

Some novel growth functions and their application with reference to growth in ostrich¹

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ABSTRACT: Four novel growth functions, namely, Pareto, extreme value distribution (EVD), Lomolino, and cumulative β - P distribution (CBP), are derived, and their ability to describe ostrich growth curves is evaluated. The functions were compared with standard growth equations, namely, the monomolecular, Michaelis-Menten (MM), Gompertz, Richards, and generalized MM (gMM). For this purpose, 2 separate comparisons were conducted. In the first, all the functions were fitted to 40 individual growth curves (5 males and 35 females) of ostriches using nonlinear regression. In the second, performance of the functions was assessed when data from 71 individuals were composited (570 data points). This comparison was undertaken using nonlinear mixed models and considering 3 approaches: 1) models with no random effect, 2) random effect incorporated as the intercept, and 3) random effect incorporated into the asymptotic weight parameter (W_f). The results from the first comparison showed that the functions generally gave acceptable values of R^2 and residual variance. On the basis of the Akaike information criterion (AIC), CBP gave the best fit, whereas the Gompertz and Lomolino equations were the preferred functions on the basis of corrected AIC (AIC_c). Bias, accuracy

factor, the Durbin-Watson statistic, and the number of runs of sign were used to analyze the residuals. CBP gave the best distribution of residuals but also produced more residual autocorrelation (significant Durbin-Watson statistic). The functions were applied to sample data for a more conventional farm species (2 breeds of cattle) to verify the results of the comparison of fit among functions and their applicability across species. In the second comparison, analysis of mixed models showed that incorporation of a random effect into W_f gave the best fit, resulting in smaller AIC and AIC_c values compared with those in the other 2 approaches. On the basis of AIC_c , best fit was achieved with CBP, followed by gMM, Lomolino, and Richards functions, respectively. The exponential, MM, Pareto, and EVD equations produced negative values for initial weight (W_0) if left unconstrained. The Gompertz equation, in spite of having a fixed inflection point and therefore being less flexible, gave accurate estimates of both W_0 and W_f and an acceptable goodness of fit favored by having fewer parameters than the other sigmoidal functions. Nevertheless, all the sigmoidal functions appeared appropriate in describing the growth trajectory of male and female ostriches to a reasonable level of accuracy.

Key words: cumulative beta- P distribution, extreme value distribution, growth curves, growth functions, Lomolino, Pareto

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INTRODUCTION

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Growth functions have been used extensively to represent change in body size with age, allowing the genetic potential of animals for growth to be evaluated (Fitzhugh, 1976; Aggrey et al., 2003). These functions

are also used to estimate feed requirements for growth to allow nutrition to be matched to optimal weight gain (López et al., 2000). Simulation models for decision making in systems of animal production require accurate estimates of growth traits for each animal category (Hancock et al., 1995). Several growth functions (e.g., Gompertz, logistic, Richards) have been fitted to the nonlinear relationship between body size (BW) and age to describe growth in animals and obtain estimates of growth traits (Aggrey, 2002; Darmani Kuhl et al., 2003). These functions have also been used to describe population growth.

Other mathematical functions, such as the extreme value statistical distribution function (Williams, 1995), the Lomolino equation (Lomolino, 2000), and the β - P statistical distribution function (Mielke and Johnson, 1974), have been used to study the species-area relationship (SAR), one of the key tools to evaluate species diversity in ecology and conservation biology (Rosenzweig, 1995). This relationship represents one of the oldest and most proven patterns in ecology (Tjørve, 2003). Despite the similarity in shape between SAR and growth curves, these mathematical functions have received relatively little attention pertaining to the description of somatic growth in animals (Faridi et al., 2014).

Four novel growth functions (1 diminishing returns and 3 sigmoidal) are derived from simple basic assumptions. Special cases include the Pareto, extreme value, and β - P distribution functions from statistics and the Lomolino SAR from ecology. These functions are evaluated and compared with popular growth equations (Thornley and France, 2007) by fitting them to growth data from ostrich and cattle.

MATERIALS AND METHODS

Research protocols followed the guidelines stated in the Guide for the Care and Use of Agricultural Animals in Research and Teaching (Federation of Animal Science Societies, 2010). Animal Care and Use Committee approval was not required for collection of the ostrich growth data (weight and age) as the birds were maintained under field conditions following standard farming practices and were raised according to the recommendations concerning ratites of the Standing Committee of the European Convention for the Protection of Animals kept for Farming Purposes (1997). Cattle growth data used were from previously published studies (López et al., 2000), and therefore, Animal Care and Use Committee approval was not required.

Derivation of Growth Functions

Pareto Distribution Function. The assumptions are as follows: The quantity of growth machinery (viz.,

mechanisms or processes) is constant and independent of the weight of the organism W (kg BW); this machinery works at a rate proportional to the substrate (viz., nutrients) level S (kg substrate); its effectiveness μ decays inversely and linearly with time t (wk); growth is irreversible. Formalizing,

$$\frac{dW}{dt} = \mu S$$

$$\mu = \frac{c}{t + \tau},$$

where c (kg BW/kg substrate) and τ (wk) are constants. These constants have to be positive as μ cannot be negative because growth is irreversible. On substituting for μ and writing S as $W_f - W$, where W_f is the asymptotic value of W , the growth rate now becomes

$$\frac{dW}{dt} = \frac{c}{t + \tau} (W_f - W). \quad [1]$$

This can be integrated analytically:

$$\int_{W_0}^W \frac{dW}{W_f - W} = c \int_0^t \frac{dt}{t + \tau},$$

giving

$$\frac{W_f - W_0}{W_f - W} = \left(\frac{t + \tau}{\tau} \right)^c, \quad [2]$$

where W_0 is the value of W at time zero. Rearranging,

$$W = W_f - (W_f - W_0) \left(\frac{\tau}{t + \tau} \right)^c. \quad [3]$$

This equation exhibits diminishing returns behavior; there is no point of inflection. Equation [3] with $W_0 = 0$ and $\tau = 0$ in the denominator corresponds to the Pareto distribution function (Prokhorov, 2001). Expressing a growth function in its rate:state form (i.e., writing dW/dt as a function of W alone) can sometimes, and unexpectedly, be meaningful biologically. Using Eq. [2] to substitute for $t + \tau$ in Eq. [1] gives

