gompertz to survey the patterns of growth of body weight and carcass components, and feed intake accumulation. They reported that the goodness of fit of the Gompertz, as expressed in terms of the proportion of variation in the data accounted for by the equation (R^2), was very high for major carcass components (0.99-1.0), although the R^2 values were considerably lower for minor components.

The Gompertz, however, has the possible limitation of a fixed point of inflexion, which occurs at $1/e$ ($= 0.368$) times the final weight (France and Thornley, 1984). Von Bertalanffy (1957) developed a function to describe growth in animals over time. Unlike the Gompertz equation, the von Bertalanffy equation has a flexible (variable) point of inflexion which occurs between 0.296 and 0.368 times the final weight. The elementary mathematical properties and functional form of the lower extreme of the von Bertalanffy (point of inflexion at 0.296 times final weight) were discussed by Fabens (1965). In the present study, the von Bertalanffy equation is evaluated with regard to its ability to describe the relationship between body weight and age in broilers, and is compared with its limiting cases: the Gompertz and the Fabens equations. A mathematical derivation of the von Bertalanffy equation is given, and the 3 equations are applied to 60 time course profiles taken from the literature.

MATERIAL AND METHODS

Mathematical derivation

The assumptions are: substrate is non-limiting; growth is the difference between the processes of anabolism and catabolism; anabolism is allometrically related to body weight W (g); catabolism is linearly related to body weight. Formalizing these assumptions:

$$\frac{dW}{dt} = \mu W^b - \lambda W \quad (1)$$

where t is time (i.e. age) (d), and μ (g^{1-b}/d) and λ ($/d$) are constants of anabolism and catabolism, respectively.

Von Bertalanffy (1957) restricted the allometric parameter b to the range $2/3 \leq b \leq 1$ on theoretical grounds. Putting $b = 1$ in Equation (1) gives exponential growth provided $\mu > \lambda > 0$. For lower values of b , Equation (1) can be integrated by first writing it as:

$$\int_{W_0}^W \left(\frac{1}{W} + \frac{(\mu/\lambda)W^{b-2}}{1 - (\mu/\lambda)W^{b-1}} \right) dW = -\lambda \int_0^t dt$$

to give the von Bertalanffy equation:

$$W = \{(\mu/\lambda) - [(\mu/\lambda) - W_0^{1-b}]e^{-\lambda(1-b)t}\}^{1/(1-b)} \quad (2)$$

Equation (2) can be expressed in a more compact form by reparameterizing it. Let $W_f = (\mu/\lambda)^{1/(1-b)}$, $k = \lambda(1-b)$ and $v = (1-b)$, where $0 < v \leq 1/3$. k and W_f are positive. Equations (1) to (2) become, respectively:

$$\frac{dW}{dt} = \frac{kW(W_f^v - W^v)}{vW^v} \quad (3)$$

$$W = [W_f^v - (W_0^v - W_0^v)e^{-kt}]^{1/v} \quad (4)$$

At $t = 0$, $W = W_0$, the initial weight; for $t \rightarrow \infty$, $W = W_f$, the final weight.

The point of inflexion is found by differentiating Equation (3):

$$\frac{d^2W}{dt^2} = \frac{k}{v} \left[(1-v) \left(\frac{W_f}{W} \right)^v - 1 \right] \frac{dW}{dt}$$

Equating this to zero at time $t = t^*$ (the inflexion point), therefore either $dW/dt = 0$, or:

$$W(t = t^*) = (1-v)^{1/v} W_f \quad (5)$$

By substituting $W = W(t = t^*)$ from Equation (5) and $t = t^*$ into Equation (4) the time to inflexion t^* is:

$$t^* = \frac{1}{k} \ln \left[\frac{W_f^v - W_0^v}{vW_f^v} \right] \quad (6)$$

The expression $(1-v)^{1/v}$ determines the proportion of the final size at which the inflexion point occurs. When $v = 1/3$, $(1-v)^{1/v} = 0.667^3 = 0.296$. When $v = 0$, Equation (3) breaks down: but since as $v \rightarrow 0$ the limiting value of $[(W_f/W)^v - 1]/v$ is $\ln(W_f/W)$, the growth rate becomes $kW \ln(W_f/W)$, which is the rate appropriate to the Gompertz (France and Thornley, 1984) whose point of inflexion occurs at $1/e$ times W_f . Therefore, the inflexion point for the von Bertalanffy occurs between 0.296 and 0.368 of the final weight.

The family of curves obtained by varying the parameter ν in Equation (4) is sketched in Figure 1. The point of inflexion is able to occur between 0.296 and 0.368 of the final body weight [Equation (5)], as ν varies over the range $0 < \nu < 1/3$.

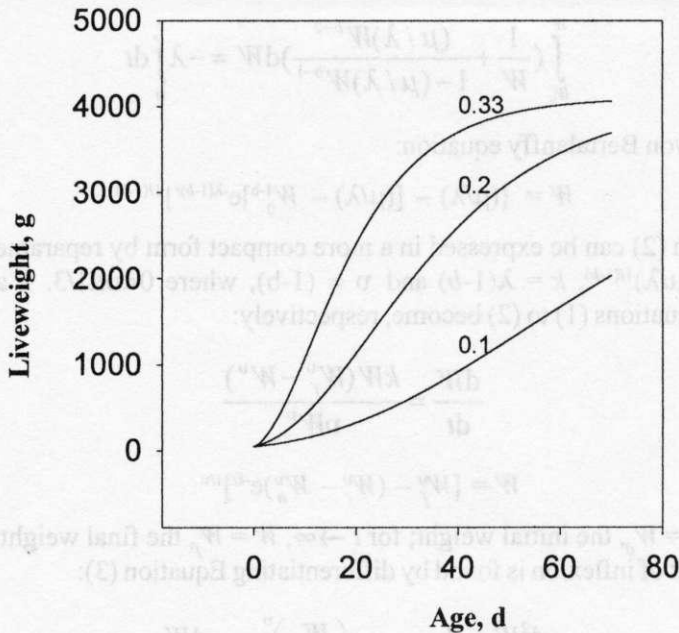


Figure 1. von Bertalanffy equation. The curves describe Equation (4) with $W_0 = 45$, $W_f = 4100$, $k = 0.24\nu$, and for three ν -values as given

