



## Analyzing population growth curves

L. L. Eberhardt, J. M. Breiwick and D. P. DeMaster

*L. L. Eberhardt (leberhardt@aol.com), 2528 West Klamath Ave., Kennewick, WA 99336, USA. – J. M. Breiwick, National Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115, USA. – D. P. DeMaster, Alaska Fisheries Science Center, NOAA Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115, USA.*

Assessing animal population growth curves is an essential feature of field studies in ecology and wildlife management. We used five models to assess population growth rates with a number of sets of population growth rate data. A ‘generalized’ logistic curve provides a better model than do four other popular models. Use of difference equations for fitting was checked by a comparison of that method and direct fitting of the analytical (integrated) solution for three of the models. Fits to field data indicate that estimates of the asymptote,  $K$ , from the ‘generalized logistic’ and the ordinary logistic agree well enough to support use of estimates of  $K$  from the ordinary logistic on data that cannot be satisfactorily fitted with the generalized logistic. Akaike’s information criterion is widely used, often with a small sample version  $AIC_c$ . Our study of five models indicated a bias in the  $AIC_c$  criterion, so we recommend checking results with estimates of variance about regression for fitted models. Fitting growth curves provides a valuable supplement to, and check on computer models of populations.

There is a long history of counting wild animals, and counts have been widely utilized in wildlife management. Population models have become popular in recent times, and many models utilize counts with sex, age and kill data. The present study seeks to extract information on population growth from counts, and to use the results to evaluate some population models. An important use of population trend data is to try to extract information on population growth curves from counts alone. A key issue then is whether recent population growth rates are likely to remain nearly constant, or to decline. Most relevant textbooks utilize a logistic growth model, which assumes that population growth rates decline continuously as the population increases. Experience with actual populations of large vertebrates indicates that population growth rates may not decline substantially until the population begins to approach an asymptotic level (Eberhardt 1977, Eberhardt and Siniff 1977, Fowler 1981). This has two consequences: (1) population projections that assume continued exponential growth may be useful below the inflection point, and (2) the ‘maximum sustainable yield (MSY)’ point is higher than predicted by the classical logistic model so that higher yields may be obtained if the population is maintained at a level above that inferred from the logistic model, which predicts MSY at half the asymptotic level (denoted as  $K$  in most studies). Effective population management thus needs to determine whether a population is growing at a relatively constant rate, and, if not, approximately the level of the MSY point. We thus need a way to assess population

growth rates, and a better model for population trend than the usual logistic model.

The main practical feature of a ‘generalized’ logistic model is that the estimated MSY point, for data sets from birds and mammals, is located above that of the classical logistic growth model. Harvests should thus be more conservative regarding the target equilibrium level of harvested population than traditionally assumed. In most expositions, the parameter determining the position of the inflection point in the generalized logistic model has been assumed to be positive, but Sibly et al. (2005) assumed that negative values should be feasible, and fit a model to 3269 time series in the Global Population Dynamics Database (GPDD), using a nonlinear least-squares procedure (their parameter estimates are available in the GPDD, maintained by the National Environmental Research Council at <[www.sw.ic.ac.uk/cpb/cpb/gpdd.html](http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html)>). Their basic assumption appears to be that a reasonably long series of observations should be sufficient to reveal any ‘density-dependent’ effects when analyzed with their model.

The present study considers only data from bird and mammal populations. We reject the notion that density-dependence can satisfactorily be revealed by fitting a model to a time series of observations of population trend, unless the population is observed below and then approaches an asymptotic level. Further, for at least species with life histories like birds and mammals, it appears that negative values for the parameter determining the inflection point on a population growth curve would be exceptional. Much effort has gone into testing for density dependence over the

past 30 or 40 years. Recent efforts include Brook and Bradshaw (2006), Dennis et al. (2006) and Freckleton et al. (2006). We believe that density dependence is a well-established phenomenon, and maintain that emphasis should now be on establishing the MSY point.

The purposes of the present study are to estimate values of the parameter ( $z$  or  $\theta$ ) that determines the inflection point of a generalized logistic model (and thus MSY) for data on various species of vertebrates, and to examine models that may be useful in determining a MSY point and thus for managing populations.

