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Gompertz – Pütter – Gompertz: Resolving two centuries of debate on laws of biological growth

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Abstract: The function of Gompertz (1825) can be derived from the growth equation of Pütter (1920), using the modified form proposed by Kühleitner et al. (2019). The genetic relative growth rate is derived as $R_G = d\ln W/dt = B_G.\ln(A_G/W)$. The genetic characteristics are A_G, mature weight, and B_G, the rate parameter; the state variable is weight, W. The integrated form is $W = A_G.\exp[-\exp-(G_0 + B_G.t)]$, where $G_0 = -\ln[-\ln(W_0/A_G)]$ and $W = W_0$ when $t = 0$. The phenotypic equation is $R_P = q_E.R_G$, where $q_E \leq 1$ is a measure of the quality of the environment. This function is consistent with data, collected where q_E can reasonably be assumed to be 1, on the post-hatching growth of domestic and wild altricial birds, and with data from both the pre-natal and post-natal growth of domestic mammals. The mean value of the rate parameter, scaled to $A_G^{0.27}$, for mammals and precocial birds unselected by humans, is about 0.037, with considerable variation in avian species. Human selection for growth traits in poultry has nearly doubled the value. The mean value for seven altricial species was found to be nearly three times that for the average precocial species. The Gompertz function is consistent with data collected where the environment is not limiting. It follows logically that any function that is inconsistent with the Gompertz is inconsistent with relevant data, and therefore not a sufficient description of genetic growth. These results indicate that the Gompertz form is not merely a convenient empirical approximation, but a sufficient and biologically grounded description of genetic growth, against which alternative theoretical growth laws can be tested. It has the additional advantages of being simple and beautiful.

Keywords: birds, Dynamic Energy Budget; mammals; ontogenetic growth; von Bertalanffy

The phylogenetic divergence that led to the classes Aves and Mammalia is generally agreed to have taken place about 300 million years ago (e.g. Benton 1990). Where members of the two classes have characteristics in common (such as a four-chambered heart, the use of haemoglobin to transport oxygen, the ADP/ATP and Krebs cycle systems, the use of rods and cones in vision) it is reasonable *a priori* to assume that these are generic and of long-standing. Figure 1 shows data for the weight by age curves of ostriches (Cilliers et al. 1995), a member of the class Aves, and sheep (Lewis et al. 2002), a member of the class Mammalia. They were chosen because they both have an estimated mature weight, A, of close to 115 kg (112 kg for the male Suffolk sheep of a genetic control line, and 119 kg for the

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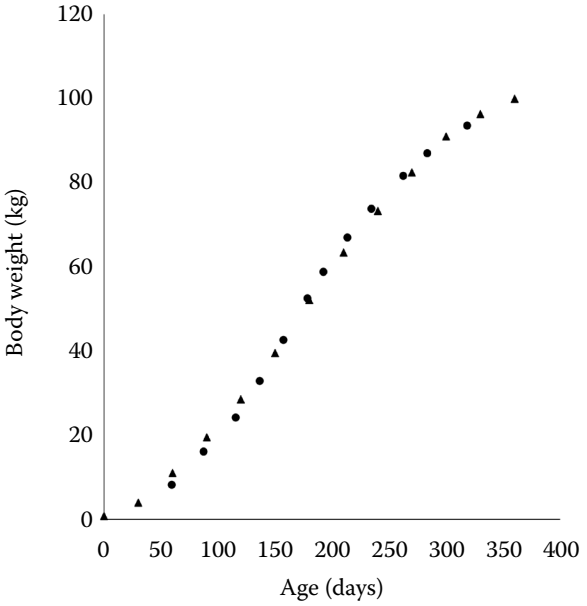

Figure 1. Body weight by age curves of ostriches (▲; Cilliers et al. 1995), a member of the class Aves, and sheep (●; Lewis et al. 2002), a member of the class Mammalia

ostrich). That the pattern of growth is virtually identical, leads to the biological hypothesis that this pattern is generic, and will be widespread in other birds and mammals. The first task of this paper is to test this hypothesis using suitable data. The second task is to examine the mathematical forms that have been used to describe the pattern, and to see how we may be able to choose between them.

The growth equation proposed by Putter (1920) was taken up by von Bertalanffy (1934, 1938, 1957). It continues to play an important part in Dynamic Energy Budget (DEB) theory (Nisbet et al. 2012; Kearney et al. 2015; Kooijman 2010, 2020; Kearney 2021; Kooijman et al. 2024; Lika and Kooijman 2024). Pütter was a chemist, and saw growth as the, almost incidental, outcome of the difference between the two "more fundamental processes" of anabolism (synthesis) and catabolism (degradation). On this view, equations are needed to describe anabolism and catabolism. The equation to describe growth then follows from these. The Ontogenetic Growth Model (OGM) of West et al. (2001) has a similar derivation. It is worth noting that ontogenesis means growth from conception through to maturity.

Others see it as useful to describe growth directly with an equation. Garcia (2005) and Zeide (1993) consider families of equations, with particular regard to forestry. Tjorve and Tjorve (2017) describe the family to which the Gompertz function belongs. Darmani Kuhi et al. (2010) deal with equations used to describe poultry growth and Lopez et al. (2000) for growth in general. France et al. (1996) describe growth functions and suggest a new one. Simpson et al. (2022) compare the ability of three of the functions of the Pütter family, as extended by Kuhleitner et al. (2019), to deal with the problem of population growth, particularly in the case of corals. Medawar (1940) deduced a growth equation directly from data generated by an elegant physiological experiment on the heart of the chicken embryo. He developed the finding into his Laws of Growth (Medawar 1941).

Gompertz (1825) brought his considerable mathematical skills to the problem of summarising the data that he found in human mortality tables, by proposing a function to describe them. It turns out that his beautiful function can also be used to describe the growth of domestic birds under non-limiting conditions (e.g. Emmans 2022).

We explore the connection between the functions of Gompertz and Pütter in a formal way. We then put forward evidence for the following propositions: (*i*) that, where simplifying assumptions hold, the two functions are equivalent, (*ii*) that the function provides a sufficient description of the genetic growth potential of, at least domestic, mammals from the early stages of pre-natal growth to maturity, (*iii*) that it provides a sufficient description of the genetic growth potential of the post-hatching growth of altricial and domestic precocial birds, (*iv*) that the value of the rate parameter of the function is scaled to mature size in the same way for domestic birds and mammals, (*v*) that the mean scaled value for the domestic species of the two Classes, while similar, shows genetic variation and, (*vi*) that the value of the scaled rate parameter for altricial birds is nearly three times higher than that of unimproved precocial ones.

The central theoretical question addressed here is whether biological growth from early development to maturity can be described by a single, sufficient functional form, and whether competing growth functions, derived from different mechanistic assumptions, are consistent with data collected under non-limiting conditions.