Models fitted

The growth functions fitted in this study take the form:

Gompertz:

$$W = (W_f - W_0) \exp(-\exp(-k(t - t^*))),$$

Fabens:

$$W = [(W_f)^{1/3}(1 - Ae^{-kt})]^3,$$

von Bertalanffy:

$$W = [W_f^\nu - (W_f^\nu - W_0^\nu)e^{-kt}]^{1/\nu},$$

where t is time, W_f is the final weight, W_0 is the initial weight, t^* is the time at which the growth rate is at its maximum and k (/d), A and ν (both dimensionless) are constants. Some properties of these growth equations are shown in Table 1.

TABLE 1

Some properties of the different growth equations

Growth equations	Growth rate (dW/dt)	Time to inflexion (t^*)	Weight at inflexion (W^*)
Gompertz	$kW \ln\left(\frac{W_f}{W}\right)$	$\frac{1}{k} \left[\ln\left(\ln\left(\frac{W_f - W_0}{W_0}\right)\right) \right]$	$0.368W_f$
Fabens	$kW \ln\left[\left(\frac{W_f}{W}\right)^{1/3} - 1\right]$	$\left[\frac{\ln A + \ln 3}{k} \right]$	$0.296W_f$
von Bertalanffy	$\mu W^{(1-\nu)} - \lambda W$	$\frac{1}{k} \ln\left[\frac{W_f^\nu - W_0^\nu}{\nu W_f^\nu}\right]$	$(1 - \nu)^{1/\nu} W_f$

Experimental data

A total of 60 time course profiles with broilers (male and female) and with meat and egg strain pullets and hens, were taken from the literature and used in this study. Details of the sources, growth phases, sex, strain and some dietary characterizations of the experimental data are given in Table 2.

Statistical procedures

The growth functions were fitted to the data using the non-linear fitting procedures of Sigmaplot (SPSS, 1998). A number of statistical analyses were used to evaluate the general goodness-of-fit of each model. The \bar{r}^2 (adjusted R^2) was calculated as $1 - \frac{RSS/(n-p)}{S_y^2/(n-1)}$, where RSS (residual sum of squares) is a measure of the variability in liveweight remaining after the age variable (the regressor variable) has been considered, n is number of data points, p is number of parameters included in the model and S_y^2 (the total variation of the y -variable) is a measure of the variability in liveweight without considering the effect of the age variable. The RSS was used to compare two different models when fitted to the data. The statistical significance between models in terms of the goodness-of-fit was assessed using an F-test described by Motulsky and Ransnas (1987) for comparing two models with

TABLE 2

Data sources used in the study

Source	Growth phase d	Sex ¹		Strain	Considerations
		M	F		
Ajang et al. (1993)	7-48	6	6	Broilers	Different dietary protein content
Grey et al. (1982)	21-364	1	1	Ross 1	-
Hancock et al. (1995)	0-77	6	6	Hubbard, Hybro, Ross 708, 788, 608 and 688	-
Leeson and Summers (1980)	0-70	1	1	Broilers	-
NRC (1994) ²	7-70	1	1	Broilers	-
Plavink and Hurwitz (1983)	7-70	1	1	White Rock	-
Waldroup et al. (1976)	7-63	6	6	Broilers	Different starter and finisher diets
Wiseman and Lewis (1998)	0-70	5	0	Ross	Different starter and finisher diets
Altman and Dittmer (1964)	0-140	1	1	New Hampshire	-
Altman and Dittmer (1964)	0-140	1	1	Cornish	-
Altman and Dittmer (1964)	0-140	0	1	White Leghorn	-
Leeson and Summers (1997)	0-154	0	1	Egg strain	-
Leeson and Summers (1997)	0-56	3	0	Broilers	-
Leeson and Summers (1997)	0-56	1	0	Broilers	-
Leeson and Summers (1997)	0-84	1	0	Broilers	-

¹ M = male, and F = female; the numbers, under M and F subheadings, refer to the number of data profiles from a specific data source

² these data are not directly experimental but were produced by compositing and smoothing data from various resources

the same or a different number of parameters. To compare models with the same parameters, the following equation was used:

$$F = \frac{SS_1}{SS_2}$$

and for models with different number of parameters the equation used was:

$$F = \frac{(SS_1 - SS_2)/(df_2 - df_1)}{SS_2/df_2}$$

where SS is the sums of squares and df is degrees of freedom.

RESULTS

The applicability of the different growth functions was examined by fitting them to the different time course profiles. The results indicated that in all cases, the models could be fitted to the females and males growth data without difficulty by non-linear regression. Figures 2 and 3 give a sample of the fitted curves, showing three different time course profiles for females and males, respectively, fitted using