## Methods

### Models

Two classes of models are considered here, integrated models and the corresponding difference equations. Three integrated models are used, the generalized logistic reported by Nelder (1961) and by Pella and Tomlinson (1969), but best known from Ayala et al. (1973), and often termed the theta-logistic:

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

The second is the traditional logistic model, used in most ecology texts to represent density-dependent growth. It is a special case of the generalized logistic with  $z = 1$ , and has three parameters, one of which ( $c$ ) depends on the initial population size:

$$N(t) = \frac{K}{1 + ce^{-rt}}, \quad c = \frac{K}{N_0} - 1 \quad (2)$$

The Gompertz model has been widely used as a model for density-dependence. The integrated form is:

$$N(t) = Ke^{-a \log(N_0/K)} \quad (3)$$

In the above three models,  $K$  is the asymptotic value,  $r$  is the maximum rate of increase,  $z$  is the parameter controlling the inflection point in a growth curve, and  $N_0$  represents initial population size, while  $a$  is a composite term.

Five models have been used here as difference equations (also known as ‘finite population growth models’). All of these can be expressed as population growth rates (pgr) by a simple rearrangement, i.e.

$$\text{pgr} = \frac{N_t}{N_{t-1}} - 1$$

We believe it is preferable to estimate population growth rate (pgr) by assuming a geometric model,  $\lambda = (1 + r)$  rather than the exponential,  $\lambda = \exp(r)$ , for the reasons suggested by Eberhardt and Simmons (1992). The apparent advantage of using pgr is that it eliminates the need to estimate an initial population size ( $N_0$ ). The work by Sibly et al. (2005) was based on pgr.

The five models are as follows:

Theta-Ricker equation (Thomas et al. 1980):

$$N_t = N_{t-1} \exp \left( r \left[ 1 - \left( \frac{N_{t-1}}{K} \right)^z \right] \right) \quad (4)$$

For ‘small’  $r$ , the first two terms of a series expansion yield the generalized logistic:

$$N_t = N_{t-1} + rN_{t-1} \left[ 1 - \left( \frac{N_{t-1}}{K} \right)^z \right] \quad (5)$$

The Ricker model (Ricker 1954), developed as a stock-recruitment model:

$$N_t = N_{t-1} \exp \left( r \left[ 1 - \left( \frac{N_{t-1}}{K} \right) \right] \right) \quad (6)$$

The first two terms of the series expansion yield the ordinary logistic model, expressed here as a difference equation:

$$N_t = N_{t-1} + rN_{t-1} \left[ 1 - \left( \frac{N_{t-1}}{K} \right) \right] \quad (7)$$

The Gompertz model in the form used by Dennis et al. (2006):

$$N_t = N_{t-1} \exp(r + b \log_e(N_{t-1})) \quad (8)$$

In this model,  $r$  corresponds to the values in the other models, but  $b$  is a complex function of  $K$ , so it is convenient to use a logarithmic transformation with  $X_t = \log(N_t)$  to linearize the model in order to use ordinary least-squares fitting to find initial values to use in final fits using nonlinear least-squares (most early studies of density dependence used the linear form as a basis for hypothesis-testing). The equations were studied on 36 data sets using nonlinear least-squares (Bates and Watts 1988), as implemented in the R-language. The primary data sets are listed in Table 1.

### Akaike’s information criterion

AIC is calculated as (Burnham and Anderson 2002):

$$\text{AIC} = n \log \hat{\sigma}^2 + 2k, \quad \text{where } \hat{\sigma}^2 = \frac{\sum \hat{e}_i^2}{n} \quad (9)$$

the  $\hat{e}_i$  are deviations (residuals) from the model fit,  $n$  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 (2002) recommended using:

$$\text{AIC}_c = \text{AIC} + \frac{2k(k+1)}{n-k-1} \quad (10)$$

Model comparisons are made using:

$$\Delta_i = \text{AIC}_c - \text{AIC}_{\min} \quad (11)$$

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

Burnham and Anderson (2002) suggested that  $\Delta$  in the range of 0–2 provides substantial empirical support for a model, while 4–7 yields ‘considerably less’ support and values  $>10$  yield essentially no support.