$$\frac{dW}{dt} = \frac{c}{\tau} \sqrt[c]{\frac{(W_f - W)^{c+1}}{W_f - W_0}}.$$

Extreme Value Distribution Function. The assumptions are as follows: The quantity of growth machinery is constant and independent of BW; this machinery works at a rate proportional to the substrate level; its effectiveness μ varies exponentially with time; growth is irreversible. We can now write

$$\frac{dW}{dt} = \mu S$$

$$\mu = ke^{kt+D},$$

where k (>0 , wk^{-1}) and D (dimensionless) are rate and shape parameters, respectively. The units of μ are

kilograms BW per kilogram substrate per week. On substituting for μ and writing S as $W_f - W$, the growth rate now becomes

$$\frac{dW}{dt} = ke^{kt+D}(W_f - W). \quad [4]$$

This can be integrated analytically:

$$\int_{W_0}^W \frac{dW}{W_f - W} = ke^D \int_0^t e^{kt} dt,$$

giving

$$\frac{W_f - W_0}{W_f - W} = \exp[e^D(e^{kt} - 1)]. \quad [5]$$

Rearranging,

$$W = W_f \left\{ 1 - \left[\frac{W_f - W_0}{W_f} \exp(e^D) \right] \exp(-e^{kt+D}) \right\}. \quad [6]$$

When W_0 and e^D tend to zero, this growth function is akin to the distribution function of the extreme value (or Gumbel) probability distribution (Gumbel, 1954, 1958). Differentiating twice,

$$\frac{d^2W}{dt^2} = k^2 \left[\frac{W_f - W_0}{W_f} \exp(e^D) \right] \times \left[\exp(kt + D - e^{kt+D}) \right] (1 - e^{kt+D}).$$

This expression is zero when

$$1 - e^{kt+D} = 0.$$

Thus, the point of inflection (t^* , W^*) is given by

$$t^* = -D/k$$

$$W^* = W_f \left[1 - \frac{W_f - W_0}{W_f} \exp(e^D - 1) \right].$$

As the growth trajectory takes place in real (positive) time, the function describes sigmoidal growth when $D < 0$ and nonsigmoidal (i.e., diminishing returns) growth when $D \geq 0$. The growth function can be written in rate:state form by using Eq. [5] to eliminate t in Eq. [4]:

$$\frac{dW}{dt} = k \left[\ln \left(\frac{W_f - W_0}{W_f - W} \right) + e^D \right] (W_f - W).$$

Beta Distribution Function. The assumptions are as follows: The quantity of growth machinery is constant and independent of BW; this machinery works at a rate proportional to the substrate level; proportionality changes with time according to a simple rational function; growth is irreversible. Formalizing,

$$\frac{dW}{dt} = \mu S$$

$$\mu = c \frac{t^{q-1}}{t^q + \tau^q},$$

where c (kg BW/kg substrate) and τ (wk) are constants. These 2 constants have to be positive as μ cannot be negative because growth is irreversible. This proportionality permits μ to decrease continually ($q \leq 1$) or increase to reach a maximum then decrease again ($q > 1$). On substituting for μ and writing S as $W_f - W$, the growth rate becomes

$$\frac{dW}{dt} = c \frac{t^{q-1}}{t^q + \tau^q} (W_f - W). \quad [7]$$

This can be integrated analytically:

$$\int_{W_0}^W \frac{dW}{W_f - W} = \frac{c}{q} \int_0^t \frac{qt^{q-1}}{t^q + \tau^q} dt,$$

giving

$$\frac{W_f - W_0}{W_f - W} = \left(\frac{t^q + \tau^q}{\tau^q} \right)^{c/q}.$$

Rearranging,

$$W = W_f - (W_f - W_0) \left[1 + \left(\frac{t}{\tau} \right)^q \right]^{-c/q}. \quad [8]$$

Equation [8] with $W_0 = 0$ and q positive corresponds to the β - P distribution function, a Pareto-type distribution (Johnson et al., 1994). Equation [8] with $c = q$ gives the generalized Michaelis-Menten growth function (López et al., 2000). A variable point of inflection occurs when d^2W/dt^2 is zero. This is possible only if $q > 1$ and occurs when

$$t = t^* = \tau \left(\frac{q-1}{c+1} \right)^{1/q}$$

$$W = W^* = W_f - (W_f - W_0) \left(\frac{c+1}{c+q} \right)^{c/q}.$$

Equation [7] cannot be expressed succinctly in rate:state form.

Lomolino Species-Area Function. The assumptions are as follows: The growth machinery works at a rate proportional to both BW and substrate level; this proportionality varies inversely and linearly with time; growth is irreversible. We now have

$$\frac{dW}{dt} = \mu WS$$

$$\mu = c' \frac{1}{t + \tau},$$

where c' (kg^{-1} substrate) and τ (wk) are positive constants. On substituting for μ and writing S as $W_f - W$ and c' as c/W_f , the growth rate becomes

$$\frac{dW}{dt} = \frac{c}{t + \tau} W \left(1 - \frac{W}{W_f} \right). \quad [9]$$

Equation [9] can be integrated analytically:

$$\int_{W_0}^W \frac{dW}{\left(1 - \frac{W}{W_f}\right)W} = c \int_0^t \frac{dt}{t + \tau},$$

i.e.,

$$\int_{W_0}^W \left[\frac{1}{(W_f - W)} + \frac{1}{W} \right] dW = c \int_0^t \frac{dt}{t + \tau},$$

giving

$$\frac{W(W_f - W_0)}{W_0(W_f - W)} = \left(\frac{t + \tau}{\tau} \right)^c. \tag{10}$$