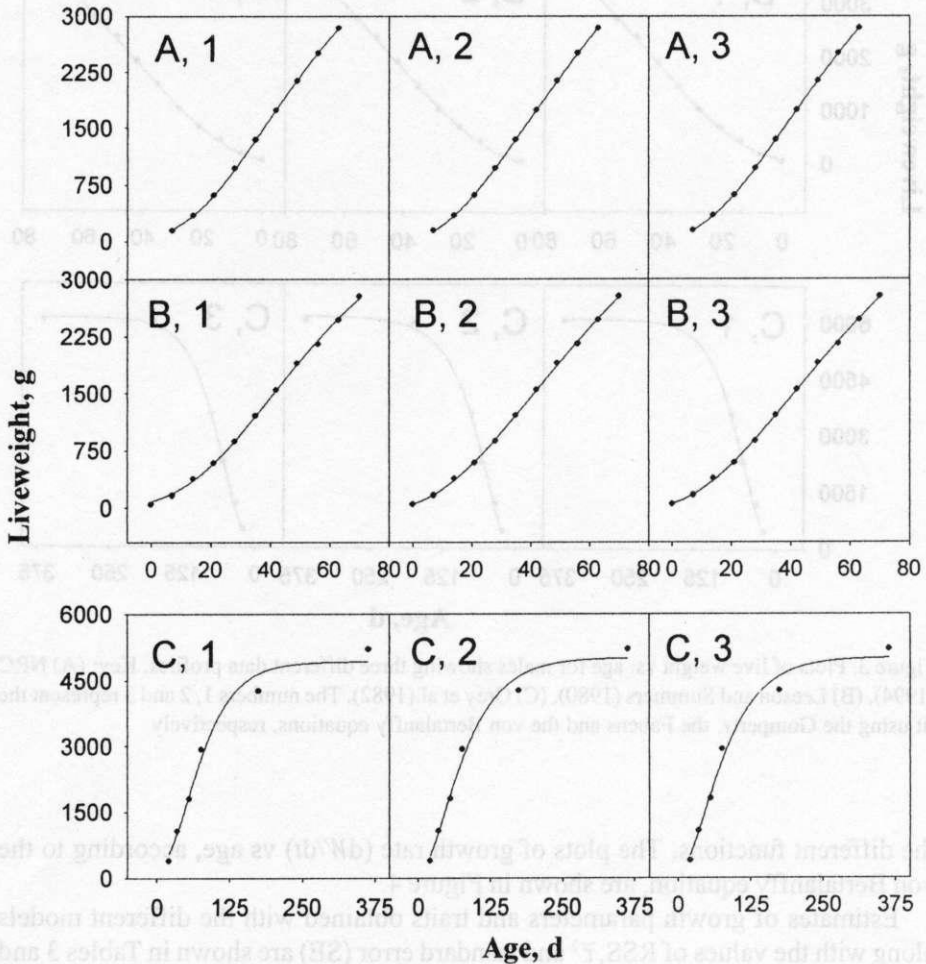


Figure 2. Plots of live weight vs. age for females showing three different data profiles. Key: (A) NRC (1994), (B) Leeson and Summers (1980), (C) Grey et al.(1982). The numbers 1, 2 and 3 represent the fit using the Gompertz, the Fabens and the von Bertalanffy equations, respectively

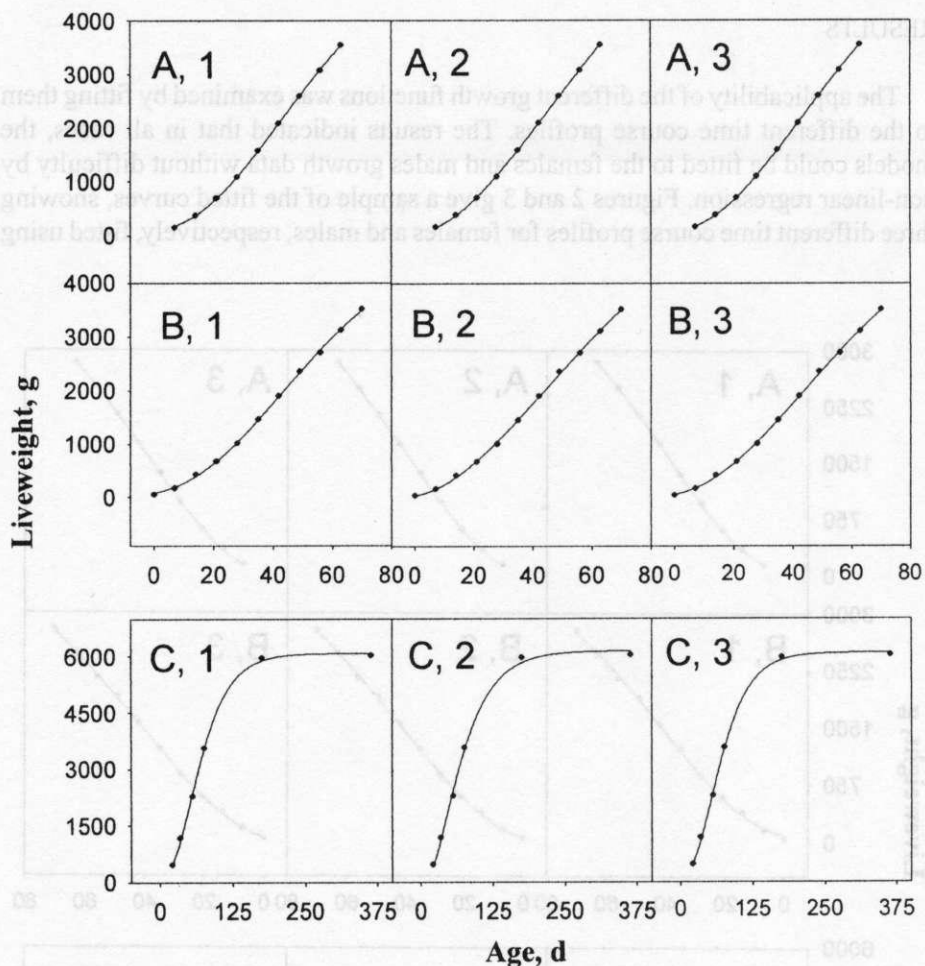


Figure 3. Plots of live weight vs. age for males showing three different data profiles. Key: (A) NRC (1994), (B) Leeson and Summers (1980), (C) Grey et al. (1982). The numbers 1, 2 and 3 represent the fit using the Gompertz, the Fabens and the von Bertalanffy equations, respectively

the different functions. The plots of growth rate (dW/dt) vs age, according to the von Bertalanffy equation, are shown in Figure 4.

