Research Article

Models for Population Growth Curves

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We examined models for population growth curves, contrasting integrated versions with various other forms. A sizable number of data sets for birds and mammals were considered, but the main comparisons were based on 27 data sets that could be fit to the generalized logistic curve. Akaike's information criterion was used to rank fits of those data sets to 5 integrated models. We found that the integrated models gave the best fits to the data examined. The difference equations examined gave much poorer fits as judged by AICc and coefficients of variation. We conclude that the integrated models should be used when possible.

1. Introduction

Most recent use of population growth curves has focused on difference equation models (also called "finite population models"). Such models may give a somewhat wider scope for applications and for theory, than do the integrated versions of these models. However, the available integrated versions appear to give much better fits to actual growth curve data, raising some questions about the practical utility of the difference equation versions. We thus examine a number of integrated and difference equation models in this paper. The data used are for birds and mammals. Rather different results may apply for insects and some species of fish.

2. Methods

2.1. Models. The first of the integrated models used here, the generalized logistic reported by Nelder [16] and by Pella and Tomlinson [17], but best known from Ayala et al. [18], and often termed the theta-logistic is:

$$N(t) = [K^{-z} - (K^{-z} - N_0^{-z})e^{-rt}]^{-1/z}. \quad (1)$$

The corresponding difference equation is

$$N(t) = N(t-1) + rN(t-1) \left[1 - \left(\frac{N(t-1)}{K} \right)^z \right]. \quad (2)$$

A rearrangement of (2) is designated here as the "Sibly model" [19–22]:

$$\text{pgr} = \left[\left(\frac{N(t)}{N(t-1)} \right) - 1 \right] = r \left[1 - \left(\frac{N(t-1)}{K} \right)^z \right]. \quad (3)$$

The Gompertz curve is

$$N(t) = K \exp \left(\log \left(\frac{N_0}{K} \right) e^{-ct} \right). \quad (4)$$

The difference equation in the form used by Dennis et al. [23] is

$$N(t) = N(t-1) \exp(r + b \log(N(t-1))). \quad (5)$$

The logistic growth curve is obtained by setting $z = 1$ in (1):

$$N(t) = \frac{K}{1 + ce^{-rt}}, \quad c = \frac{K}{N_0} - 1. \quad (6)$$

The difference equation is

$$N(t) = N(t-1) + rN(t-1) \left[1 - \left(\frac{N(t-1)}{K} \right) \right]. \quad (7)$$

The exponential model is

$$N(t) = N_0 \exp(rt). \quad (8)$$

TABLE 1: Comparison of the generalized logistic (1) with the corresponding difference equation (2) and the ordinary logistic (6) compared with the corresponding difference equation (7). Numbers in square brackets refer to references and other numbers are GPDD numbers. Values given are residual mean squares from the fits.

Source	Generalized logistic	Difference equation	Ratio	Logistic	Difference equation	Ratio
Red deer 6585	2.16	2.47	1.14	3.1	2.8	0.90
Gray fox 319	283	591	2.09	378.2	566.7	1.50
Gray fox 342	1311	1440	1.10	1254	1399	1.12
Coyote 263	2528	2729	1.08	2451	2681	1.09
Gray seals [1]	56.83	93.2	1.64	65.93	90.88	1.38
Bison [2]	5.81	7.86	1.35	5.64	7.81	1.38
Macaque 6068	1.11	1.32	1.19	1.45	1.43	0.99
Beaver 151	15960	16490	1.03	15850	16410	1.04
Beaver 156	40960	43800	1.07	43400	44070	1.02
Elephant seals [3]	48.61	63.44	1.31	50.06	62.79	1.25
Seneca deer [4]	29.93	50.78	1.70	28.99	50.44	1.74
Badger 78	375	453	1.21	372.5	438.8	1.18
Gentoo penguins (Fraser pers. comm.).	61.19	113.2	1.85	57.88	108.6	1.88
Polar bear 143	89.9	68.1	0.76	95.09	67.49	0.71
Coyote 247	308	380	1.23	335.7	362.4	1.08
Gray fox 328	549.3	901.3	1.64	526.1	850.1	1.62
Marten 9695	17020	22010	1.29	16630	22390	1.35
Squirrel 9699	347100	393400	1.13	339100	398500	1.18
Gray fox 334	3383	3332	0.98	3280	3155	0.96
Camargue horses [5]	0.58	1	1.72	1.42	1.74	1.23
Argentine horses [6]	5.01	8.04	1.60	5.38	7.8	1.45
Przewalski's horses [5, 7]	0.89	1.39	1.56	1.23	1.47	1.20
Red kite [8]	3.27	4.56	1.39	3.2	4.46	1.39
Medians and Mean Ratios	89.9	113.2	1.35	95.09	108.6	1.20