The position of the inflection point in the generalized logistic, as a proportion ( $p$ ) of the asymptotic level ( $K$ ), can be calculated from (Eberhardt 1987):

Table 1. Sample sizes, species names, ID numbers from the GPDD and references. Plot numbers are those used in the present study.

ID	n	Plot no.	Family	Genus and species	Common name	Used	Reference
8	21	8	Haematopodidae	<i>Haematopus ostralegus</i>	Eurasian oystercatcher	all	GPDD
50	21	283	Phalacrocoracidae	<i>Phalacrocorax carbo</i>	great cormorant	all	GPDD
85	11	315	Mustelidae	<i>Taxidea taxus</i>	American badger	all	GPDD
298	10	506	Canidae	<i>Canis latrans</i>	coyote	all	GPDD
320	26	528	Mustelidae	<i>Martes pennanti</i>	fisher	all	GPDD
362	12	565	Canidae	<i>Urocyon cinereoargenteus</i>	grey fox	all	GPDD
377	12	580	Canidae	<i>Urocyon cinereoargenteus</i>	grey fox	all	GPDD
379	12	582	Canidae	<i>Urocyon cinereoargenteus</i>	grey fox	all	GPDD
385	12	588	Canidae	<i>Urocyon cinereoargenteus</i>	grey fox	all	GPDD
387	12	590	Canidae	<i>Urocyon cinereoargenteus</i>	grey fox	all	GPDD
1314	11	1010	Rodentia	<i>Dipodomys ordii</i>	ord's kangaroo rat	all	GPDD
1593	18	1169	Anatidae	<i>Anser caerulescens</i>	lesser snow goose	all	GPDD
2733	12	1993	Cercopithecidae	<i>Macaca fuscata</i>	Japanese macaque	all	GPDD
2738	15	1998	Cercopithecidae	<i>Macaca fuscata</i>	Japanese macaque	all	GPDD
3263	13	2516	Cervidae	<i>Cervus elaphus</i>	red deer	all	GPDD
3341	26	2594	Bovidae	<i>Connochaetes taurinus</i>	blue wildebeest	all	GPDD
3623	13	2863	Felidae	<i>Lynx lynx</i>	Eurasian lynx	all	GPDD
3654	14	2889	Suidae	<i>Sus scrofa</i>	wild boar	all	GPDD
3946	18	3170	Sylviidae	<i>Sylvia atricapilla</i>	blackcap	all	GPDD
3955	18	3179	Fringillidae	<i>Carpodacus erythrinus</i>	common rosefinch	all	GPDD
332	15	540	Corvidae	<i>Corvus monedula</i>	jackdaw	33–47	GPDD
77	15	308	Mustelidae	<i>Taxidea taxus</i>	American badger	33–47	GPDD
83	15	313	Mustelidae	<i>Taxidea taxus</i>	American badger	17–31	GPDD
172	44	390	Castoridae	<i>Castor canadensis</i>	beaver	20–63	GPDD
177	46	395	Castoridae	<i>Castor canadensis</i>	beaver	18–63	GPDD
234	18	452	Felidae	<i>Lynx rufus</i>	bobcat	13–30	GPDD
258	20	466	Felidae	<i>Lynx rufus</i>	bobcat	19–38	GPDD
294	17	502	Canidae	<i>Canis latrans</i>	coyote	8–24	GPDD
295	16	504	Canidae	<i>Canis latrans</i>	coyote	9–24	GPDD
1036	24	804	Corvidae	<i>Cyanocitta cristata</i>	blue jay	5–28	GPDD
	16		Phocidae	<i>Halichoerus grypus</i>	gray seals		Bonner 1975
	13		Bovidae	<i>Bison bison</i>	bison		Fredin 1984
	26		Phocidae	<i>Mirounga angustirostris</i>	elephant seals		Stewart et al. 1994
	37		Cervidae	<i>Cervus elaphus</i>	elk		Lubow et al. 2002
	11		Cervidae	<i>Odocoileus virginianus</i>	deer		Hesselton et al. 1965
	19		Phocidae	<i>Phoca vitulina</i>	harbor seals		Jeffries et al. 2003

$$p = \left( \frac{1}{1+z} \right)^{1/z} \quad (12)$$

where  $z$  is the parameter of the generalized logistic (Eq. 1).