Estimates of growth parameters and traits obtained with the different models along with the values of RSS, \bar{r}^2 and standard error (SE) are shown in Tables 3 and 4 for females and in Tables 5 and 6 for males. Although the analyses were carried out for all time course profiles (both male and female data), limitations on space prevent the presentation of the results for all of the profiles through Tables 3 to 6.

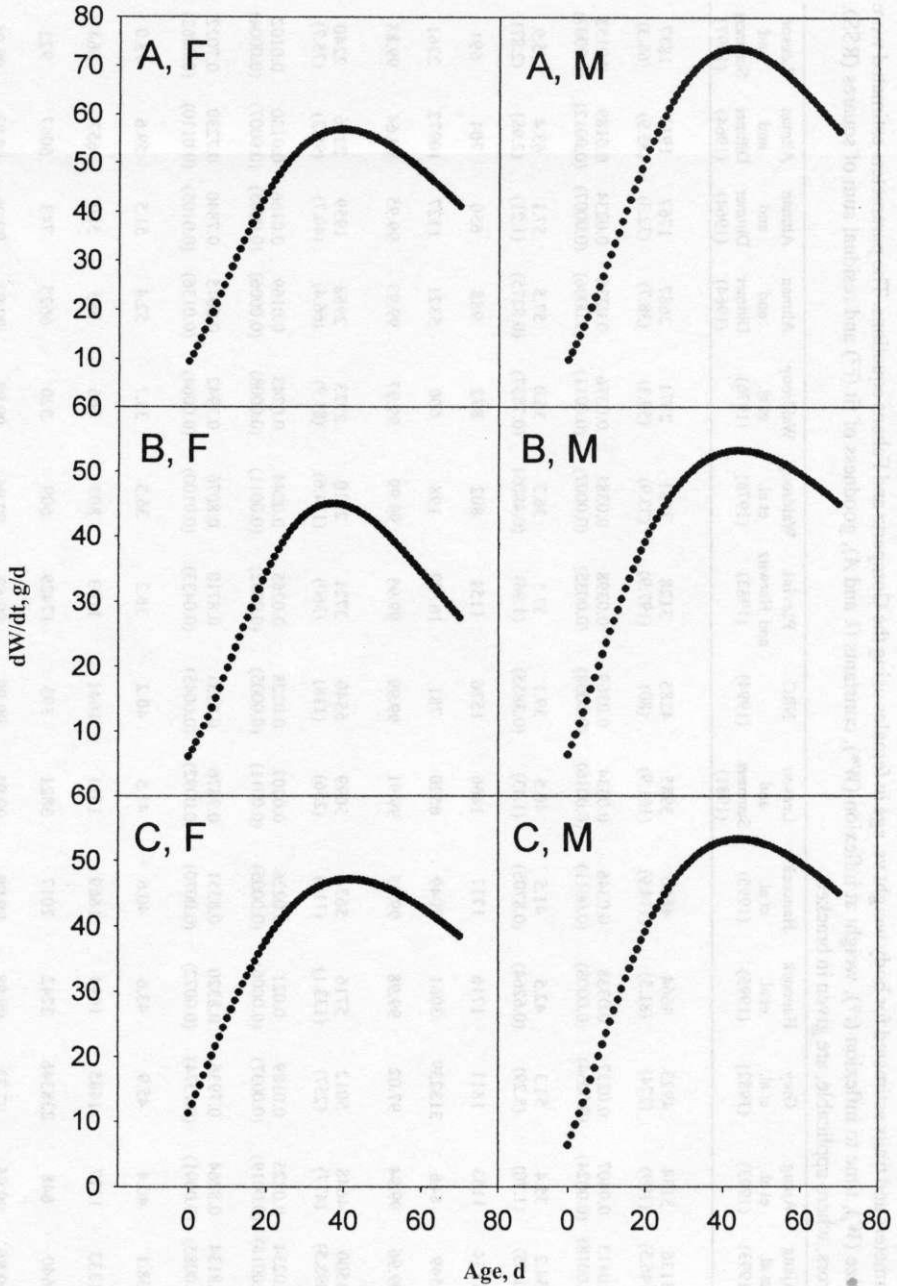


Figure 4. Plots of the estimated values of growth rate, dW/dt , vs. age for the von Bertalanffy equation using three different data profiles. Key: (A) NRC (1994), (B) Plavink and Hurwitz (1983), (C) Leeson and Summers (1980), (F) Female, and (M) Male

TABLE 3

Growth parameters and traits estimated for body weight vs. age in females using the Gompertz and Fabens equations. The parameters estimated were final body size (W_f), time to inflexion (t^*), weight at inflexion (W^*), constants (k and A), goodness of fit (r^2) and residual sum of squares (RSS). Standard errors, where applicable, are given in brackets