Domestic animals provide extensive, relevant, data and these are mainly used here. Supplementary data from altricial birds in the wild are used in support.

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MATERIAL AND METHODS

Growth laws and their mathematical consequences

While the phenomenon of growth applies more widely than just to that of an individual animal e.g. the growth of biological populations (e.g. Simpson et al. 2022), we will confine our arguments to animal growth, specifically the growth of birds and domestic mammals.

Gompertz

The Gompertz (1825) function, as a growth Equation (1), can be written as:

$$W = A.\exp[-\exp-(G_0 + B.t)] \quad (1)$$

This form emphasises the journey as having a starting point, G_0, a destination, A, and a rate of travel, B. The shape of the path is set by the function. The mature, or final, weight is A, and B is the rate parameter; $G_0 = -\ln[-\ln(W_0)]$, is a transformed initial condition where $W = 0$ when $t = 0$. The Equation (2) can be written as a linear function:

$$G_t = G_0 + B.t \quad (2)$$

where $G_t = -\ln[-\ln(W_t/A)]$.

The function follows from the assumption that the relative growth rate, $R = \mathrm{d}\ln(W)/\mathrm{d}t = (\mathrm{d}W/\mathrm{d}t)/W$, declines linearly with $\ln(W)$, at the rate B, to be zero when $W = A$.

$$R = B.\ln(A/W) \quad (3)$$

Emmans and Gous (2025) have shown how this equation can be derived from first principles. The linear forms of Equations (2) and (3) confer the great advantage that calculations can be visibly done, for example, in Microsoft Excel (Microsoft Corporation, 2024) rather than having to use complex statistical packages.

Pütter

Kuhleitner et al. (2019) present two versions of the Putter (1920) function. The first (our notation) is:

$$\mathrm{d}W/\mathrm{d}t = a\cdot W^m - b\cdot W^n \quad (4)$$

where the exponents must differ. We will call this the Pütter equation. There are different views about what the values of the exponents (m, n) should be, as shown in Table 1. The different growth equations that result can usefully be seen as the consequence of different assumptions about the way in which R is predicted to relate to W, as shown in Table 1. Suitable data can be used to test which, if any, of these proposed relationships agrees with the facts.

The second form, proposed by Kuhleitner et al. (2019) to deal with the case where $m = n$, and where there is heterogeneous variance in W, which is the normal case, is (our notation):

$$\mathrm{d}W/\mathrm{d}t = a\cdot W^m - b\cdot\ln(W)\cdot W^n \quad (5)$$

We will call this the Kühleitner equation. When $m = n = 1$ and (5) is divided through by W we have:

$$(\mathrm{d}W/\mathrm{d}t)/W = \mathrm{d}\ln(W)/\mathrm{d}t = R = a - b\cdot\ln(W) \quad (6)$$

At maturity in weight $\ln(W) = \ln(A)$, and $R = 0$. It follows that $a = b\cdot\ln(A)$. By substitution, with $a = b = B$, we have:

$$R = B.\ln(A/W) \quad (7)$$

The consequence is that, on these assumptions, the Gompertz Equation (3) and the Pütter Equation (7)

Table 1. Growth functions derived from two forms of the Putter (1920) equation [Equations (4) and (5) in this paper] and their predictions of the relationship between $\mathrm{d}\ln W/\mathrm{d}t$, the relative growth rate, R, and W

Equation	Exponents		Source	Development	Linear function of R on W
	m	n			
Pütter	⅔	1	von Bertalanffy (1934)	Dynamic Energy Budget	$1/W^{⅓}$
	¾	1	West et al. (2001)	Ontogenetic Growth Model	$1/W^{¼}$
	1	2	Verhulst (1845)	Logistic	W
Kühleitner	1	1	Kuhleitner et al. (2019)	Gompertz	$\ln W$

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are the same. Both equations are intended to apply only to cases where the environment is not limiting the genetic potential for growth. To make this explicit, Equations (3) and (7), can be written as:

$$R_G = B_G.\ln(A_G/W) \quad (8)$$

The subscript emphasises that the two animal parameters are genetic in nature. The equation can then be generalised (Emmans 2022) to:

$$R_P = q_E.R_G = q_E.B_G.\ln(A_G/W) \quad (9)$$

where the quality of the environment, $q_E \leq 1$, may modify genetic growth, R_G, to produce phenotypic growth, R_P. Figure 2 shows the results of the experiment of Lister et al. (1966) where one treatment may well have provided $q_E = 1$ and the other, by design, $q_E = 0$ for about six months. It is unrealistic to expect the same function to be able to describe the outcomes of both treatments. When data are used to estimate the values of parameters in (8), or any other function, it is necessary to check that $q_E = 1$ throughout.

Data

The data sets used to test where (8) could apply, come from experiments on pre- and post-natal domestic mammals, and post-hatching domestic precocial and altricial birds. The tests are not intended to be exhaustive, but relevant and illustrative. For both mammals and birds, species are chosen to give a wide range in mature weight. The cases for precocial birds are selected from much more comprehensive sets (Emmans 2022; Emmans and Gous 2025)

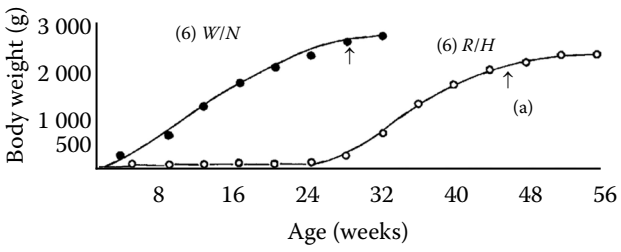

Figure 2. Growth curves of normal (●) and rehabilitated (restricted) (○) birds

The first may describe genetic, potential, growth; the second cannot. The numbers of each group are given in parentheses. Rhode Island Red birds: experimental group (*R*/*H*) hatched in February, control group (*W*/*N*) hatched in July. After Lister et al. (1966)

because they are unlikely to have been the subject of human selection to any great extent. Human selection can greatly change the values of the growth parameters, *A* and *B* (Emmans and Kyriazakis 2000).

The scaling rule of Taylor (1968, 1980) is assumed to apply, rather than being tested. Using this rule the relation expected between *A* and *B* in Equation (8) is that the value of the scaled rate parameter $B^* = B.A^{0.27}$, will be uncorrelated with *A*. The definition of metabolic age, *MA*, of Taylor (1980) as $MA = (t - 3.5)/A^{0.27}$ is used. The data in any given case were used to estimate the values of *A*, *B* and *B** either by regressing *R* on ln*W*, or by plotting G_t, from Equation (2), against *MA*. In this latter case the value of *A* was first estimated by finding the value that gave the same estimate of *B* for early and late sub-sets of the data. This method made it easier to detect any growth checks.