TABLE 2: Contrast of fit to Gompertz (4) with difference equation (5) using residual mean squares.

Source	Gompertz	Difference equation	Ratio
Red deer 6585	4.01	3.5	0.87
Gray seals [1]	68.58	91.91	1.34
Bison [2]	6.34	7.59	1.20
Macaque 6068	1.57	1.5	0.96
Beaver 156	46930	46160	0.98
Elephant seals [3]	62.24	69.86	1.12
Seneca deer [4]	35.4	53.87	1.52
Badger 78	392.7	487	1.24
Gray fox 328	569.8	867.9	1.52
Marten 9695	16850	23060	1.37
Camargue horses [5]	1.84	2.49	1.35
Argentine horses [6]	5.67	8.18	1.44
Przewalski's horses [5, 7]	1.4	1.68	1.20
Mean			1.24

The difference equation is

$$N(t) = N(t-1) + rN(t-1). \quad (9)$$

The equation of Morris and Doak [24] is

$$\hat{\mu} = \left(\frac{1}{q}\right) \sum_{i=0}^{q-1} \log\left(\frac{N_{i+1}}{N_i}\right) \quad (10)$$

with variance estimate:

$$\text{var } \hat{\mu} = \left(\frac{1}{q-1}\right) \sum_{i=0}^{q-1} \left(\log\left(\frac{N_{i+1}}{N_i}\right) - \hat{\mu}\right)^2. \quad (11)$$

In the notation used here $\mu = r$. A modification of (1), with $z = 2$, is considered here, as it has significant advantages. It is here denoted as a modified logistic:

$$N(t) = [K^{-2} - (K^{-2} - N_0^{-2})e^{-2rt}]^{-1/2}. \quad (12)$$

In the aforementioned models, K is the asymptotic value, r is a rate of increase, z is the parameter controlling the inflection point in a growth curve, N_0 represents initial population size, and b and c are functions of r and K in the Gompertz equations. The models have been fit by using nonlinear least-squares, [25], as implemented in the R-language [26].

TABLE 3: Contrasts between the Sibly model (3) and the corresponding difference equation (2). Due to structural differences in the models, coefficients of variation are used for contrasts. An asterisk (*) indicates cases where counts reached or closely approximated an asymptotic value (K).

Source	Difference equation K	CV (K)	Sibly model K	CV (K)	Generalized logistic K
Red deer 6585*	166	0.020	167	0.028	168
Gray fox 319*	10520	0.052	10760	0.574	10600
Gray fox 342*	15590	0.003	15060	0.139	15290
Coyote 263*	19340	0.063	19120	0.173	19110
Gray seals* [1]	2044	0.155	2016	0.167	2013
Bison [2]	2120	1.314	no fit		1356
Macaque 6068*	24	0.026	24	0.054	24
Beaver 151*	156400	0.055	158500	0.057	164.500
Beaver 156*	422700	0.069	429300	0.083	421200
Elephant seals [3]	1752	0.072	no fit		1862
Seneca deer [4]	4134	0.396	2672	0.343	4425
Badger 78	2550	0.162	no fit		3009
Gentoo penguins (Fraser pers comm.)	949	0.534	no fit		1027
Polar bear 143	738	0.097	no fit		700
Coyote 247*	3273	0.046	3310	0.103	3231
Gray fox 328	9200	0.296	no fit		9723
Marten 9695	98330	0.062	no fit		104000
Squirrel 9699*	$2.19E + 06$	0.069	$2.04E + 06$	0.199	$2.17E + 06$
Gray fox 334	$3.59E + 05$	0.059	$3.54E + 05$	0.217	22790
Camargue horses* [5]	75	0.031	77	0.074	78
Argentine horses* [6]	209	0.051	209	0.069	213
Przewalski's horses* [5, 7]	44	0.093	43	0.131	44
Red kite [8]	139	7.45	no fit		182