Item	Ajang et al. (1993)	Ajang et al. (1993)	Grey et al. (1982)	Hancock et al. (1995)	Hancock et al. (1995)	Leesson and Summers (1981)	NRC (1994)	Plavink and Hurwitz (1983)	Waldroup et al. (1976)	Waldroup et al. (1976)	Altman and Dittmer (1964)	Altman and Dittmer (1964)	Leesson and Summers (1997)
Gompertz:													
W_f	3136 (146.5)	3134 (199)	4923 (274)	4664 (81.5)	4666 (114.9)	3985 (161.9)	4285 (80)	3128 (197.9)	2181 (33.9)	2371 (59.3)	2687 (38.7)	1767 (32.3)	1877 (68.3)
k	0.0413 (0.0018)	0.0407 (0.0024)	0.0237 (0.0054)	0.0338 (0.0008)	0.0346 (0.0011)	0.0334 (0.0016)	0.0369 (0.0008)	0.0398 (0.0035)	0.0381 (0.0007)	0.0376 (0.0011)	0.0236 (0.0006)	0.0234 (0.0007)	0.0153 (0.0007)
t^*	34.2 (1.25)	35.4 (1.70)	54.3 (5.29)	42.5 (0.6264)	41.5 (0.8705)	40.5 (1.43)	39.1 (0.3855)	37.5 (1.96)	36.3 (0.4805)	36.0 (0.7837)	57.5 (0.8275)	57.1 (1.21)	75.9 (2.87)
W^*	1154	1153	1811	1716	1717	1466	1576	1151	802	872	988	650	704
RSS	549	846	313239	3061	7049	6520	781	16740	198	600	5321	1127	2361
r^2	99.96	99.94	97.02	99.98	99.95	99.91	99.99	99.95	99.99	99.97	99.93	99.95	99.88
Fabens:													
W_f	4500 (398.5)	4648 (477)	5012 (257)	5716 (133.1)	5634 (114)	5099 (256)	5540 (118)	3721 (360)	2710 (114.6)	2923 (81.9)	2988 (66.4)	1959 (40.7)	2240 (75.7)
k	0.0234 (0.0018)	0.0225 (0.0019)	0.0189 (0.0037)	0.021 (0.0006)	0.0226 (0.0005)	0.0207 (0.0011)	0.0228 (0.0005)	0.0265 (0.0032)	0.0244 (0.0011)	0.0243 (0.0008)	0.0169 (0.0006)	0.0166 (0.0005)	0.0102 (0.0004)
A	0.8134 (0.0085)	0.8264 (0.0091)	0.7936 (0.1374)	0.8320 (0.0072)	0.8351 (0.0070)	0.7876 (0.0092)	0.8331 (0.0045)	0.8710 (0.0433)	0.8076 (0.0100)	0.7942 (0.0064)	0.8075 (0.0136)	0.7840 (0.0105)	0.7022 (0.0062)
t^*	38.1	40.4	45.9	43.6	40.6	41.5	40.2	36.2	36.3	35.7	52.4	51.5	73.0
W^*	1333	1377	1485	1694	1669	1511	1641	1103	803	866	885	580	664
RSS	640	648	238346	2242	2017	3821	393	17429	609	320	6625	743	922
r^2	99.96	99.95	97.73	99.98	99.99	99.95	99.99	99.63	99.96	99.98	99.92	99.96	99.95

TABLE 4
 Growth parameters and traits estimated for body weight vs. age in females using the von Bertalanffy equation. The parameters estimated were initial body size (W_0), final body size (W_f), time to inflexion (t^*), weight at inflexion (W^*), constants (k and v), goodness of fit (\bar{r}^2) and residual sum of squares (RSS). Standard errors, where applicable, are given in brackets

Item	Ajang et al. (1993)	Ajang et al. (1993)	Grey et al. (1982)	Hancock et al. (1995)	Hancock et al. (1995)	Leeson and Summers (1981)	NRC (1994)	Plavink and Hurwitz (1983)	Waldroup et al. (1976)	Waldroup et al. (1976)	Altman and Dittmer (1964)	Altman and Dittmer (1964)	Altman and Dittmer (1964)	Leeson and Summers (1997)
von Bertalanffy														
W_f	3494 (717.8)	3975 (1319)	5015 (366.7)	5159 (162.4)	5427 (240.2)	4933 (638.6)	4895 (87.8)	3299 (622.8)	2243 (105)	2713 (187.5)	2784 (84)	1876 (63.4)	2216 (243.9)	2240 (211.6)
k	0.0342 (0.0115)	0.028 (0.0133)	0.0188 (0.012)	0.0268 (0.0017)	0.0244 (0.0021)	0.0219 (0.005)	0.0283 (0.0009)	0.0347 (0.0147)	0.0357 (0.0036)	0.0281 (0.0037)	0.1464 (0.013)	0.1330 (0.0131)	0.0912 (0.0213)	0.0715 (0.0132)
v	0.1317 (0.2114)	0.2341 (0.2388)	0.3333 (0.9997)	0.1943 (0.0453)	0.2831 (0.0588)	0.3019 (0.1260)	0.2036 (0.0208)	0.1274 (0.3641)	0.0586 (0.086)	0.2397 (0.0905)	0.1342 (0.0872)	0.2174 (0.0885)	0.3333 (0.1585)	0.3333 (0.117)
W_0	43.9 (15.2)	31.3 (17.4)	45.4 (355.6)	46.1 (6.65)	32.5 (8.86)	52.3 (16.5)	40.9 (2.54)	25.8 (35)	37.1 (5.6)	32.9 (7.50)	42 (9.74)	27 (6.09)	47.1 (12.9)	59.2 (8.45)
t^*	35.1	38.0	46.0	42.1	40.7	41.3	39.5	37.1	36.2	35.7	55.7	53.6	59.4	72.9
W^*	1196	1272	1486	1697	1675	1500	1600	1132	800	865	951	607	657	664
W^*/W_f	0.349	0.296	0.329	0.324	0.349	0.304	0.327	0.343	0.357	0.319	0.342	0.324	0.296	0.296
RSS	486	643	238376	996	1827	3799	43	16426	181	260	4508	453	5067	922
\bar{r}^2	99.96	99.94	96.60	99.99	99.99	99.94	100	99.59	99.99	99.98	99.94	99.97	99.82	99.95

TABLE 5

Growth parameters and traits estimated for body weight vs. age in males using the Gompertz and Fabens equations. The parameters estimated were final body size (W_f), time to inflexion (t^*), weight at inflexion (W^*), constants (k and A), goodness of fit (r^2) and residual sum of squares (RSS). Standard errors, where applicable, is given in brackets