Mammals

Emmans (1997) used the pre-weaning data presented in the first 10 rows of Table 8 of Taylor (1980) to estimate the value of *B** for 8 species of domestic mammal. Re-examination of these data revealed that in 5 cases (cattle, pig, sheep, goat, and guinea pig) the graph of G_t on *MA* was essentially linear as shown by the high r^2 values in Table 2. The data in the other three cases (mouse, rat, and rabbit) were much noisier and less convincing, although the estimates of the regression coefficient were similar. That the problem probably lay with the data, rather than the species, is supported by the mouse data of Balinsky (1950) used below. The results for the three cases are shown in Table 2 but were excluded from the means.

Mouse. The pre-natal data of Balinsky (1950) and the post-natal data of Sutherland et al. (1974) for two genetic lines were used. The estimates of *A* were 0.030, 0.024 and 0.034 kg respectively. The latter two were estimated from the data; the first was taken from Taylor (1980).

Rabbits. No pre-natal data, but two sources for post-natal data, were used. The data of Larzul and Rochambeau (2004) were the initial weights for the ten lines, from their Table 1, and the weights at 35, 56, 77 and 98 d from their Table III. The data for 0, 35 and 56 d were called "early" and those at 56, 77 and 98 d "late". The value of *A* that gave the same value for *B* for each subset when G_t was regressed on age was estimated for each line. This was done to check that the data were consistent with

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Table 2. The regression of $d\ln W/dt$ on $\ln W$ for pre-weaning data for domestic mammals

Sub-set	Species	A (kg)	Intercept	B^*	R^2
	guinea pig	0.85	–2.881	0.035 5	0.999
	goat	45	–2.708	0.035 2	0.994
Well-ordered	sheep	75	–2.690	0.037 3	0.991
	swine	200	–2.592	0.038 3	0.987
	cattle	600	–2.734	0.036 7	0.986
Mean		–	–2.721	0.036 6	–
SD		–	0.104	0.001 28	–
	mouse	0.030	–2.866	0.042 8	0.957
Less well ordered	rat	0.25	–2.619	0.037 2	0.922
	rabbit	3.0	–2.386	0.040 4	0.951

Data from first 10 rows of Table 8 of Taylor (1980)

a linear relationship. It was in all cases. Gestation length was assumed to be 30 days. The regression of G_t on MA was fitted for each of the ten lines to estimate B^*.

The data of Putter (1920; Table 24) were used to calculate the mean $\ln W$ and R values for each period. The calculated regression excluded the low value for R following weaning.

Sheep. The pre-natal data of Cloete (1939), Stephenson and Lambourne (1960) for two breeds, and Thurley et al. (1973), and the post-natal data of Lewis et al. (2002) for female Suffolks of a genetic control line, are used. The value of A was estimated from the relevant post-natal data and then used for both the pre- and post-natal periods.

Swine. We used the pre-natal data of Mitchell (1931), Moustgaard (1962) and van Oijen et al. (1993), and the post-natal data of Doornenbal (1971). The value of 280 kg for A was estimated from the Doornenbal data and then used for all four sets.

Cattle. The pre-natal data to 250 d of gestation of Ferrell et al. (1982) were used. The 280-day value given in their Table was beyond the range of the data that they had. The post-natal data of Archer et al. (1997) for heifers were chosen because they had high absolute growth rates consistent with a non-limiting environment. The value of A was chosen *a priori* as 600 kg (Taylor 1980) and then B, and B^*, were estimated from both sets of data.

Birds

Data for the post-hatching growth of domestic species, believed to have been unselected for growth traits by humans, were used. The analyses came from Emmans (2022) and Emmans and Gous (2025) where the full details can be found. The intention was to use well-formed data sets with a wide geographical range. The birds used were most unlikely to have been a random genetic sample of their population, nor that population a random sample of that species. The data can thus be seen as only indicative. The estimates of the values of A, B, and hence B^*, were from either the regression of R on $\ln W$ or from that of G_t on t, as described above.

Data for six species of altricial bird were used: sparrows (Weaver 1942; Banks 1959), Robins (Hamilton 1935); Jays (Ritter 1984), Pigeons (Zannah et al. 2022), Eagle Owls (Penteriani et al. 2005) and Snowy Owls (Holt et al. 2016). The Gompertz parameter estimates for Bald Eagles were taken directly from Bortolotti (1984) as the data were not available.

RESULTS

Mammals

Mouse. G_t is plotted against MA in Figure 3. The pre-natal and post-natal data are consistent with a single function. The range in weight is about 2 500-fold.

Rabbits. The graph of R against $\ln W$ for the data of Putter (1920) is in Figure 4. With the deviant immediately post-weaning point (indicated) omitted, the data are consistent with a linear relationship. The data of Larzul and De Rochambeau (2004) are in Figure 5. The overall estimate of B^* was 0.038 5. The mean B^* for the 10 individual lines was 0.038 4 (SE 0.000 75). The range in weight was about 70-fold.

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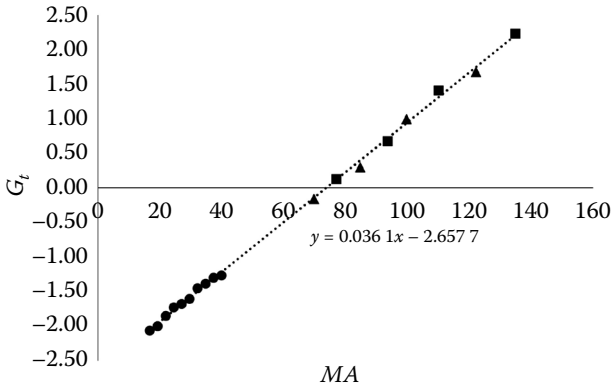

Figure 3. Growth in the mouse

The Gompertz variable, $G_t = -\ln[(-\ln(W/A)]$, plotted against metabolic age, $MA = (t - 3.5)/A^{0.27}$. Pre-natal data (●) are from Balinsky (1950) and post-natal from Sutherland et al. (1994) (line 2; ▲ and line 4; ■). The assumed values of A are 0.030, 0.024 and 0.034 kg, respectively

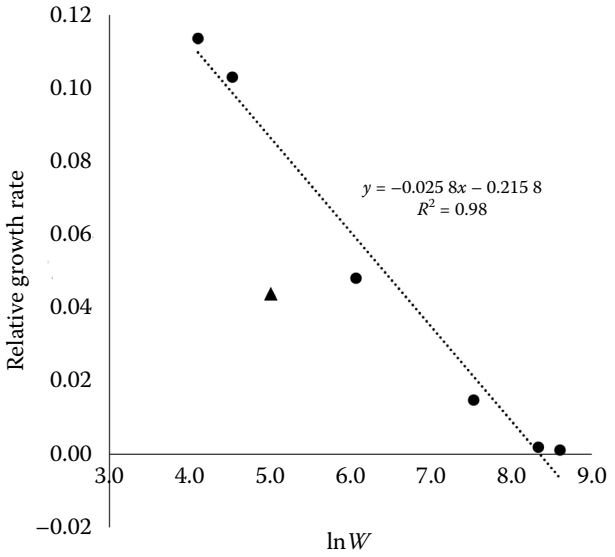

Figure 4. Relative growth rate, R, plotted against $\ln W$ for the rabbits of Putter (1920)