2.2. *Akaike's Information Criterion.* AIC is calculated as [27]

$$AIC = n \log \hat{\sigma}^2 + 2k, \quad \text{where } \hat{\sigma}^2 = \frac{\sum \hat{e}_i^2}{n}, \quad (13)$$

the $\hat{e}_i$ are deviations (residuals) from the model fit (assumed to be normally distributed), n is sample size, and k is the number of parameters in the model plus 1. Most of the available data sets have small samples, so Burnham and Anderson [27] recommended using

$$AIC_c = AIC + \frac{2k(k+1)}{n-k-1}. \quad (14)$$

Model comparisons are made using

$$\Delta_i = AIC_c - AIC_{\min}, \quad (15)$$

where $AIC_{\min}$ is the minimum value calculated for a set of models.

2.3. *Data Sources.* Part of the data used here was obtained in 2006 from the Global Population Dynamics Database (GPDD) maintained by the National Environmental Research Council at <http://www.sw.ic.ac.uk/cpb/gpdd.html>. ID numbers for data used from the GPDD appear in the

tables. Data sets from the GPDD were obtained by searching the entire data set (over 4000 entries) by inspecting plots of each data set and attempting to fit curves. An up-to-date version of the GPDD data was obtained in 2008 and searched for additional examples. Over 100 data sets were examined in detail, but those that could be fit to (1) are the primary data sets used here.

3. Results

3.1. *Integrated Models versus Difference Equations.* Table 1 contrasts the generalized logistic (1) with the corresponding difference equation (2), and the ordinary logistic (6) with its corresponding difference equation (7), using residual mean squares in consequence of the experience of Eberhardt et al. [28], who found that residual mean squares performed better on data similar to those used here. We believe that the “adjustment factor” of Burnham and Anderson [27] (in (14)) may discriminate against models with the larger number of parameters. In nearly all instances, the integrated version is to be preferred, as shown by residual mean squares. The two apparent exceptions in Table 1 have highly variable data.

Table 2 makes the same contrast for the Gompertz equation (4) with the corresponding difference equation (5).

TABLE 4: Estimates of the parameter z in (1).

Species	z	CV
Red deer 6585	3.89	0.720
Boar 9428	4.99	1.138
Gray fox 319	3.78	0.407
Gray fox 342	1.85	1.151
Coyote 263	1.93	1.482
Gray seals [1]	11.76	0.882
Bison [2]	0.75	0.627
Macaque 6068	16.26	1.545
Beaver 151	0.46	1.739
Beaver 156	7.43	1.027
Elephant seals [3]	1.86	0.360
Seneca deer [4]	0.69	0.652
Badger 78	1.76	2.290
Fur seals [9]	4.05	0.783
Blue Springs manatees [10]	5.08	2.108
Chinstrap penguins (Fraser, pers. commun.)	0.45	5.778
Gentoo penguins (Fraser, pers. commun.)	0.69	2.087
Polar bear 143	6.13	1.127
Coyote 247	6.42	1.673
Gray fox 328	1.88	1.293
Boar 9429	1.66	0.596
Marten 9695	1.2	1.892
Squirrel 9699	0.98	2.920
Gray fox 334	0.45	2.480
Camargue horses [5]	6.06	0.240
Argentine horses [6]	7.99	0.95
Przewalski's horses [5, 7]	6.81	0.690
Red kite [8]	1.47	3.380
Median	1.93	

Smaller samples are available due to the fact that the Gompertz did not fit a number of the data sets. That the “Sibly” model gives even more variable results is illustrated in Table 3, where the Sibly model (3) has a larger coefficient of variation in all cases where a comparison could be made, with the exception of the Seneca deer data which has essentially an exponential trend.