### Diagnostic ‘test’

Plotting logarithms of counts of populations following a generalized logistic growth curve against time gives plots that are concave downwards (Eberhardt 1992). This result can be used as a rapid test. A linear regression is fit to logarithms of the counts over time, and residuals of the fits plotted. If the residuals follow a roughly parabolic curve (concave downwards), then there is a good prospect that a generalized logistic can be fitted to the data. If no pattern in the deviations is detected, then one might expect the ordinary exponential curve to approximate the data. Successful nonlinear least-squares fitting depends on finding good initial estimates of parameters, which may occasionally be difficult. This test can thus provide a useful screening device. Once convergence is achieved, plots of observations and the curves given above, can then be used to assess the fit, along with estimated standard errors.

### Data sources

Fits of Eq. 1 to 12 sets of population growth data appear in Fig. 1. Three other data sets (Fisher 320, Badger 85 and Harbor seals) could be fit with Eq. 1. None of the other data sets of Table 1 could be fit with Eq. 1. 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 if the plot appeared roughly s-shaped. Ten of the data sets obtained from the GPDD were truncated below, using only the range of data indicated in Table 1. All of the remaining data sets were used in their entirety except that the elephant seal data was truncated above due to erratic fluctuations in the later counts. The last six data sets in Table 1 were obtained from the references cited. Because nonlinear least-squares fitting requires provision of trial values of parameters, it is possible that we did not locate all suitable data sets that might be fitted with Eq. 1, but we did try varying parameters until plots of curves appeared to ‘fit’ the data points and used the difference equation version (Eq. 5) as an alternative plotting approach, as well as considering trial values of parameters obtained by fitting other models. We also used the logistic model (Eq. 2) in screening for usable data sets.