The deviant point (▲) following weaning is indicated and omitted from the regression

Sheep. The four sources (Cloete 1939; Stephenson and Lambourne (1960) for the Romney cross and Merinos; Thurley et al. 1973) for the pre-natal period were in very good agreement (not shown). The pre-natal data for Cloete (1939) agreed with the post-natal data for the females of the genetic selected line of Lewis et al. (2002), as shown in Figure 6. The common value of A was 112 kg. The overall range in the weights was about 20 000-fold. The values of the two regression coefficients are in good agreement with each other, and with the value for sheep in Table 2 that used data from another source.

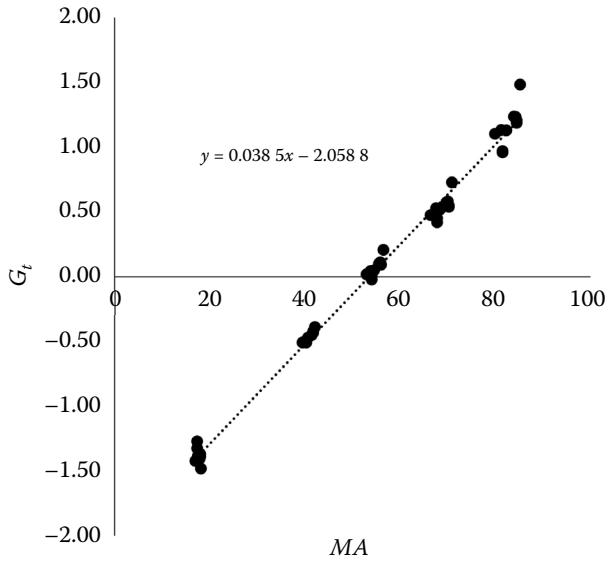

Figure 5. The Gompertz variable, $G_t = -\ln[(-\ln(W/A)]$, plotted against metabolic age, $MA = (t - 3.5)/A^{0.27,}$ for the post-natal growth of 10 lines of rabbits of Larzul and De Rochambeau (2004)

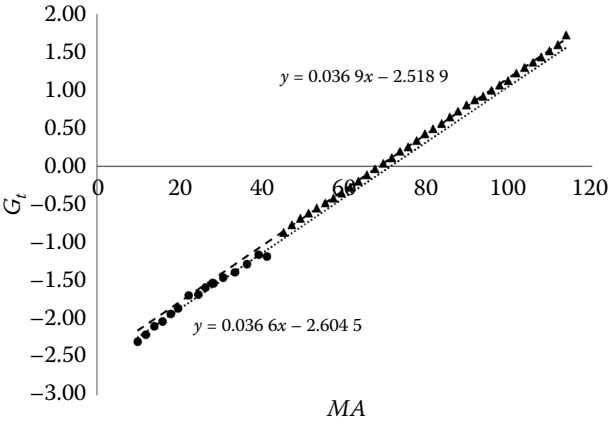

Figure 6. Growth in sheep

The Gompertz variable, $G_t = -\ln[-\ln(W/A)]$, plotted against metabolic age, $MA = (t - 3.5)/A^{0.27}$. The pre-natal data (●) are from the Merinos of Stephenson and Lambourne (1960) and the post-natal (▲) from Lewis et al. (2002). The assumed value of A is 100 kg for both

Swine. The three sources for the pre-natal period were in very good agreement as found by Wellock et al. (2004). The representative pre-natal data of Moustgaard (1962) agreed with the post-natal data of Doornenbal (1971) as shown in Figure 7. The overall range in the weights was about 1 500-fold.

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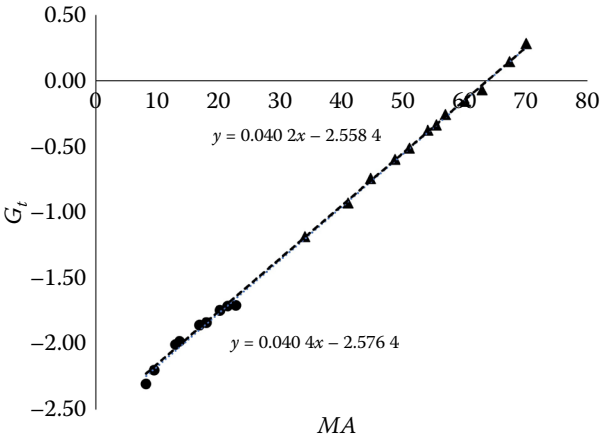

Figure 7. Growth in the pig
The Gompertz variable, $G_t = -\ln[-\ln(W/A)]$, plotted against metabolic age, $MA = (t - 3.5)/A^{0.27}$. The pre-natal data (●) are from Moustgaard (1962) and the post-natal (▲) from Doornenbal (1971). The assumed value of A is 280 kg for both

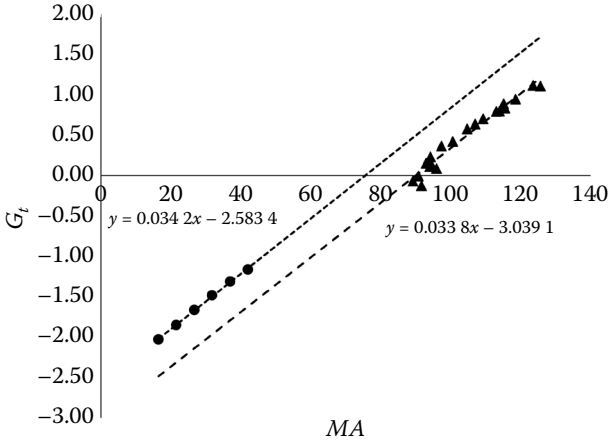

Figure 8. Growth in cattle
The Gompertz variable, $G_t = -\ln[-\ln(W/A)]$, plotted against metabolic age, $MA = (t - 3.5)/A^{0.27}$. The pre-natal data (●) are from Ferrell et al. (1982) and the post-natal (▲) from Archer et al. (1997). The assumed value of A is 600 kg for both

Cattle. The data are plotted in Figure 8. Given a common value of A of 600 kg the slopes for the two stages of growth were in very good agreement. The difference in the values of the intercepts was consistent with a growth check of 9 d of MA between birth and the start of the test of Archer et al. (1997). For the 10 post-natal cases the mean value of B^* of 0.035 9 (SE 0.002 5) was in good agreement with the mean pre-natal value of 0.036 7 (Table 2). The overall range in the weights was more than 1 000-fold.