Rearranging,

$$W = \frac{W_0 W_f}{W_0 + (W_f - W_0) \left(\frac{\tau}{t + \tau} \right)^c}. \tag{11}$$

Differentiating Eq. [9],

$$\frac{d^2W}{dt^2} = \frac{c}{(t + \tau)^2} W \left(1 - \frac{W}{W_f} \right) \left[c \left(1 - \frac{2W}{W_f} \right) - 1 \right].$$

Therefore, a point of inflection occurs when the term in the square brackets is zero, i.e.,

$$W = W^* = \frac{c - 1}{2c} W_f.$$

Substituting this value of W into Eq. [11], the point of inflection occurs at time

$$t = t^* = \tau \left[\sqrt[c]{\frac{c - 1}{c + 1} \left(\frac{W_f}{W_0} - 1 \right)} - 1 \right].$$

The species-area relationship of ecology (Lomolino, 2000),

$$y = \frac{y_{\max}}{1 + s^{\ln(x_{50}/x)}}, \tag{12}$$

$$\frac{dy}{dx} = \frac{\ln s}{y_{\max} x} y (y_{\max} - y), \tag{13}$$

where y denotes species richness, x is land area, and parameters s (>0) and x_{50} are a measure of the slope of the curve at the point of inflection and the area yielding a richness of 50% of the maximum, respectively, follows a trajectory similar to that of Eq. [11] when $c = \ln s$ and $\tau \rightarrow 0$ (compare Eq. [9] and [13]). Also, Eq. [12] can be written in the alternative form

$$y = \frac{y_{\max}}{1 + \left(\frac{x_{50}}{x} \right)^b}, \tag{14}$$

where $b = \ln s$. A variable point of inflection occurs when $d^2y/dx^2 = 0$. This occurs when

Table 1. Mathematical equations fitted to ostrich growth data

Growth function	Functional form ¹
Monomolecular ²	$W = W_f - (W_f - W_0)e^{-kt}$
Gompertz ²	$W = W_0 \exp \left[\frac{k}{D} (1 - e^{-Dt}) \right]$
Richards ²	$W = \frac{W_0 W_f}{\left[W_0^n + (W_f^n - W_0^n) e^{-kt} \right]^{1/n}}$
Michaelis-Menten ²	$W = \frac{W_0 \tau + W_f t}{\tau + t}$
Generalized Michaelis-Menten (aka López) ²	$W = \frac{W_0 \tau^q + W_f t^q}{\tau^q + t^q}$
Pareto	$W = W_f - (W_f - W_0) \left(\frac{\tau}{t + \tau} \right)^c$
Extreme value distribution	$W = W_f \left\{ 1 - \left[\frac{W_f - W_0}{W_f} \exp(e^D) \right] \exp(-e^{kt+D}) \right\}$
Cumulative β -P distribution	$W = W_f - (W_f - W_0) \left[1 + \left(\frac{t}{\tau} \right)^q \right]^{-c/q}$
Lomolino	$W = \frac{W_0 W_f}{W_0 + (W_f - W_0) \left(\frac{\tau}{t + \tau} \right)^c}$

¹Symbols: W_0, W_f initial and final weights; k (>0), rate parameter; τ (>0), time parameter; c (>0), $N \geq -1$, D, q , other parameters.

²From Thornley and France (2007, chapter 5).

$$x = x^* = x_{50} \sqrt[b]{\frac{b - 1}{b + 1}}$$

$$y = y^* = \frac{(1 - 1/b)}{2} y_{\max},$$

Equation [14] is equivalent to the generalized Michaelis-Menten growth function with initial weight W_0 set at zero (López et al., 2000). Using Eq. [10] to substitute for $t + \tau$ in Eq. [9] gives the rate:state form:

$$\frac{dW}{dt} = \frac{c}{\tau} \sqrt[c]{\frac{W_0 W^{c-1} (W_f - W)^{c+1}}{W_f^c (W_f - W_0)}}.$$

Comparative Analysis

The Functions. Nine functions (Table 1) were assessed using ostrich and cattle growth data. Five of these functions, namely, monomolecular, simple (**MM**) and generalized (**gMM**) Michaelis-Menten, Gompertz, and Richards, have been used widely to fit animal growth data (Thornley and France, 2007). The other 4 functions, namely, Pareto distribution (Eq. [3]), extreme value distribution (**EVD**; Eq. 6), cumulative β -P distribution (**CBP**; Eq. [8]), and Lomolino (Eq. [11]), were derived and discussed in the previous section.

Table 2. Summary of data used to compare growth functions

Item	No. of birds	No. of data points	Observations per bird	Interval between consecutive records, wk	Age, wk		Weight, kg	
					Initial	Final	Initial	Final
Commercial farm data								
Data set 1: Males	5	50	10	3 to 8.6	1.4	60	1.1 to 1.4	90 to 95
Data set 2: Females	35	327	9 to 10	3 to 8.6	1.4	60	1.1 to 1.4	87 to 93
Experimental farm data								
Data set 3: Growing females	15	138	8 to 10	4 to 6	15	55	26 to 40	85 to 125
Data set 4: Young chicks	21	105	5	1	0	4	0.8 to 1.1	2.9 to 4.2

The Data. The data were obtained from 3 sources: one was a commercial farm (Africa Atruches, Sidi Bou Ali, Tunisia), and the other 2 were trials conducted at the experimental farm of the Ecole Supérieure d'Agriculture de Mograne (Mograne, Zaghuan, Tunisia).

The data from the commercial farm comprised 377 weight records from 5 male and 35 female ostriches (*Struthio camelus australis*). First weight was recorded when the chicks were 10 d old, and subsequently, all birds were weighed at 1, 2, 3, 4, 6, 8, 10, and 12 mo of age. In addition, the weights for 12 of the females and for all the males were recorded at 14 mo of age. Birds were fed concentrate feeds ad libitum (starter from 4 d after hatching until 6 mo and grower from 6 to 12 to 14 mo).