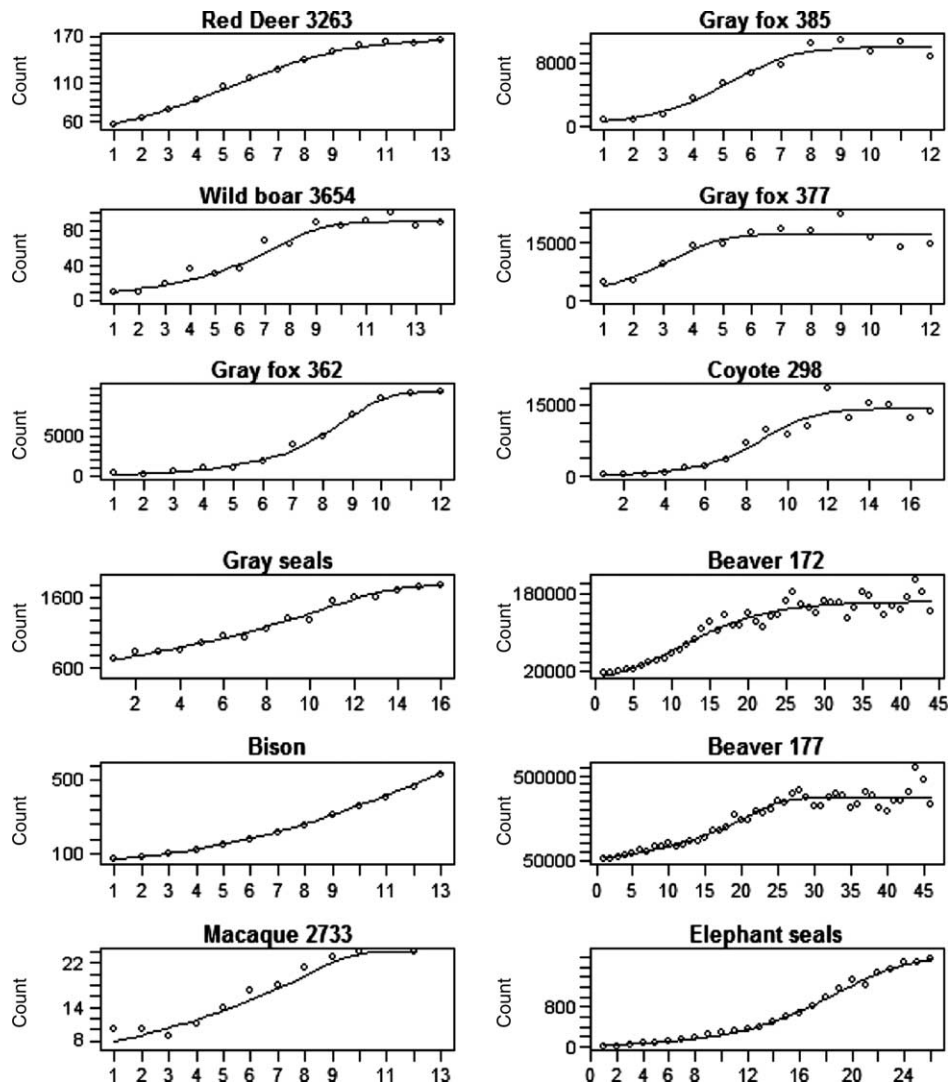


Figure 1. Plots of integrated generalized logistic to population growth data.

## Results

### Using population growth models

We found that the fits of Eq. 1, 2 and 3 gave results that were generally in accord with fits to the corresponding difference equations, hence further analyses were conducted using the difference equations, so that we could also study the theta-Ricker (Eq. 4) and Ricker (Eq. 6) models, which are not available in integrated form. We calculated AICc for five models, getting the  $\Delta_i$  values for each data set. The results (Table 2) were quite variable with no one model consistently favored. We then used the variance estimate (Eq. 9) as a measure of 'goodness-of-fit' and found (Table 3) that the generalized logistic gave the best overall fit to the data, with the theta-Ricker favored in a few cases. As noted under Methods, the series expansion of the theta-Ricker model yields the generalized logistic so long as the rate of increase ( $r$ ) is small or moderate. Those examples in Table 3 where the variance of the theta-Ricker model is slightly smaller than that of the generalized logistic have larger values of  $r$ . It thus appears that the generalized logistic is the

preferred model among the five cases examined here. Estimated values of  $z$  (Table 4) have a mean of 4.48 and standard error of 1.11, so that approximate 95% confidence limits are about 2.3 to 6.7.

### Using population growth rates

The population growth rates (pgr) for Eq. 4–8 have one fewer parameters than do the corresponding difference equations, and can be fit to most of the data sets used in this study (Table 1). Because pgr is estimated from values of successive counts, the data are highly variable. Inasmuch as the individual counts appear in the numerator and denominator of successive ratios, there is also the prospect of serial correlations.

We believe that the high variability evident in plots of pgr suggests that it may not be suitable for selecting among a set of models. As pointed out by Eberhardt (2003), in the face of substantial variability, one needs another criterion besides AIC to select 'good' models. In the case of multiple regression models,  $R^2$  provides a possible such criterion

Table 2. Delta AIC<sub>c</sub> values for 5 models. k = number of parameters + 1. ID numbers are those used by the GPDD.

Species k	ID	Theta-Ricker 4	Generalized logistic 4	Logistic 3	Ricker 3	Gompertz 3
Red deer		0.23	0	4.26	5.71	12.36
Wild boar	3654	2.89	2.9	0	0.67	3.22
Gray fox	362	2.74	2.95	0	2.6	nc
Gray fox	385	5.44	5.2	0	0.38	1.36
Gray fox	377	5.16	5.2	0	0.12	0.69
Coyote	294	0.61	2.09	107.49	0	nc
Gray seals		0	1.69	67.99	2.79	4.09
Bison		5.08	4.51	1.48	0	2.61
Macaque	2733	0	0.01	2	2.28	2.14
Beaver	172	2.14	2.5	1.1	0.6	0
Beaver	177	0	0.3	0.76	0.76	3.76
Elephant seals		0.38	1.72	0.1	0	10
Seneca deer		0.68	8.16	4.65	0	1.45
Badger	85	1.45	4.99	1.64	0	nc
Gray fox	387	1.44	1.4	0	0.99	3.4

(Eberhardt 2003), but unfortunately a similar measure is not available for nonlinear models.