Birds

The results of the analyses are in Table 3. The mean value of B^* was close to the mean mammalian value, Table 2. The variation was large. The species for which data were available were far from being a random, or systematic, sample of the Class Aves. However, it is possible that, even within domestic precocial species, there is considerable natural genetic variation in the value of B^*. The functional form of the equations applied to all the species.

The results for the altricial birds are in Table 4. As an example, G_t, calculated for a mature weight of 0.082 kg, is plotted against age in Figure 9 for the jays.

Other functions

Over a small range of data, it is difficult to show that any more complex function gives a better fit to W, t data than a simple linear one. As the range is extended curvature becomes apparent, but it is still difficult to distinguish between different functional forms with three parameters.

In order to be able to distinguish between functions, such as those shown in Table 1, data collected over a considerable range are needed. The data also need to be "clean" in the sense that there are no errors, in the values of either W or t, and the environment was such as to allow the genetic potential to be expressed at all times (Emmans and Gous 2025).

The Logistic function rapidly fails as the weight range is extended. Wellock et al. (2004) describe this for the case of pigs. Other examples, for birds, are in Emmans (2022).

Two widely used functions, also with three parameters, are the von Bertalanffy (1934) function and the OGM function (West et al. 2001). These are first evaluated for post-natal growth using, as an example, the data for the males of a genetic control line of Suffolk sheep (Lewis et al. 2002). The derived values for the post-natal parameters are then used to predict pre-natal growth. These predictions were assessed and compared with the actual data of Thurley et al. (1973). The two sets of data used, when taken together, have a wide range in weight from 0.07 to 93 kg, about 1 300-fold and were found to be consistent with a single Gompertz function, Figure 10.

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Table 3. Estimates of the values of A, B, and hence B^*, from either the regression of R on $\ln W$ (a) or from that of G_t on t (b), as described in the text, using data for the post-hatching growth of domestic species of birds

Species	Author	Note	A (kg)	B (a)	$B^* = B.A^{0.27}$ (a, b)	Species mean B^*
Quail	Aggrey and Cheng (1992))	male	0.112	0.076 0	0.042 1	–
	Haqani et al. (2021)		0.122	0.070 1	0.039 7	–
			0.155	0.069 9	0.042 3	–
			0.158	0.073 4	0.044 6	–
			0.204	0.061 9	0.040 3	0.041 8
Guinea fowl	Nahashon et al. (2006)		0.221	0.033 4	–	0.022 2
Partridge	Iqbal et al. (2019)		0.510	0.038 1	–	0.031 8
Tinamou	dos Santos Correia et al. (2018)		0.782	–	–	0.017 4
Pheasant	Ipek and Dikmen (2007)		1.08	–	0.031 4	–
	Kuzniacka and Adamski (2010)	female	0.988	–	0.035 7	–
		male	1.43	–	0.032 8	–
	Yamak et al. (2020)		1.65	–	0.022 0	0.030 5
Duck	Asiamah et al. (2020)	female	1.16	0.032 0	0.045 2	–
		male	1.23	–	0.043 6	0.044 4
Chicken	Singsen (1949)	females	1.80	–	0.037 6	–
	Kumar et al. (2022)	males	2.50	–	0.038 2	–
			2.51	–	0.019 5	–
	Nguyen Hoang et al. (2021)	males	2.60	–	0.031 4	–
	Sohn et al. (2022)	as-hatched	3.16	–	0.047 1	–
	Yang et al. (2006)		2.89	–	0.027 2	0.033 5
Goose	Al-Muzani and Al-Asadi (2021)		3.69	–	0.060 6	–
			3.79	–	0.063 0	–
			4.01	–	0.058 6	–
			4.25	–	0.060 3	–
	Hrncar et al. (2016)		5.43	–	0.071 1	–
			5.69	–	0.060 6	–
			6.24	–	0.083 1	0.065 3
Turkey	Funk (1930)		7.134	–	0.026 2	–
			10.386	–	0.025 2	–
			11.642	–	0.028 7	–
			14.234	–	0.029 7	0.027 5
Ostrich	Cilliers et al. (1995)	11–100 kg	119.4	–	0.032 0	–
	Bo et al. (2025)	0.9–102 kg	133	–	0.033 5	–
			135	–	0.035 1	0.033 5
Mean			–	–	–	0.034 8
SD			–	–	–	0.013 4

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Table 4. Estimates of the values of A, B, and hence B^*, from either the regression of R on ln$W$ (a) or from that of G_t on t (b), as described in the text, using data for the post-hatching growth of altricial species of birds (*u is the degree of maturity)

Species	u range*	A	B (a)	B^* (a, b)	Source	ln$A$	ln$B$
Bald Eagles, female	0.020 to 0.95	5.172	0.068 3	0.106 4	Bortolotti (1984)	1.643 3	−2.683 9
Bald Eagles, male	0.020 to 0.95	4.066	0.068 3	0.099 7	Bortolotti (1984)	1.402 7	−2.683 9
Owls	0.080 to 0.80	1.650	0.074 5	0.085 3	Penteriani et al. (2005)	0.500 8	−2.597 0
Snowy Owl	0.027 to 0.95	1.650	0.085 7	0.098 1	Holt et al. (2016)	0.500 8	−2.456 9
Pigeons, male	0.041 to 0.94	0.350	0.140 2	0.105 6	Zannah et al. (2022)	−1.049 8	−1.964 7
Pigeons, female	0.042 to 0.91	0.329	0.141 6	0.104 9	Zannah et al. (2022)	−1.111 7	−1.954 8
Jays	0.066 to 0.77	0.082	0.166 0	0.084 5	Ritter (1984)	−2.501 0	−1.795 8
Robins	0.070 to 0.55	0.094	0.195 0	0.103 0	Hamilton (1935)	−2.364 5	−1.634 8
Sparrows1	0.098 to 0.71	0.029	0.233 7	0.089 5	Weaver (1942)	−3.554 4	−1.453 7
Sparrows2	0.110 to 0.83	0.023	0.294 5	0.106 1	Banks (1959)	−3.781 0	−1.222 5
			mean	0.098 3			
			SD	0.008 73			
			SE	0.002 76			

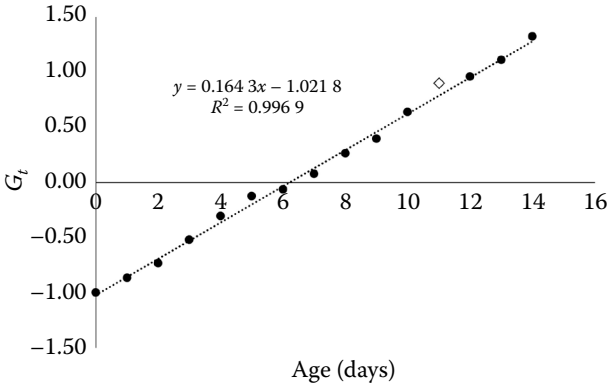

Figure 9. The Gompertz variable, $G_t = -\ln[-\ln(W/A)]$, calculated for a mature weight of 82 g, plotted against age for male pigeons using the data of Zannah et al. (2022)