The data from the experimental farm were from 2 different trials, and female ostriches (*Struthio camelus australis*) were used in both. One set of data comprised 138 weight records from 15 ostriches (8 to 10 records per bird) between 15 and 55 wk of age. The birds were maintained in individual stalls (35 × 4 m²) and were fed a mixture of germinated barley grain, alfalfa, and a concentrate feed. The other set of data comprised 105 data points from 21 chicks weighed weekly from hatching (artificially) to 4 wk of age (5 records per chick). From d 4, chicks were fed ad libitum a mixture of a granulated concentrate feed, leaves from *Medicago arborea*, and crumbled hard-boiled egg. The ostrich growth data from each source are summarized in Table 2.

Sample growth data for cattle were also used in evaluating the newly derived growth functions. Average growth for 2 breeds of cattle, namely Charolais (beef cattle) and Holstein (dairy cattle), were taken from López et al. (2000). Each curve contained 19 observations of weight, recorded monthly from calving to 3 mo of age and then every 3 mo until 48 mo of age.

Comparison 1: Fit to Individual Growth Curves. The first comparison between growth functions was based on goodness of fit to the individual growth curves of 2 data sets (a total of 40 individual curves, 5 for ostrich males and 35 for females, with 9 to 10 data points each from 1.4 to 60 wk of age; see Table 2). All the functions were fitted to the data by nonlinear regression using the NLIN procedure of SAS (SAS Inst. Inc., Cary,

NC). Statistical criteria used to evaluate goodness of fit were root-mean-square error (RMSE), R^2 , Akaike information criterion (AIC), and corrected AIC (AIC_c). The Durbin-Watson statistic (DW), accuracy and bias factors, and number of runs of sign were used to analyze the residuals obtained when each curve was fitted.

A similar comparison among all 9 functions was conducted using the sample growth data for 2 cattle breeds. Goodness of fit was assessed using residual mean squares (RMS), R^2 , RMSE, AIC, and AIC_c.

Comparison 2: Fitting Mixed Models. In this comparison, the functions were fitted to a pooled set of 570 data points (corresponding to all the records for the 71 female ostriches included in data sets 2 to 4; Table 2). The NLMIXED procedure of SAS (SAS Inst. Inc.) was used to fit the models employing 3 different approaches:

1) No random effects were included in the model. Each function only contained fixed-effect parameters, and residual errors e_j (subscript j denotes observation) were assumed to be $N(0, \sigma_e^2)$.

2) Each function was fitted with fixed-effect parameters and a random-effect intercept u_i .

3) Each function was fitted with fixed-effect parameters, and a random effect of animal u_i was incorporated into the W_f parameter (asymptotic weight).

In approaches 2 and 3, the random effect u_i (where i denotes each individual animal or growth curve) was assumed to be $N(0, \sigma_u^2)$, and residual errors e_{ij} (i is animal and j is observation within each animal) were taken to be $N(0, \sigma_e^2)$ and independent of u_i . In both cases, the random-effect parameters u_i entered the model linearly.

The performance of each approach was assessed within each function based on AIC_c and residual variance. Comparison between models within the best approach was also based on AIC_c. The estimates of W_f , W_0 , and age (t^*) and weight (W^*) at point of inflection were estimated using the different functions.

RESULTS AND DISCUSSION

Modeling growth patterns of animals is important for optimizing their management and efficiency

of production. There are many studies dealing with modeling the growth of livestock to improve their husbandry and care. The Gompertz, Richards, and monomolecular equations are considered classical growth functions and have been used extensively to describe growth of farm animals (Cilliers et al., 1995; Aggrey, 2002; Nahashon et al., 2006). The gMM was derived by López et al. (2000) by reparameterization of the Michaelis-Menten equation. The Lomolino function, EVD, and CBP were applied and developed in the ecological sciences for the relationship between species and area (Scheiner, 2004). However, these 3 functions have rarely been used to study growth patterns (Faridi et al., 2014). To our knowledge, ours is the first study to derive Pareto, EVD, CBP and Lomolino equations from basic principles to be used as functions to interpret animal growth data. These functions are evaluated and compared with popular growth equations (Thornley and France, 2007) by fitting them to growth data from ostriches. This avian species has received relatively little attention despite ostrich farming being considered among the most profitable of agricultural enterprises (Shanawany, 2014). Ostriches are raised commercially for their meat, hide, and feathers. They produce red meat, similar in taste and texture to veal and beef depending on age of slaughter, that is higher in protein and lower in fat and cholesterol than either beef or chicken. Sample growth data from cattle were also used in the analysis, with the aim of extending the comparison to more conventional farm species.

Results observed with ostrich growth curves will be described first. Suitable initial values for the parameter estimates needed to be provided to achieve convergence within a reasonable number of iterations. If the initial values were very different from the final estimates, the regression algorithm failed to converge in some cases. Results showed that convergence was easily achieved with the monomolecular, MM, EVD, Gompertz, and Pareto functions for all growth curves. Estimates of W_0 , if left unconstrained, were negative with the non-sigmoidal functions (monomolecular, MM, Pareto) and with the EVD function. The Richards function was sensitive to initial values, and problems occurred when W_0 was small (in 25/40 curves). In these situations, a reparameterized Richards function was fitted so that W_0 was omitted from the equation and t^* became the fourth parameter. Previous animal growth studies have also reported difficulties in fitting the Richards function (López et al., 2000; Porter et al., 2010). The gMM was easy to fit, but in 14/40 curves, W_0 was negative. The Lomolino equation could not be fitted effectively when W_0 was close to zero (26/40 curves). In these cases W_0 had to be set at an arbitrarily small value to obtain a solution. The CBP failed to converge for 10/40 curves,

with W_f increasing in successive iterations. In such cases we limited the number of iterations. The goodness of fit was not noticeably affected, but the solutions cannot be considered definitive. The CBP also gave unrealistically high values of W_f for a further 24 curves.