### Estimation with data subject to removals

When removals (harvests) are involved, pgr may be the only useful approach to estimating population parameters from count data. In principle, Eq. 5 can be used with data subject to removals, by adding the numbers removed to a census conducted after the removals, assuming the removals take place near the time of the census. This approach necessarily results in data that are more variable than when there are no removals, so that a fairly long data series is desirable. Such a set is available for captive longhorn cattle (Fredin 1984). The fit (Fig. 2) using Eq. 5 yielded an estimate of  $z$  of 3.7 (SE = 5.7), and  $K = 388$  (SE = 265). One very interesting aspect of the data is that the population was held at 100 individuals for 13 years, giving the considerable variation in pgr shown in Fig. 2. Two other data sets (bison and George Reserve deer, data of Eberhardt 1987) were also assessed with the removal method. The bison data are from the same series listed in Table 1, but were collected after removals started, and yielded an estimate of  $z$  of 1.2 (SE = 1.5) as compared to  $z = 1.6$  (SE = 1.3) from the initial series of observations with no removals, using pgr.

### Using the logistic model

The only substantial reason for using pgr, other than in analyzing removal data, is that it is readily fit to data that do not fit the integrated generalized logistic (Eq. 1), and might thus be useful to estimate  $K$ , the asymptotic level for such data. However, estimates of  $K$  from fitting the logistic curve are very close to those obtained with the generalized logistic, and the logistic curve fits a somewhat wider range of data than does the pgr. Table 5 compares estimates of  $K$  from the logistic and the generalized logistic, and shows that the estimates are very much the same for most examples, with gray seals the only example with a substantial difference in estimates of  $K$ . This may be a consequence of the fact that the gray seal counts were of pups only. Regression of logistic estimates of  $K$  on values from the generalized logistic gave an  $R^2$  of 0.9994.

## Discussion

### Generalized logistic curves

Because a major interest in fitting growth curves lies in estimating  $K$ , the asymptotic level, we compared estimates of  $K$  from a generalized logistic with estimates of the same quantity from the ordinary logistic. The results are

Table 3. Variances (Eq. 9) as a measure of 'goodness-of-fit' for five models.

Species	Theta-Ricker	Genl Logistic	Logistic	Ricker	Gompertz
Red deer 3263	3.02	2.97	5.915	6.61	11.04
Boar 3654	39.32	39.34	43.57	45.73	54.84
Gray fox 362	54072	55014	66373	82698	nc
Gray fox 385	$1.10 \times 10^6$	$1.08 \times 10^6$	$1.08 \times 10^6$	$1.12 \times 10^6$	$1.22 \times 10^6$
Gray fox 377	$7.64 \times 10^6$	$7.65 \times 10^6$	$7.67 \times 10^6$	$7.77 \times 10^6$	$8.15 \times 10^6$
Coyote 294	$4.23 \times 10^6$	$3.02 \times 10^6$	$4.80 \times 10^6$	$4.86 \times 10^6$	nc
Gray seals	2454	1638.00	3498.00	3514	3805
Bison	24.81	15.54	26.53	25.93	30.86
Macaque 2733	0.824	0.83	1.51	1.54	1.8
Beaver 172	$2.31 \times 10^8$	$1.62 \times 10^8$	$2.37 \times 10^8$	$2.35 \times 10^8$	$2.33 \times 10^8$
Beaver 177	$1.77 \times 10^9$	$1.29 \times 10^9$	$1.88 \times 10^9$	$1.89 \times 10^9$	$2.04 \times 10^9$
Elephant seals	2004	828.40	2107.00	2156	3229
Seneca deer	576.73	102.40	735.00	667	761.7
Badger 85	192329	$3.28 \times 10^4$	$1.07 \times 10^5$	109050	nc
Gray fox 387	$5.914 \times 10^8$	$5.893 \times 10^8$	$8.088 \times 10^8$	$8.10 \times 10^8$	$1.059 \times 10^9$

Table 4. Values of  $z$  estimated with integrated generalized logistic (Eq. 1).