In those cases marked by an asterisk in Table 3, the estimates of the asymptotic value (K) are nearly the same for the difference equation (2), the Sibly model (3), and the generalized logistic (1). In all of these cases, the data reach an asymptotic value or closely approximate an asymptote. Coefficients of variation (standard error/ K) show that the “Sibly” model (3) gives much more variable estimates than do the other two models considered. These are cases where no gaps existed in the count data. The “Sibly” model does not accommodate isolated data points and has to be fit in segments (yielding more variable estimates), whereas the integrated models can be applied directly in such cases.

Table 4 gives estimates of the coefficient (z) governing the inflection point in the generalized logistic model, suggesting

FIGURE 1: Plot of r versus z from the 27 data sets that fit the generalized logistic model.

use of 2.0 in the modified logistic (12). Table 5 contrasts the 5 integrated models using AIC_c , showing that the modified logistic is generally superior. Clark et al. [29] found, using simulations, that there appeared to be a linear relationship between r and z in the generalized logistic model. Using our data set on birds and mammals, we found a correlation between r and z (-0.51) and a distinctly nonlinear relationship. The data appear in Figure 1.

Table 6 compares the Morris and Doak [24] ((10) and (11)) with exponential models fitted by nonlinear least-squares or a linear fit with log-transformation. The median values indicate that all 3 methods give much the same values, but the Morris and Doak approach is far more variable, as indicated by coefficients of variation. The coefficients of variation show essentially no difference between the two approaches using exponential models. It should be noted that the Morris and Doak estimator (10) can be used with virtually any data set giving nonsensical results in some cases (only exponential-type data were used in Table 6). Thus Morris and Doak [24] used 39 observations on the Yellowstone grizzly bear data, as shown in their Figure 3.6 and Table 3.1. The problem is that the population was initially decreasing and then, as protective measures began to take effect, started to increase in the early 1980s and continued to do so for the remainder of the series. Consequently, the resulting estimate of r (or μ) is of no practical value. Eberhardt and Breiwick [11] give details and cite 7 published papers that largely ignore the change in trend and thus give largely meaningless results.

3.2. Scope of Models. Clark et al. [29] extracted 99 data sets from the 1198 published by Brook and Bradshaw [20] using a set of criteria that included a minimum number (19) of “transitions” (used because they used difference equations), so all of the data they used had at least 20 observations. This data set contained 42 cases involving birds and mammals, which we screened with linear regression, of which 20 could

TABLE 5: Contrasting the 5 integrated models using AIC_c and Δ_i . Zeros indicate minimum AIC_c (15).

Species		Sample size	Generalized logistic	Modified logistic	Logistic	Exponential	Gompertz
Red deer 6585	<i>Cervus elaphus</i>	13	0	0.85	13.77	13.14	13.46
Gray seals [1]	<i>Halichoerus grypus</i>	16	0	2.17	10.67	15.21	4.62
Beaver 156	<i>Castor canadensis</i>	46	0	0.84	10.41	52.9	6.34
Polar bear 143	<i>Ursus maritimus</i>	51	0	6.3	6.3	72.75	no fit
Boar 9428	<i>Sus scrofa</i>	14	2.78	0	9.37	28.37	5.2
Gray fox 319	<i>Urocyon cinereoargenteus</i>	12	1.95	0	12.4	37.79	no fit
Gray fox 342	<i>Urocyon cinereoargenteus</i>	12	4.81	0	7.2	27.4	no fit
Coyote 247	<i>Canis latrans</i>	11	4.46	0	1.84	22.88	no fit
Coyote 263	<i>Canis latrans</i>	17	3.1	0	35.68	165.69	no fit
Elephant seals [3]	<i>Mirounga angustirostris</i>	26	1.16	0	10.25	61.16	13.95
Gray fox 328	<i>Urocyon cinereoargenteus</i>	12	4.81	0	0.38	13.75	2.29
Badger 78	<i>Taxidea tatus</i>	15	2.97	0	12.37	8.47	6.71
Fur seals [9]	<i>Callorhinus ursinus</i>	12	3.57	0	8.37	3.47	3.47
Blue springs manatees [10]	<i>Trichechus manatus</i>	19	1.6	0	7.6	0.7	0.7
Boar 9429	<i>Sus scrofa</i>	14	3.26	0	36.04	35.97	5.09
Camargue horses [5]	<i>Equus caballus</i>	8	7.34	0	4.53	16.97	8.6
Przewalski horses [5, 7]	<i>Equus ferus</i>	8	14.09	0	2.1	4.18	7.67
Marten 9695	<i>Martes americana</i>	25	1.27	0	0.99	13.37	0.27
Squirrel 9699	<i>Sciurus virginianus</i>	25	1.27	1.27	0	18.23	0.65
Bison [2]	<i>Bison bison</i>	13	1.28	0.26	0	23.29	0.51
Seneca deer [4]	<i>Odocoileus virginianus</i>	11	2.58	5.73	0	40.94	3.52
Gentoo penguins**	<i>Pygoscelis papua</i>	12	5.24	5.77	0	31.14	4.4
Beaver 151	<i>Castor canadensis</i>	44	4.73	0.8	0	13.94	no fit
Chinstrap penguins**	<i>Pygoscelis antarcticus</i>	22	2.77	2.22	0	62.75	0.05