Fitted lines obtained with the 9 candidate functions are shown in Fig. 1 and 2 for representative individual male and female ostrich growth curves, respectively. The 3 diminishing returns functions (monomolecular, MM, Pareto) exhibited similar behavior, with a negative intercept on the y axis and a trend toward increasing weight at mature age without approaching an upper asymptote. The Pareto and monomolecular functions produced almost identical fits to the growth curves in data set 1. With the exception of the EVD, the sigmoidal functions exhibited similar fitted curves for all the growth profiles. The EVD has an inflection point at a later age than the other functions, resulting in a negative intercept and a slightly lower upper asymptote. The other 5 sigmoidal functions showed appreciable differences in the position of the inflection point, but visual assessment of the fitted lines revealed that the values were, in general, close to observed data points for all functions, with small differences among them that can be determined only by statistical analysis of goodness of fit.

There is no means of recommending a priori what equation to use in any given case (Motulsky and Ransnas, 1987). Therefore, the growth functions investigated here were compared using well-established goodness of fit indices. The results for the comparison of fit of 9 functions to 40 individual growth curves are shown in Table 3. All the functions yielded significant R^2 values, ranging from 0.977 to 0.999. However, the diminishing returns (monomolecular, MM, Pareto) and EVD functions gave smaller values of R^2 than the other sigmoidal functions. The smallest RMSE were obtained with CBP and Lomolino functions (Table 3). Mielke and Johnson (1974) claimed that the CBP possesses very desirable computational properties because it is very flexible and has great ability to fit data sets closely, although a function giving a good fit for some curves may not do so for others. The conventional EVD function (no intercept) has a fixed inflection point that occurs at 63.2% of its asymptote (Tjørve, 2009). The EVD derived herein has an additional parameter and is therefore more flexible regarding the inflection point, but the inflection point still occurs at a heavier weight than with other the functions. This difference probably explains the relatively poor performance of the EVD when applied to our growth data. Considering AIC values, all the sigmoidal functions except for EVD outperformed the diminishing returns equations (Table 3). These sigmoidal functions (Gompertz, Richards, gMM, Lomolino, CBP) seem to be appropriate for describing ostrich growth patterns, with

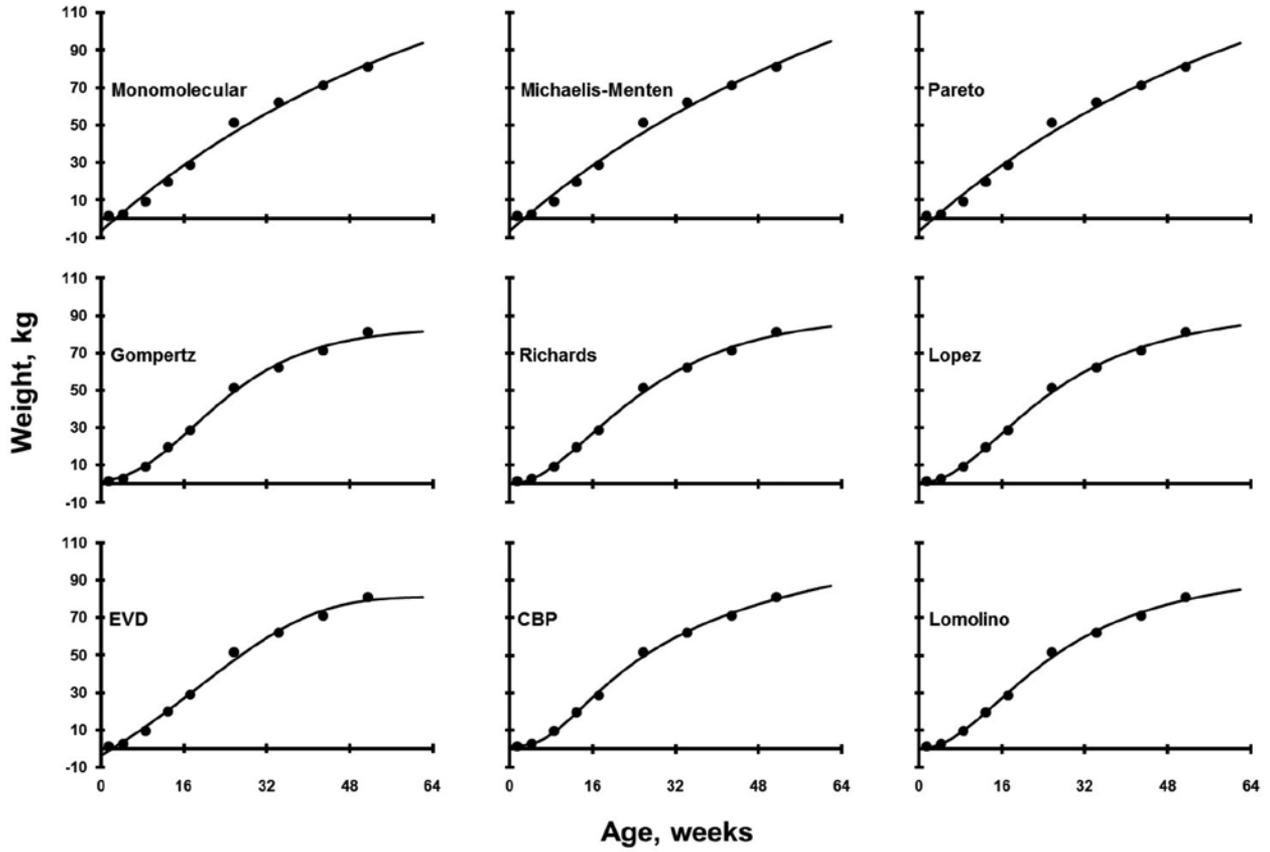


Figure 1. Observed (dots) and fitted (solid line) values for a randomly selected individual male ostrich growth curve. EVD: extreme value distribution; CBP: cumulative beta- P distribution.