Item	Ajang et al. (1993)	Ajang et al. (1993)	Grey et al. (1982)	Hancock et al. (1995)	Hancock et al. (1995)	Leeson and Summers (1980)	NRC (1994)	Plavink and Hurwitz (1983)	Waldroup et al. (1976)	Waldroup et al. (1976)	Wiseman Lewis (1998)	Wiseman Lewis (1998)	Altman and Dittmer (1964)	Altman and Dittmer (1964)	Leeson and Summers (1997)	Leeson and Summers (1997)	Leeson and Summers (1997)	Leeson and Summers (1997)
Gompertz:																		
W_f	4191 (178.8)	4610 (594.1)	6080 (65.3)	5475 (100.3)	5621 (61.6)	5145 (186.9)	5698 (114.5)	4368 (435)	2487 (82.8)	2628 (88.7)	4362 (169.5)	4680 (314.4)	4440 (294.5)	2599 (42.1)	4896 (132.9)	5333 (160.4)	4860 (91)	6937 (254.4)
k	0.0394 (0.0014)	0.0353 (0.0034)	0.0283 (0.0013)	0.0358 (0.0009)	0.0358 (0.0005)	0.0358 (0.0014)	0.0356 (0.0007)	0.0344 (0.0039)	0.0380 (0.0015)	0.0408 (0.0018)	0.0464 (0.0030)	0.0361 (0.0028)	0.0206 (0.0016)	0.0209 (0.0005)	0.0387 (0.0010)	0.0427 (0.0014)	0.0331 (0.0005)	0.0261 (0.0009)
t^*	37.6 (1.16)	42.5 (3.7)	54.1 (0.9220)	42.7 (0.6260)	42.6 (0.3746)	42 (1.26)	42.2 (0.6383)	43.2 (3.37)	37.7 (1.03)	35.3 (0.9934)	33.4 (1.11)	43.9 (2.18)	71.2 (3.48)	68 (1.09)	39.7 (0.7801)	37.1 (0.8097)	45.7 (0.5918)	57.8 (1.57)
W^*	1542	1696	2237	2014	2068	1893	2096	1607	915	967	1605	1722	1633	956	1801	1962	1788	2552
RSS	477	2305	20523	5281	2028	7777	1069	32541	1031	1828	32314	21067	83355	906	1000	2474	178	9728
r^2	99.97	99.89	99.88	99.97	99.99	99.93	99.99	99.54	99.95	99.93	99.77	99.79	99.53	99.98	99.98	99.97	100	99.95
Fabens:																		
W_f	6733 (699.4)	8741 (1920)	6131 (114.5)	6652 (349.8)	6800 (236)	6717 (387.9)	7830 (311)	5599 (847.1)	3173 (284.3)	3209 (255)	4885 (289.1)	6134 (803.8)	5296 (494.6)	3049 (60.2)	7342 (851.5)	7292 (675.2)	8925 (1131)	10020 (410.8)
k	0.0205 (0.0016)	0.0165 (0.0024)	0.0231 (0.0017)	0.0232 (0.0014)	0.0234 (0.0010)	0.0206 (0.0012)	0.0208 (0.0008)	0.0214 (0.0033)	0.0236 (0.0022)	0.0265 (0.0024)	0.0330 (0.0030)	0.0218 (0.0029)	0.0136 (0.0016)	0.0138 (0.0003)	0.0210 (0.0021)	0.0249 (0.0022)	0.0156 (0.0014)	0.0146 (0.0005)
A	0.8419 (0.0072)	0.8513 (0.0074)	0.6700 (0.0792)	0.8844 (0.0219)	0.8825 (0.0146)	0.8185 (0.0114)	0.8570 (0.0069)	0.8574 (0.0374)	0.8566 (0.0205)	0.8375 (0.0255)	0.9246 (0.0501)	0.9027 (0.0385)	0.8503 (0.0363)	0.8157 (0.0071)	0.8647 (0.0151)	0.8957 (0.0216)	0.8508 (0.0059)	0.8537 (0.0056)
t^*	45.2	56.8	30.2	42.1	41.6	43.6	45.4	44.1	40.0	34.8	30.9	45.70	68.9	64.8	45.4	39.7	60.1	64.4
W^*	1995	2590	1817	1971	2015	1990	2320	1659	940	951	1447	1817	1569	903	2175	2161	2644	2969
RSS	769	1491	56708	17975	8523	7180	1435	29401	2900	4289	37829	28552	98833	589	5209	7685	1785	3755
r^2	99.97	99.93	99.66	99.91	99.96	99.94	99.98	99.59	99.85	99.83	99.73	99.72	99.44	99.98	99.92	99.92	99.96	99.98

TABLE 6
 Growth parameters and traits estimated for body weight vs. age in males using the von Bertalanffy equation. The parameters estimated were initial body size (W_0), final body size (W_∞), time to inflexion (t^*), weight at inflexion time (W^*), constants (k and u), goodness of fit (\bar{r}^2) and residual sum of squares (RSS). Standard errors, where applicable, is given in brackets