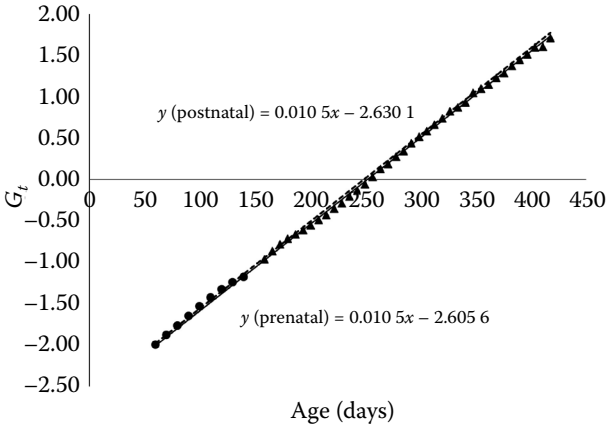

Figure 10. The Gompertz variable, $G_t = -\ln[-\ln(W/A)]$ plotted against age for the post-natal data of sheep (▲; Lewis et al. 2002) and using the same derived parameters for pre-natal data also of sheep (●; Thurley et al. 1973)

von Bertalanffy. The post-natal data were used to estimate the value of the rate parameter of the vB growth function, given that W = 6.2 kg at t = 0 and A = 112 kg. The actual and vB predicted ln$W$ values are plotted against age in Figure 11. Although not perfect, the agreement is very good as can be seen. The same values of the parameters were then used to predict ln$W$ for pre-natal ages. Figure 12 shows the vB predictions of ln$W$ together with the pre-natal data. There is no agreement and the predictions become increasingly absurd as age goes back towards conception.

OGM. The post-natal data were used to estimate the value of the rate parameter of the OGM growth function, given that W = 6.2 kg at t = 0 and A = 112 kg. The actual and OGM predicted ln$W$ values are plotted against age in Figure 11. Although

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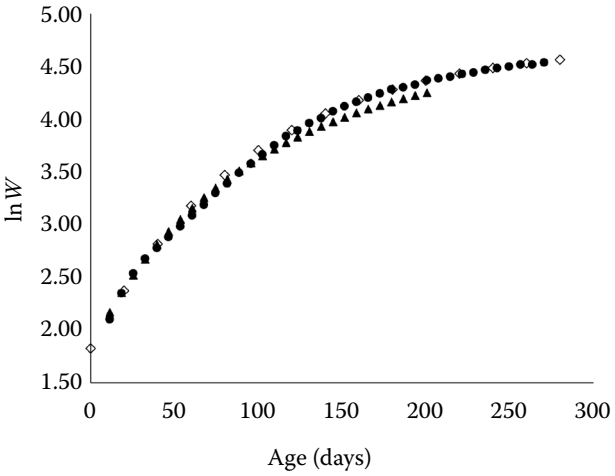

Figure 11. Using post-natal data of sheep (Lewis et al. 2002) values of ln*W* are plotted against age
Actual data (●) are compared with those predicted by the von Bertalanffy (1934) function (◊) and the OGM function (West et al. 2001) (▲)

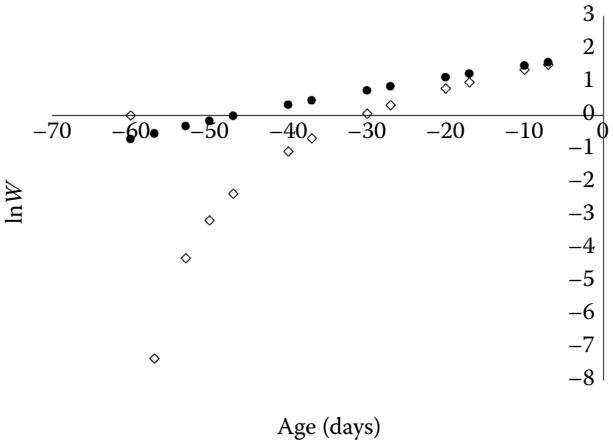

Figure 12. Using pre-natal data from sheep (Thurley et al. 1973), values of ln*W* are plotted against age, comparing actual data (●) with those predicted by the von Bertalanffy (1934) function (◊)

not perfect, the agreement is very good as can be seen. The same values of the parameters were then used to predict ln*W* for pre-natal ages. The predicted ln*W* by *t* relationship becomes increasingly absurd as age moves back towards conception, Figure 13. Beyond a particular pre-natal age weight starts to increase as age moves backwards towards conception when it is predicted to be 13 kg.

With the Gompertz function able to describe the ontogenetic growth of mammals, there is no good reason to use either the vB or the OGM functions for post-natal growth.

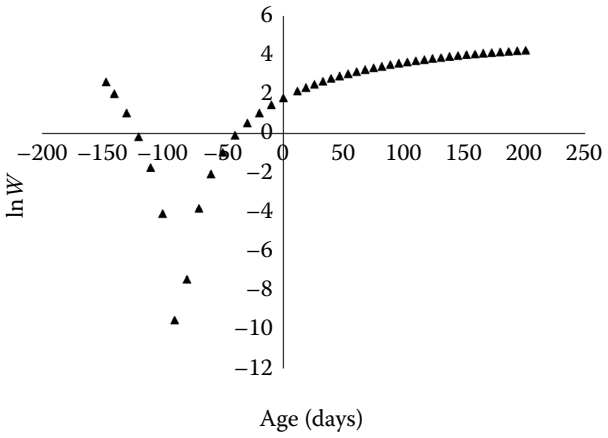

Figure 13. Using pre-natal (Thurley et al. 1973) and post-natal data (Lewis et al. 2002) from sheep, values of ln*W* predicted by the OGM function (West et al. 2001) (▲) are plotted against time

DISCUSSION

It is intriguing that a function that Gompertz (1825) invented two centuries ago to describe data on human mortality, turns out, under certain assumptions, to be equivalent to one proposed one century later in relation to animal metabolism and growth. The equation of Putter (1920) was developed by von Bertalanffy (1934) and it is usually given his name. Kearney (2021) has tried recently to set the record straight.