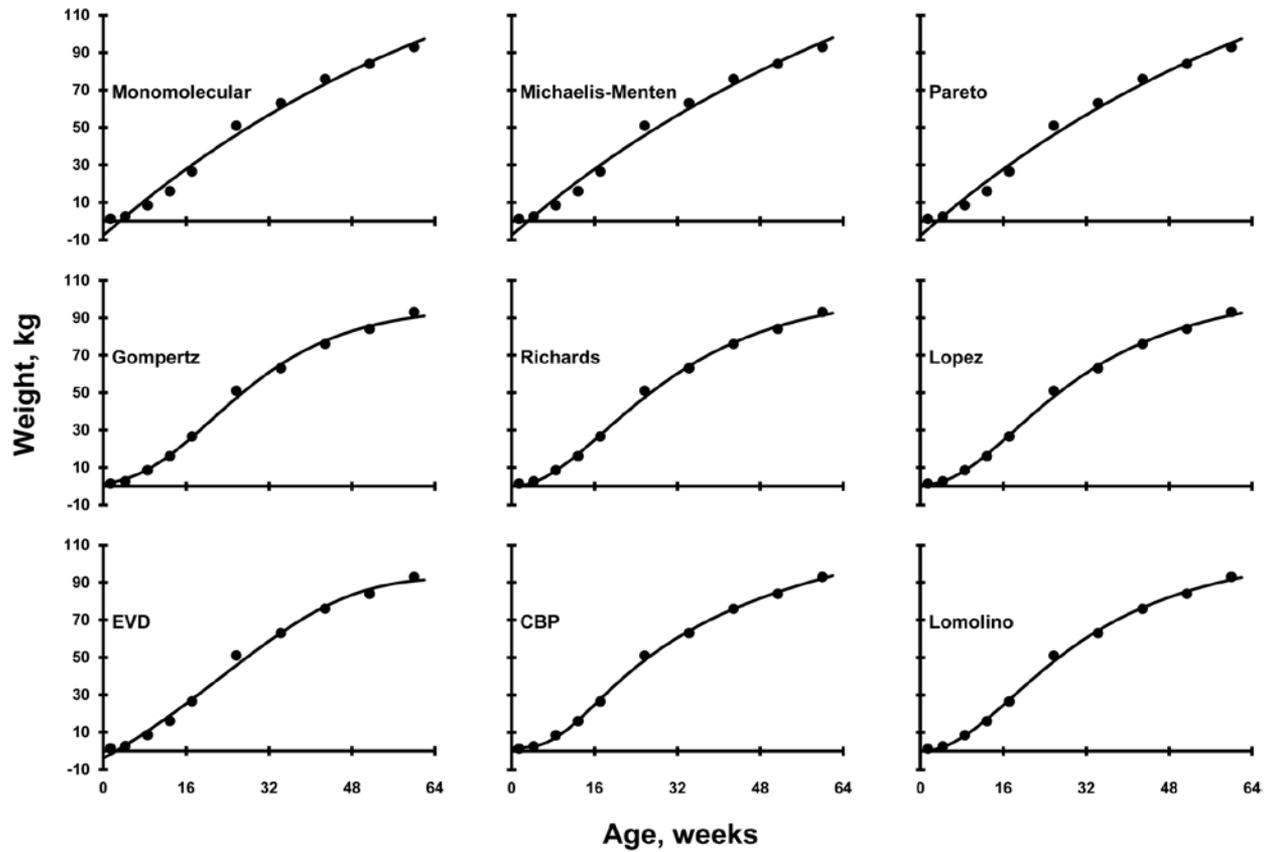


Figure 2. Observed (dots) and fitted (solid line) values for a randomly selected individual female ostrich growth curve. EVD: extreme value distribution; CBP: cumulative beta- P distribution.

Table 3. Goodness of fit statistics for comparison 1

Goodness of fit statistic ¹	Growth function ²								
	MON	MM	PAR	EVD	GOM	RIC	gMM	LOM	CBP
RMSE									
Mean	16.97	17.54	20.12	11.10	6.40	4.72	4.35	4.00	3.72
Minimum	8.14	8.42	9.50	5.87	2.87	1.78	1.67	1.40	1.31
Maximum	32.28	32.63	38.74	19.24	11.79	9.36	8.92	7.65	7.22
Average rank	6.9	8.0	9.0	6.0	4.8	4.1	2.6	2.3	1.6
No. with smallest RMSE	0	0	0	0	0	0	7	4	29
R²									
Mean	0.988	0.987	0.988	0.993	0.996	0.997	0.997	0.997	0.998
Minimum	0.977	0.977	0.977	0.989	0.992	0.995	0.995	0.995	0.996
Maximum	0.994	0.994	0.994	0.996	0.998	0.999	0.999	0.999	0.999
AIC									
Mean	57.2	57.5	59.2	53.8	47.8	45.3	44.6	43.5	43.0
Minimum	49.3	49.4	51.3	46.2	39.4	35.1	34.9	32.9	32.7
Maximum	66.0	66.4	68.0	62.8	57.3	55.5	55.2	53.2	53.2
Average rank	6.9	7.9	9.0	6.0	4.6	4.0	2.7	2.2	1.8
AIC_c									
Mean	66.3	66.6	77.0	71.7	56.9	63.1	62.5	56.0	79.0
Minimum	59.3	59.4	70.8	66.2	49.4	55.1	54.9	42.9	68.1
Maximum	74.0	74.4	83.2	77.8	65.3	70.5	70.2	66.7	90.0
Average rank	4.6	5.6	8.4	7.2	1.8	4.2	3.2	1.8	8.4
AIC weight									
Mean	—	—	—	0.003	0.070	0.113	0.159	0.281	0.374
Minimum	—	—	—	0.000	0.002	0.041	0.049	0.099	0.099
Maximum	—	—	—	0.014	0.282	0.194	0.280	0.467	0.770
AIC_c weight									
Mean	—	—	—	0.000	0.364	0.009	0.014	0.613	0.000
Minimum	—	—	—	0.000	0.007	0.001	0.002	0.005	0.000
Maximum	—	—	—	0.001	0.985	0.065	0.134	0.981	0.001

¹RMSE: root-mean-square error; AIC: Akaike information criterion; AIC_c: corrected AIC.