Item	Ajang et al. (1993)		Ajang et al. (1993)		Grey et al. (1982)		Hancock et al. (1995)		Hancock et al. (1995)		Leeson and Summers (1980)		NRC (1994)		Pisavik and Hurwitz (1983)		Waldroup et al. (1976)		Waldroup et al. (1976)		Wiseman and Lewis (1998)		Wiseman and Lewis (1998)		Altman and Dittmer (1964)		Leeson and Summers (1997)		Leeson and Summers (1997)	
	4556 (847.3)	5659 (3518)	6080 (99.5)	5475 (118.9)	5778 (147.1)	5859 (688.2)	6397 (320.8)	5598 (2536)	2488 (110.5)	2626 (103.6)	4442 (383.3)	4683 (306.6)	4815 (57.4)	2817 (161.6)	4892 (40.5)	5324 (116)	9329 (1023)													
k	0.0345 (0.0096)	0.0266 (0.0232)	0.0283 (0.0017)	0.0358 (0.0009)	0.0334 (0.0019)	0.0261 (0.0053)	0.0288 (0.0024)	0.0214 (0.0163)	0.0379 (0.0018)	0.0409 (0.0007)	0.0437 (0.0107)	0.0360 (0.0030)	0.0208 (0.0006)	0.0167 (0.0008)	0.0428 (0.0017)	0.0331 (0.0006)	0.0161 (0.0025)													
u	0.0855 (0.1686)	0.1603 (0.4002)	0.0000 (0.0001)	0.0000 (0.0004)	0.0638 (0.0494)	0.1945 (0.1299)	0.1547 (0.0533)	0.3333 (0.3993)	0.0000 (0.0014)	0.0000 (0.0000)	0.0662 (0.2496)	0.0000 (0.0000)	0.0000 (0.0000)	0.1956 (0.0370)	0.0000 (0.0001)	0.0000 (0.0001)	0.2885 (0.0692)													
W_0	45.7 (12.8)	40 (27.5)	59.7 (22.8)	54.3 (5.78)	48.7 (7.53)	58.5 (19.16)	45.7 (7.13)	16.2 (47)	38.2 (5.36)	38.4 (1.62)	31.4 (33.3)	35.8 (13.2)	56.1 (2.07)	28.9 (2.90)	46.5 (5.79)	51.8 (11)	37.9 (11)													
t^*	38.7	46.2	54.1	42.7	42.4	42.6	43.0	44.2	38.7	35.2	33.0	44.0	70.9	66.3	39.7	45.7	63.0													
W^*	1602	1903	2237	2014	2056	1927	2159	1659	1602	966	1578	1723	1624	926	1800	1788	2867													
W^*/W_0	0.352	0.336	0.368	0.368	0.356	0.329	0.337	0.296	0.352	0.368	0.355	0.368	0.368	0.329	0.368	0.368	0.307													
RSS	437	1898	20524	5281	1696	6106	417	29402	1032	1823	31987	21066	83335	149	1001	2477	3579													
\bar{r}^2	99.97	99.89	99.82	99.97	99.99	99.94	99.99	99.52	99.94	99.91	99.74	99.77	99.49	99.99	99.98	99.97	99.99													

von-Bertalanffy:

Therefore, in Tables 3 to 6 the results for Waldroup et al. (1976), Ajang et al. (1993) and Wiseman and Lewis (1998) are shown only for two extreme dietary conditions and for the Hancock et al. (1995) only for two strains, Ross 708 and Hybro. The statistical criterion of r^2 shows that most of the total variation of growth in body weight is accounted for by non-linear regression using the different growth functions ($\bar{r}^2 > 0.99$). Tables 3-6 show that for each of the different data profiles there was no significantly different fit among the models compared, based on the coefficients of determination (\bar{r}^2). However, the RSS values showed significant differences between the different models in their ability to describe the relationship between live body weight and age for the different time course profiles. Based on this criterion, fitting the different models to the data, both female and male, led to a smaller or the same estimated values of RSS by the von Bertalanffy equation compared to the Gompertz and the Fabens. A comparison between the different models in terms of percentage of cases in which one model was statistically superior to the other is shown in Table 7. The results (Table 7) show that the von Bertalanffy is superior to the Gompertz and the Fabens, because fitting the von Bertalanffy to the different data profiles led to statistical significances in 12 and 50% of cases in males and to 54 and 42% of cases in females when compared to the Gompertz and the Fabens, respectively. Comparing the estimated values of the final body weight for the same data source using the different growth functions (Tables 3-6), with the exception of few cases in which the models gave approximately the same estimated values, showed that the values are greater for the Fabens than for the von Bertalanffy, and are greater for both the Fabens and the von Bertalanffy than for the Gompertz.

TABLE 7

The statistical significances¹ between the models based on the estimated RSS values

Models	Gompertz	Fabens	von Bertalanffy
Males			
Gompertz	-	29 ²	0
Fabens	6	-	0
von Bertalanffy	12	50	-
Females			
Gompertz	-	4	0
Fabens	12	-	0
von Bertalanffy	54	42	-

¹ based on an F test (Motulsky and Ransnas, 1987)

² percentage of cases in which the model specified in the row was statistically ($P \leq 0.05$) superior to the model specified in the column

Considering the growth rate of the von Bertalanffy equation in males and females (Figure 4), it is evident that values for the maximum gain in weight (g/d), which occur at the time to inflexion, are greater for males than for females and that the growth rate will approach zero as the birds reach maturity.

DISCUSSION

The Gompertz equation has been the function of choice for describing growth in broilers in the literature. The Gompertz, however, has the possible limitation of a fixed point of inflexion. Therefore, in the present study, the von Bertalanffy equation (a flexible growth function) was evaluated with regard to its ability to describe the relationship between body weight and age in broilers, and was compared to its limiting cases: the Gompertz and the Fabens equations.

The purpose of curve fitting is to describe the course of mass increase with age by simple equations with few parameters, which in the most useful models are biologically interpretable (Ricklefs, 1985). However, there is no single, simple method to evaluate similarities and differences between non-linear models and to recommend which model should be used (Motulsky and Ransnas, 1987). Hence, the comparison of the models in this study was carried out according to three criteria: model behaviour when fitting the curves using non-linear regression, statistical performance, and comparison of biologically meaningful parameters estimated by each model.