Gompertz started with data on human mortality, seen as relevant to his problem (how to set annuity rates), and then invented a functional form that could describe them. Taylor (1980) used data to find that the time taken to pass between two degrees of maturity in domestic mammals was related to $A^{0.27}$. The approach of starting with what Nature is telling us through data, is in marked contrast to another that starts with theoretical assumptions about what Nature ought to be like. Kooijman and Metz (1984) agreed with von Bertalanffy (1957) that $m = 2/3$ and $n = 1$ in Equation (4) to develop Dynamic Energy Budget (DEB) theory. At best the vB function gives a close, but not perfect, description of post-natal growth in mammals. When extrapolated to pre-natal growth it breaks down, Figure 12.

West et al. (2001) proposed $m = ¼$ and $n = 1$ to derive the OGM. Recent developments in these models are described by Kearney (2021). Although West et al. (2001) use the term "ontogenetic", implying that their equations apply from concep-

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tion to maturity, they say nothing about pre-natal growth in mammals. While our results show that the Gompertz function applies over the pre- and post-natal stages with the same values of the parameters, Figure 13 shows that the OGM does not, and cannot properly be seen as "ontogenetic".

Ricklefs (1968) examined 105 sets of data on the growth of species of wild birds. Although he recognised that there were environmental effects, he initially ignored these to classify the observed growth patterns as Logistic, Gompertz or von Bertalanffy (vB). The numbers in each group were 81, 21 and 3 respectively. In contrast, the data from all the domestic species of birds of Emmans (2022) and Emmans and Gous (2025), when collected in non-limiting conditions, were found to be consistent with the Gompertz function. They also showed that data collected in limiting environments could be accounted for.

Kuhleitner et al. (2019) made no a priori assumptions about the values of the exponents in Equation (4). They proposed a method for directly estimating the values of the four parameters in the Pütter growth equation, plus the initial condition, from suitable data. Unfortunately, they chose a set of data, that of Aggrey and Cheng (1992) for chickens, that had a serious flaw. The very earliest data were grossly aberrant. Part of the difficulty in estimating the values of the five parameters was probably a reflection of the inclusion of the early aberrant data.

Even so they found that a = 0.89 and b = 0.93. These values are close to both being equal, and to a common value of 1, which leads to the Gompertz function as we have seen earlier. Other data on chickens, Table 3, do not have the problem of the Aggrey and Cheng (1992) set.

The interplay between theory and data is important. Hiraiwa (1929) was interested in the growth of the Wistar rat in Japan. He weighed male and female rats over 250 days from birth. He compared his data with that of Donaldson (1924) and concluded that "we find some inferiority in our results". Figure 14 shows the female/male ratio of weights plotted against age in the two sets of data. The data of Hiraiwa make biological sense; those of Donaldson do not and are contrary to the consensus (Slob and Van der Werff Ten Bosch 1975). The ratio in the data of King et al. (2014) is also shown in Figure 15 to support those of Hiraiwa. Despite this, it is the data of Donaldson (his publication has been cited 669 times according to Google Scholar) that were subsequently used extensively as if they, in some generic sense, described the growth of the rat. The paper of Hiraiwa has been cited once. Figure 14 shows his data for the males, assuming a mature weight of 224 g. The data, over a range in degree of maturity of 0.024 to 0.91, are consistent with a Gompertz function. The number of animals decreases rapidly at later ages, and the data become more erratic (not shown).

The DEB and OGM frameworks derive growth equations from specific mechanistic, (either geometric or chemical), assumptions. The present results suggest that these assumptions lead to growth laws that are not consistent with observed genetic growth trajectories for mammals and birds under non-limiting conditions. Their assumptions lead to predictions that the relative growth rate is a lin-

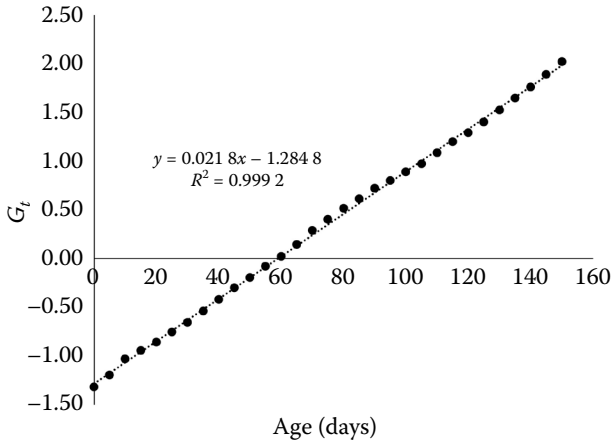

Figure 14. The Gompertz variable, $G_t = -\ln[-\ln(W/A)]$ plotted against age for male rats (Hiraiwa 1929)

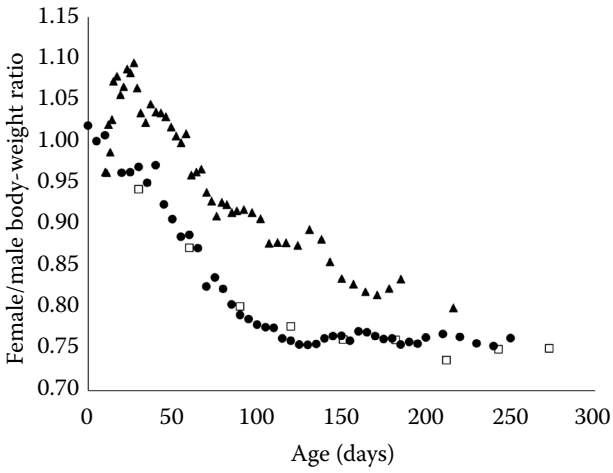

Figure 15. Ratio of female to male body weights of rats plotted against age (Donaldson 1924, ▲; Hiraiwa 1929, ●; and King et al. 2014, □)

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ear function of either $W^{-⅓}$ or $W^{-¼}$ respectively. The data from the male chickens of Gous et al. (2024), were chosen because they cover a nearly 200-fold range in weight.

In Figure 16A–D the chicken data are used to plot R against $\ln W$ (Gompertz), W (Logistic), $W^{-⅓}$ (von Bertalanffy) and $W^{-¼}$ (OGM) respectively. The linear relationship with $\ln W$ is clear. All of the other three relationships are not the linear one predicted, but are clearly curved.