²MON: monomolecular; MM: Michaelis-Menten; PAR: Pareto; EVD: extreme value distribution; GOM: Gompertz; RIC: Richards; gMM: generalized MM; LOM: Lomolino; CBP: cumulative β -P.

small differences between them. Discrimination between the functions was possible using AIC_c to assess goodness of fit (Table 3). On the basis of this index, the functions with fewer parameters (Gompertz, Lomolino) gave the best fit across the 40 curves. The AIC and AIC_c weights were also used to compare goodness of fit of the sigmoidal functions (Table 3), showing that differences among the functions for weights >0.1 were small, and evidence ratios derived from the weights (not shown) failed to suggest a strong case against any of these functions, so all (Richards, gMM, Lomolino, CBP) may be considered appropriate. The evidence ratios calculated from AIC_c indicated that the Lomolino and Gompertz equations would be the best choices to fit our growth curves. All the sigmoidal functions again seemed appropriate, but as the curves had only 9 or 10 data points, functions with more parameters were penalized by the AIC_c criterion. These functions could well be useful for growth curves with more data points, whereas functions having fewer parameters are clearly more appropriate if the number of data points is limited. The AIC_c criterion favored the

Lomolino function because when the fit converged to a solution with W_0 preset, the model was deemed to have 3 parameters and thus was not penalized.

Results of the analysis of residuals for the comparison across 40 individual growth curves are summarized in Table 4 for the sigmoidal functions. Bias and accuracy factors are indices of closeness between observed and predicted values (best when indices equal unity). Functions resulting in negative or very small (close to zero) predicted values at $t = 0$ or early age are penalized for both bias and accuracy. This is the reason for weak bias or accuracy factors (bias < 1 and accuracy > 1) obtained with the EVD, Richards, gMM, Lomolino, and CBP functions. The DW statistic is used to test serial correlation and random distribution of the residuals and thus whether a function is successful in describing the underlying trend. A significant DW value indicates there is serial correlation because of the presence of cycles in the plot of residuals (López et al., 2004). As Table 4 shows, all functions generally behaved well, and only the CBP showed evidence of

Table 4. Analysis of residuals for the sigmoidal functions used in comparison 1

Item	Growth function ¹					
	EVD	GOM	RIC	gMM	LOM	CBP
Bias						
Mean	0.82	1.10	0.80	0.91	0.87	1.01
Minimum	0.78	0.91	0.70	0.70	0.70	0.96
Maximum	0.85	1.20	0.97	1.01	0.99	1.04
Accuracy factor						
Mean	2.28	1.27	1.99	1.53	1.61	1.10
Minimum	2.12	1.07	1.19	1.04	1.17	1.03
Maximum	2.44	1.49	2.43	3.37	2.47	1.22
Durbin-Watson (DW)						
Mean	1.93	2.05	2.47	2.48	2.48	2.86
Minimum	1.52	1.27	1.76	1.77	1.73	1.87
Maximum	2.60	2.89	3.13	3.16	3.16	3.31
No. of curves with significant DW ($P < 0.05$)	0	2	0	0	0	8
Number runs of sign						
3	0	60	0	0	0	0
4	100	15	60	52.5	60	10
5	0	25	0	2.5	0	67.5
6	0	0	40	45	40	17.5
7	0	0	0	0	0	5

¹EVD: extreme value distribution; GOM: Gompertz; RIC: Richards; gMM: generalized Michaelis-Menten; LOM: Lomolino; CBP: cumulative β -P.

autocorrelation (in 8/40 curves). The number of runs of sign test evaluates random distribution of residuals (Motulsky and Ransnas, 1987). A smaller number of runs of sign is obtained when the residuals are not randomly distributed, so that residuals of the same sign tend to cluster together on certain parts of the curve. The Gompertz and EVD functions showed the worst random distribution of residuals according to the number of runs of sign observed (Table 4).

For the comparison of functions when fitted to the pooled set of 570 data points using mixed models, goodness of fit (i.e., AIC_c , residual variance) and parameter estimates obtained are presented in Table 5. Incorporating a random animal effect into W_f (approach 3) provided the best fit with all functions, resulting in smaller AIC and AIC_c than the other 2 approaches (i.e., mixed models either with no random animal effect or with a random intercept). The AIC_c values show the sigmoidal functions provided better fits to the growth data than the diminishing returns functions. There was clear indication that the nonsigmoidal functions are inappropriate for fitting ostrich growth curves. Among the sigmoidal functions, CBP provided the best fit, and the EVD, Gompertz, and Lomolino functions provided the worst fits (Table 5). In this mixed-model analysis, growth data for 71 individual birds were amalgamated and used; therefore, a large number of data points (570 points) was available. In such a situation, the number of parameters a function possessed was not a problem, and equations were hardly penalized for having more parameters when AIC_c was calculated. The monomolecu-

lar, MM, Pareto, and EVD functions resulted in negative estimates for W_0 . Only the Gompertz, CBP, and, to a lesser extent, gMM functions gave estimates of W_0 close to observed values (0.957 kg; SE = 0.023). The other functions (Richards, Lomolino) gave estimates of $W_0 \leq 0$. Negative or insignificant estimates of W_0 should be considered a weakness of a particular growth function, reflecting limited adaptability at early ages. Mature weight W_f was unrealistically overestimated with some of the functions (monomolecular, MM, Pareto, CBP) and appeared slightly underestimated with others (EVD, Gompertz). The other functions seemed to provide more appropriate estimates. On the basis of ostrich growth curves reported by du Preez et al. (1992) and Sabbioni et al. (1999), weight of 1-yr-old birds appears to represent, on average, 0.80 of mature weight. Imposing bounds on the initial and final weights, namely, $W_0 > 0$ and $W_f < 1.25 \times$ weight at 1 yr, taking them either together or individually, failed to improve the goodness of fit or alter the relative performance and ranking of the models. Time to inflection t^* varied from 15 wk (CBP) to 21 wk (EVD). Cooper and Mahroze (2004) determined maximum weight gain at 28.4 wk of age for ostrich hens using the Gompertz function. Ramos et al. (2013) estimated the inflection point to be at 24.3 wk (Gompertz) or at 26.4 wk (logistic) of age, showing that it is model dependent. Time and weight at inflection can vary in different studies depending on the growing conditions (environment and feeding).