The results of this study indicated that the different data profiles both male and female can be described by the different growth functions with a very high degree of accuracy ($r^2 > 0.99$). However, in spite of this similarity there are some important differences between the growth functions. Although, fitting the Gompertz and the Fabens to the different data profiles led to statistically very significant parameters (parameters with significantly lower standard errors at $P < 0.0001$) in all cases, fitting the von Bertalanffy to the same data profiles resulted in 91%, 76%, 12% and 85% significant parameters in males and to 92%, 81%, 35% and 77% significant parameters in females for W_p , W_0 , v and k , respectively. But, since the estimated standard error of the parameters are based on linearizing assumptions and will always underestimate the true uncertainty of any nonlinear equation, these values should not be taken into account too seriously (Motulsky and Ransnas, 1987). With the logistic (results not shown), for example, the RSS values and biologically meaningful parameters did not suggest a suitable fit to the different data profiles, but fitting the equation in all cases led to statistically very significant parameter estimates. Comparisons based on the statistical significances between the estimated RSS values (Table 7) indicated that there are significant differences between the models. Here the really interesting choice lies between the generalized von Berta-

lanffy model and its special cases, the Gompertz and the Fabens. Based on this criterion and dependent on the sex (for female more than male data profiles), the von Bertalanffy showed superiority to the Gompertz and the Fabens. The results, especially for females, show the point of inflexion based on the von Bertalanffy equation occurred between 0.296 and 0.357 of final weight, confirming the initial assumption of the possible limitation of a fixed point of inflexion with the Gompertz equation.

In conclusion, the results of this study confirmed our initial reservation about the adoption a single growth function with a fixed point of inflexion for describing the relationship between live body weight and age in broilers. Therefore, consideration of flexible growth functions such as von Bertalanffy equation as an alternative to the Gompertz is recommended. This recommendation is based on model testing and evaluation, an essential part of the model development process.

REFERENCES

- Ajang O.A., Prijono S., Smit W.K., 1993. Effect of dietary protein content on growth and body composition of fast and slow feathering broiler chickens. *Brit. Poultry Sci.* 34, 73-91
- Altman P.L., Dittmer D.S., 1964. *Biology Data Book*. Federation on American Societies for Experimental Biology. Washington, DC
- Fabens A.J., 1965. Properties and fitting of the von Bertalanffy growth curve. *Growth* 29, 265-289
- France J., Thornley J.H.M., 1984. *Mathematical Models in Agriculture*. Butterworth, London
- Grey T.C., Robinson D., Jones J., 1982. Effect of age and sex on the eviscerated yield, muscle and edible offal of a commercial broiler strain. *Brit. Poultry Sci.* 23, 289-298
- Hancock C.E., Bradford G.D., Emmans G.C., Gous R.M., 1995. The evaluation of the growth parameters of six strains of commercial broiler chickens. *Brit. Poultry Sci.* 36, 247-264
- Leeson S., Summers J.D., 1980. Production and carcass characteristics of the broiler chicken. *Poultry Sci.* 59, 786-798
- Leeson S., Summers J.D., 1997. *Commercial Poultry Nutrition 2nd Edition*. University Books, Guelph, Ontario (Canada)
- Motulsky H.J., Ransnas L.A., 1987. Fitting curves to data using nonlinear regression: A practical and nonmathematical review. *FASEB J.* 1, 365-374
- National Research Council, 1994. *Nutrient Requirements of Poultry. 9th revised Edition*. National Academy Press, Washington, DC
- Plavink I., Hurwitz S., 1983. Organ weight and body composition in chicken as related to the energy and amino acid requirements: Effects of strain, sex and age. *Poultry Sci.* 62, 152-163
- Ricklefs R.E., 1985. Modification of growth and development of muscles in poultry. *Poultry Sci.* 64, 1563-1576
- SPSS, 1998. *SigmaPlot 5.0 User's Guide*. SPSS Inc., Chicago, IL
- Tzeng R.Y., Becker W.A., 1981. Growth patterns of body and abdominal fat weights in male broiler chickens. *Poultry Sci.* 60, 1101-1106
- Von Bertalanffy L., 1957. Quantitative laws for metabolism and growth. *Quart. Rev. Biol.* 32, 217-231
- Waldroup P.W., Mitchell R.J., Payne J.R., Johnson Z.B., 1976. Characterization of the response of broiler chickens to diets varying in nutrient density content. *Poultry Sci.* 55, 130-145

- Wilson B.J., 1977. Growth curves: their analysis and use. In: K.N. Boorman, B.J. Wilson (Editors). Growth and Poultry Meat Production. British Poultry Science Ltd., Edinbrough, pp. 89-115
- Wiseman J., Lewis C.E., 1998. Influence of dietary energy and nutrient concentration on the growth of body weight and of carcass components of broiler chickens. J. Agr. Sci. 131, 361-371

STRESZCZENIE

Zastosowanie równania von Bertalanffy'ego do opisu wzrostu brojlerów

Przyrosty masy ciała brojlerów są opisywane w literaturze zazwyczaj przy pomocy równania (krzywej) Gompertza. Przedmiotem przeprowadzonych badań jest ocena przydatności równania von Bertalanffy'ego do opisu zależności między masą ciała i wiekiem brojlerów w porównaniu z innymi metodami (równania Gompertza i Fabensa). Analizą objęto 60 zestawów danych pochodzących z różnych populacji, takich jak: brojlery (obu płci), rasy mięsne i nieśne. Analiza porównawcza opierała się na kryteriach adekwatności modelu – wielkości estymatorów wybranych parametrów (wariancji błędu i współczynnika determinacji). Uzyskane wyniki, opierające się na analizie sum kwadratów dla błędu, potwierdzają wcześniejsze przypuszczenia dotyczące możliwości aplikacyjnych równania (krzywej) Gompertza dla iloczynu ustalonego punktu nachylenia ($1/e = 0.368$) i masy ciała. Tendencja ta jest szczególnie widoczna w przypadku osobników żeńskich. W przypadku analizowanych zestawów danych, punkt nachylenia w równaniu von Bertalanffy'ego osiągnął większą efektywność, od 0.296 do 0.357, niż w przypadku równań Gompertza i Fabensa.