** Fraser, pers. comm.

TABLE 6: Comparison of Morris and Doak estimates with exponential models.

Species	Morris and Doak		Nonlinear LS		Log transform	
	r	CV	r	CV	r	CV
Grizzlies [11]	0.055	1.440	0.054	0.137	0.056	0.126
Bison [2]	0.203	0.08	0.188	0.037	0.201	0.03
Muskox [12]	0.145	0.104	0.169	0.022	0.146	0.027
Calif. Sea otters D. Siniff, pers. comm.	0.047	0.422	0.055	0.073	0.052	0.076
Gray seals [1]	0.066	0.256	0.068	0.054	0.069	0.041
Albatross [13]	-0.007	3.260	-0.008	0.290	-0.008	0.302
Sparrow [14]	-0.061	0.477	-0.055	0.094	-0.052	0.088
Red kite [8]	0.058	0.320	0.058	0.035	0.059	0.034
YNP Bison [15]	0.163	0.112	0.141	0.024	0.156	0.028
Seneca deer [4]	0.391	0.080	0.386	0.068	0.411	0.003
Medians	0.058	0.256	0.058	0.054	0.059	0.034

be fit with the modified logistic (12) or with an exponential model (4 cases). Those that did not have significant slopes were examined with (10) and appeared to be essentially stationary series (correlation = 0) with the exception of a few instances (3) with an erratic pattern. There were just 4 cases in the Clark data that also fell in our sample (Fulmar 6527, Blue Wildebeest 7060, Sandhill crane 9990, and Blue tit 6830).

4. Discussion

The results given here indicate that, for any practical purposes, the integrated models should be used for species like those considered here (birds and mammals). The Gompertz model may be preferred for some species of fish and for insects. Our analyses here have largely been restricted to data sets that can be fit by the generalized logistic (1). The

modified logistic (12) and the ordinary logistic (6) can be fit to a much wider range of data. In a few cases, the exponential (8) may appear to give a better fit, but these appear to be largely instances where the data are limited to the early stages of population increase.

The recent ecological literature contains a wide range of difference equations (finite population growth models). We have studied 5 of these [28], but there are additional examples [20–23, 30–35]. One reason for the popularity of difference equation models is that they provide a wide range of models, some of which have no integrated analogs. A popular example is the Ricker model [36, 37]:

$$N(t) = N(t-1) \exp\left(r\left[1 - \frac{N(t-1)}{K}\right]\right), \quad (16)$$

where r is the rate of increase and K the asymptotic value, as before. This model was originally developed for cases where r is quite large and thus may be useful for such situations. If r is not large (as in all of the cases examined here), the model reduces to the difference equation version of the ordinary logistic, so that the ordinary logistic or (preferably the modified logistic) can be used. There may thus be some practical reasons to consider difference equations. In many other cases, it appears that the principal goals are the development of ecological theory.

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