All the growth functions were fitted to sample data for cattle. The goodness of fit statistics (i.e., R^2 , RMSE,

Table 5. Goodness of fit (corrected Akaike information criterion, AIC_c) and parameter estimates for comparison 2

Item	Model ¹								
	MON	MM	PAR	EVD	GOM	RIC	gMM	LOM	CBP
Approach 1 (no random effect)									
AIC_c	4,014	4,019	4,025	3,919	3,893	3,892	3,887	3,888	3,888
Residual variance	66.0	66.6	67.0	55.7	53.4	52.9	52.6	52.7	52.5
Approach 2 (random effect incorporated as intercept)									
AIC_c	3466	3,473	3,471	3,292	3,220	3,212	3,203	3,210	3,203
Residual variance	17.2	17.5	17.4	12.7	10.6	10.4	10.2	10.4	10.2
Approach 3 (random effect incorporated in W_f)									
AIC_c	3,291	3,299	3,293	3,121	3,065	2,935	2,921	3,136	2,882
Residual variance	13.5	13.7	13.5	9.79	8.88	6.86	6.68	9.96	6.17
Parameter estimates									
Initial weight W_0 , kg	-4.33	-4.28	-4.33	-2.54	1.60	4.2×10^{-18}	0.43	2.0×10^{-5}	1.16
SE	0.321	0.326	0.321	0.288	0.207	—	0.234	—	0.232
Final weight W_f , kg	234.8	436.1	236.5	94.5	95.9	110.4	124.3	117.3	274.3
SE	13.08	27.7	14.03	1.91	1.71	2.7×10^{-5}	3.26	1.5×10^{-4}	50.63
Age at inflection t^* , wk	—	—	—	21.1	20	16.1	16.6	16.2	14.9
Weight at inflection W^* , kg	—	—	—	38.5	35.3	27.8	28.8	28.3	24.6

¹MON: monomolecular; MM: Michaelis-Menten; PAR: Pareto; EVD: extreme value distribution; GOM: Gompertz; RIC: Richards; gMM: generalized MM; LOM: Lomolino; CBP: cumulative β -P.

AIC , and AIC_c) are presented in Table 6. These statistics demonstrate that the relative performance of all the functions considered was very similar for both the ostrich and cattle data, verifying the applicability of the new functions across species.

Results of the present study have shown that the novel growth functions developed herein appear capable of describing the growth curves of animals such as the ostrich (and cattle), despite the EVD, CBP, and Lomolino functions having been adopted primarily for the study of the species-area relationship in ecology. The results obtained, however, should be interpreted with an element of caution as the data used, although novel, are nonideal. The ideal data set would contain weights from hatching to 5 yr of age (data points at ages close to mature weight being desirable); weights should probably be more frequent near hatching and less frequent as maturity is approached (Cilliers et al., 1995). Such data sets are rarely available for almost

any agriculturally relevant species. Nonetheless, the new functions appear flexible enough to be considered potential alternatives to classical growth equations such as the Gompertz and Richards functions. Like their classical counterparts, these functions benefit from the advantage of having relatively few parameters. More parameters in a model are something of a mixed blessing. On the one hand, such models are more flexible, but on the other, they are more prone to difficulty when fitting (Faridi et al., 2011). The criterion of choosing the function with fewer parameters is, of course, an application of that long-established maxim Occam's razor (Thorburn, 1915). As a result of the mathematical derivation, biological meaning can be ascribed to the parameters of the novel functions. The parameters of a growth function should be capable of being ascribed meaning. Using a function that makes biological sense has much more to recommend it than a mathematical equation that only provides a close fit

Table 6. Goodness of fit to the average growth curves reported by López et al. (2000) for 2 breeds of cattle¹

Item	R^2		RMS		RMSE		AIC		AIC_c	
	Charolais	Holstein								
MON	0.994	0.993	965.5	758.2	28.5	25.3	189.2	184.6	192.1	187.5
MM	0.990	0.987	1,619.2	1,339.6	36.9	33.6	199.1	195.5	201.9	198.3
PAR	0.994	0.992	1,093.9	875.4	29.4	26.3	192.4	188.2	197.0	192.8
EVD	0.982	0.984	3,094.0	1,777.7	51.0	38.7	287.9	200.8	290.7	203.7
GOM	0.999	0.999	164.1	79.1	11.8	8.2	155.6	141.7	158.4	144.5
RIC	0.999	1.000	93.9	55.0	8.6	6.6	145.7	135.6	150.3	140.2
gMM	1.000	0.999	47.8	56.5	6.1	6.7	132.9	136.1	137.5	140.7
LOM	1.000	1.000	48.9	25.9	6.2	4.5	133.4	121.2	138.0	125.8
CBP	1.000	1.000	48.3	45.8	6.0	5.8	150.4	132.8	157.4	139.8

¹RMS: residual mean squares; RMSE: root-mean-square error; AIC: Akaike information criterion; AIC_c : corrected AIC; MON: monomolecular; MM: Michaelis-Menten; PAR: Pareto; EVD: extreme value distribution; GOM: Gompertz; RIC: Richards; gMM: generalized MM; LOM: Lomolino; CBP: cumulative β -P.

to the data. Although important, goodness of fit alone is not a justification for adopting a given function as several others may fit the data equally well (Kowalski and Guire, 1974).

Conclusions

In summary, the growth functions introduced here (Pareto, EVD, Lomolino, and CBP) can serve as alternatives to classical equations such as the monomolecular, Gompertz, and Richards functions in describing the BW of food-producing and other animals over time. These functions possess desirable attributes such as flexibility and relatively few parameters, each with biological interpretation. However, this is probably the first study to apply these generalized equations to animal growth patterns, and therefore, further comparative application of these functions to different animal species is recommended.

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