It appears that evolution chose the Gompertz form for the genetic growth of domestic, and possibly other, mammals at least 300 million years ago. This was when the lines leading to Aves and Mammalia diverged. The same form is used for the post-hatching growth of, at least, domestic birds and, likely, wild altricial birds. It may be that the range of applicability can be extended. Laberge et al. (2025) used data on the growth of seals to conclude that "all model validation criteria suggested

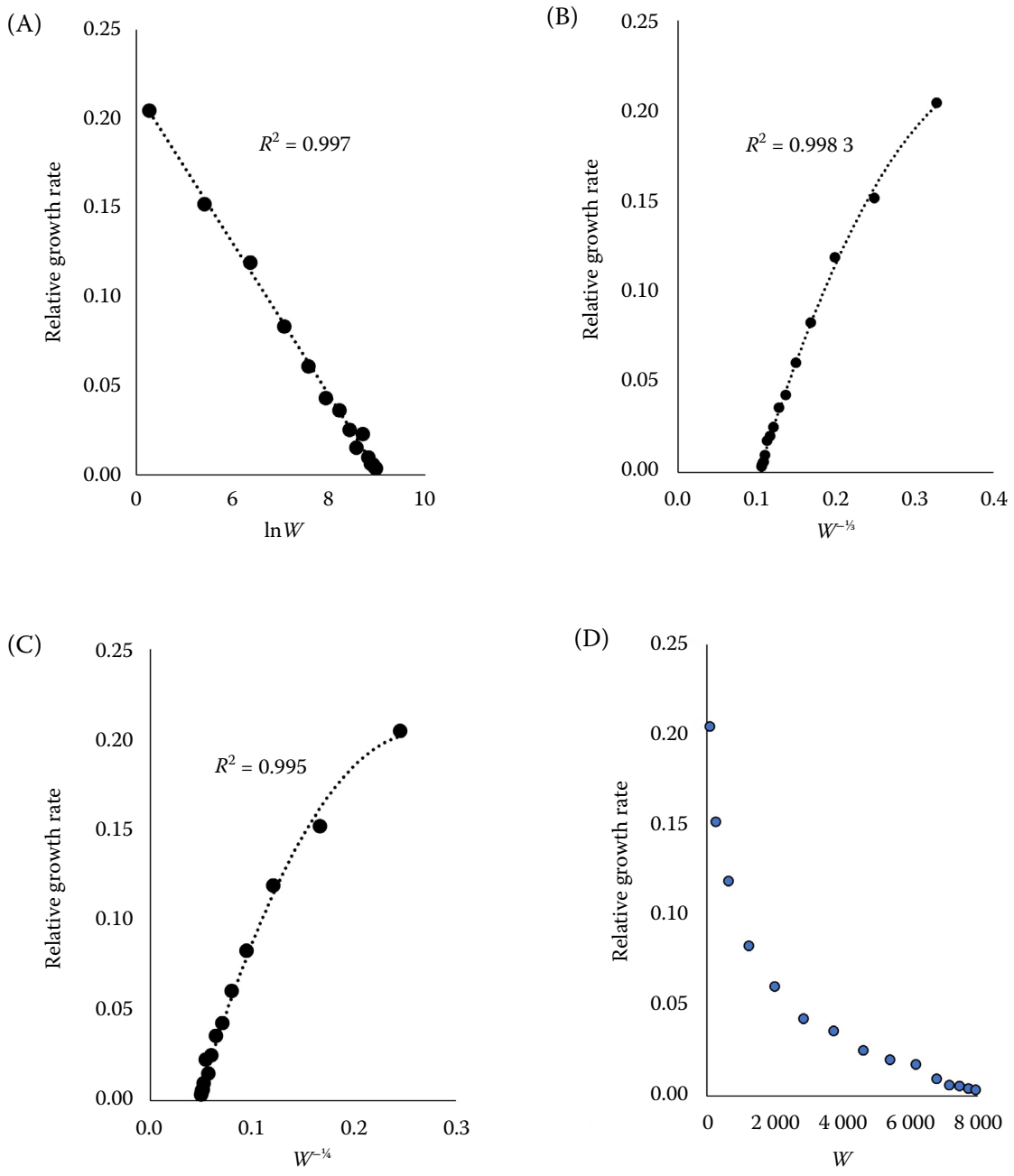

Figure 16. Data from the male chickens of Gous et al. (2024) were used to plot relative growth rate, R against $\ln W$ (Gompertz) (A), $W^{-⅓}$ (von Bertalanffy) (B), $W^{-¼}$ (OGM) (C), and W (Logistic) (D), respectively

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that harbour seal neonatal growth patterns, as derived from our data, can be best described using a Gompertz curve".

Two biologically relevant questions are: can the genetic growth of mammals and birds be sufficiently described by a simple functional form and, if so, what is it? The evidence presented here and elsewhere (Wellock et al. 2004; Emmans 2022; Emmans and Gous 2025) is that the answers are "yes", and "the Gompertz function". No function is expected to apply to any set of phenotypic data as the value of q_E may vary in a wide variety of ways.

In nature an animal would be expected to seek an environment where $q_E = 1$, subject to other considerations such as avoiding predation. In animal production the human decision maker seeks to make the value of the many dimensions that comprise q_E as close to 1 as is economically justified (Gous and Fisher 2017). Where the aim of an experiment is to evaluate a genotype then it is important that $q_E = 1$ throughout. Where this is not the case, for at least some of the time, it may wrongly be concluded that functions other than the Gompertz are better.

For domestic precocial birds, altricial birds, and domestic mammals, the data presented here suggest that the qualitative similarity can usefully be extended to an examination of the quantitative similarities and differences. The value of the scaled rate parameter, B^*, is strikingly similar in the different species of domestic mammals with a wide range in A. In the domestic birds used, all of which are precocial, in the post-hatching period there is considerable genetic variation, but the mean value is close to that of mammals.

For the seven species of altricial birds in Table 4 the range in A was about 200-fold. Over this range the regression coefficient for ln$B$ on ln$A$ was 0.264 (SE = 0.018). This was not significantly different to the exponent used here of 0.27. The mean value of $B^* = B.A^{0.27}$ was 0.098 3 (SE 0.002 76), which is nearly three times as great as that for the mammals and the precocial birds.

Weight, W, has been used here as the measure of size throughout. It is conventional to analyse the empty body into the four major chemical components – protein, lipid, ash, and water. The Gompertz function can then be extended to each of these (Emmans 1988; Gous et al. 2024). As the carbon contents of protein (6.25N) and lipid are close to constant (at 0.524 and 0.765 respectively) these components can, in turn, be resolved into N and C where this is thought to be necessary. As virtually all the energy in the body is in its protein and lipid contents the function can be extended to energy and, by extension, to the prediction of feed intake (Emmans 1997).

CONCLUSION

This paper shows that, under clear and biologically reasonable assumptions, the Gompertz growth function and a modified version of the Pütter equation describe the same genetic growth process. Evidence from a wide range of data demonstrates that the Gompertz function provides a sufficient and consistent description of genetic growth in domestic mammals from early development to maturity, and in domestic birds after hatching, when the environment does not limit growth. Growth functions that depart from the Gompertz form are not supported by these data.

These results indicate that the Gompertz form is not merely a convenient empirical approximation, but a sufficient and biologically grounded description of genetic growth, against which alternative theoretical growth laws can be tested. It has the additional advantages of being simple and beautiful.

More generally, this work illustrates how long-standing theoretical growth laws can be evaluated and refined by requiring consistency with data across the full ontogenetic trajectory.

Conflict of interest

The authors declare no conflict of interest.

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