Source	$Z$	Coef. of variation
Red deer 3263	3.89	0.27
Boar 3654	4.99	1.14
Fox 362	3.78	0.41
Fox 385	1.85	1.15
Fox 377	3.48	1.9
Coyote 294	1.93	1.53
Gray seals	11.78	0.88
Bison	0.74	0.64
Macaque 2733	16.3	1.54
Beaver 172	0.45	0.18
Beaver 177	7.43	1.03
Elephant seals	1.86	0.36
Seneca deer	0.89	0.51
Fisher 320	0.4	5.35
Badger 85	4.22	1.64
Harbor seals	7.72	1.5

encouraging, suggesting that the ordinary logistic should provide useful estimates of  $K$ , even though a generalized logistic may be indicated for other purposes. Estimating  $z$  from removal data is more difficult. Until more and better data is available on removals, we suggest assuming a fixed value of  $z$  in cases where a direct fit of the generalized logistic model is unsuccessful. This is important in that many practical applications may be possible in situations where removals are encountered. We propose that an interim 'typical' value of  $z$  may be about 4.5. Quite surely individual estimates are influenced by changing environmental circumstances, so espousing a 'universal' value of  $z$  may not be realistic, but an interim value should be useful. The major practical use of estimates of  $z$  lies in estimating  $MSY$ , and the mean value using Eq. 12 is 0.68 (approximate 95% CI 0.60 to 0.73).

Sæther et al. (2006) examined data on a number of European stork *Ciconia ciconia* populations and estimated  $z$  for Eq. 2 for 8 of 17 populations studied, with a range of values of  $z$  from 1.18 to 3.93. Jeffries et al. (2003) studied harbor seal data from Washington State, and estimated values of  $z$  for Eq. 2 for a coastal and inland stock, obtaining  $z = 2.43$  for the inland stock ( $SE = 1.75$ ), and  $z = 1.75$  ( $SE = 1.47$ ) for the coastal stock. We used their coastal stock average data in our study and obtained  $z = 7.7$ , but the estimate is unreliable ( $SE = 12$ ). Their estimates were based on replicate data sets, not reported in their paper.

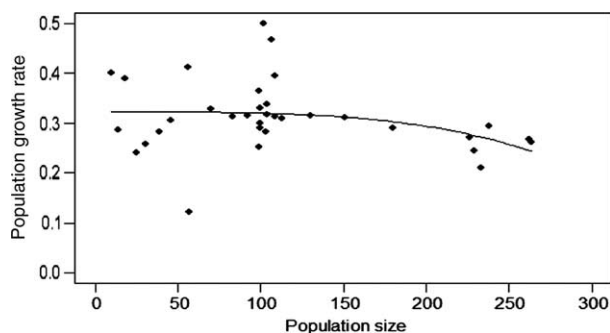


Figure 2. Population growth rates for longhorn cattle based on pgr model (Eq. 5).

Table 5. Estimates of  $K$  from generalized logistic curve and logistic model.

Species	Integrated generalized logistic	Logistic
Red deer 3263	168.1	180
Wild boar 3654	91	95
Gray fox 362	10600	11560
Gray fox 385	15290	15410
Gray fox 377	22790	22970
Gray fox 379	19110	19250
Gray seals	2013	3096
Bison	1356	1159
Macaque 2733	24	30.4
Beaver 172	164500	162300
Beaver 177	421200	444100
Elephant seals	1862	2056
Seneca deer	4425	3836
Fisher 320	2003	1993
Badger 85	2431	2592

## Serial correlations

Most of the models found in the recent literature are of the form  $N_{t+1} = f(N_t)$ , expressed as difference equations like Eq. 4–8, and often described as 'finite population models'. Some have the dependent variable,  $N_{t+1}/N_t = f(N_t)$ , including the population growth rate of Sibly et al. (2005). Such models involve a serial correlation, discussed by Watt (1964, 1968). Eberhardt (1970) indicated the sizable degree of correlation thus induced when the underlying data are constructed only from random numbers. Such correlations can be dealt with by time series methods, but these require sizable samples, which are not usually available with population growth curve data, as indicated in Table 1. We thus recommend using the integrated growth curves of the form of Eq. 1–3 when possible. Our experience thus far suggests that some, but not all, of the parameters estimated from the integrated models may be close to those obtained from the corresponding difference equation.

## Modeling population trends

Computer modeling of populations has been a very popular area for several decades. A serious drawback is that almost all such models are truly understood only by those who do the actual construction of a given model, and readers of reports on the results have to take a lot on faith. Hence, it is important to use curve-fitting by nonlinear least-squares to check on the elements of a model whenever that is feasible. In other cases, curve-fitting may provide useful checks and sidelights on the modeling.

Lubow et al. (2002) used the methodology of White and Lubow (2002) to model an unharvested elk herd in Rocky Mountain National Park. They provided a record of the counts from 1965 to 2001. Due to the high variability in successive counts, the best approach appears to be fitting the ordinary logistic, which gives an estimate of  $K$  of 1020, with a standard error of 82 elk. Essentially the same result was obtained from the rather complex computer model of Lubow et al. (2002), i.e. 1069 elk with  $SE$  of 55, so it appears that the desired result (estimating the asymptotic population size)

could be obtained directly from the population counts. Data on gray whales (Rugh et al. 2005) do not fit a generalized logistic model, but  $K$  can be estimated as 23 910 (SE = 2470) from the ordinary logistic (Eq. 2).

Most of the results of this study are concerned with fitting a generalized logistic curve to data, and developing criteria for assessing and improving the fits. Results of the analyses indicate that the models are suitable for actual population data, and that the inflection, or MSY, point is appreciably higher than the commonly assumed  $K/2$  level associated with the ordinary logistic. If these results are accepted, then the major management implication is that improved long-term yields from a harvested population can be achieved by maintaining the population significantly above  $K/2$ . Ascertaining  $K$ , the asymptotic population level, by using the generalized logistic model, requires a sequence of fairly precise counts or population estimates. When the data are quite variable, it appears to be feasible to fit the ordinary logistic to estimate  $K$ . We believe that the curve-fitting and estimation methods presented here may give useful direction to management, without the need for the elaborate computer simulations often found in the literature.

The Gompertz curve (Eq. 3) has been popular in testing for density dependence since the paper of Bulmer (1975), very likely because a log transform yields a linear model, which is much easier to use in statistical tests than the nonlinear models considered here. However, the theoretical inflection point,  $p$ , is  $0.385 K$ , much too low for the data studied here, and the variance about regression is much larger than that for the other models studied (Table 3). We thus do not believe that it is an appropriate model for data on birds and mammals, but have included it due to the wide use in the literature.

AICc is widely used in recent ecological literature, usually comparing a number of models on one or a few sets of data. In the present study we studied it on five models over 15 data sets and found it did not discriminate at all well when contrasted with the variance about regression (Table 2, 3). We thus recommend that users should also check the variance about regression, when the range in number of parameters is not large.

**Acknowledgements** – We thank Dr G. H. M. Dawkins and others concerned with the Global Population Dynamics Database for access to the data files.

## References

- Ayala, F. J. et al. 1973. Competition between species: theoretical models and experimental results. – *Theor. Popul. Biol.* 4: 331–356.
- Bates, D. M. and Watts, D. G. 1988. Nonlinear regression analysis and its applications. – Wiley.
- Bonner, W. N. 1975. Population increase of grey seals at the Farne Islands. Biology of the seal. – In: Ronald, K. and Mansfield, A. W. (eds), *Rapports et Proces-Verbaux des Reunions, Conseil International pour l'Exploration de la Mer* 169: 366–370.
- Brook, B. W. and Bradshaw, C. J. A. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. – *Ecology* 87: 1445–1451.
- Bulmer, M. 1975. The statistical analysis of density dependence. – *Biometrics* 31: 901–911.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multi-model inference (2nd ed). – Springer.
- Dennis, B. et al. 2006. Estimating density dependence, process noise and observation error. – *Ecol. Monogr.* 76: 323–341.
- Eberhardt, L. L. 1970. Correlation, regression, and density dependence. – *Ecology* 51: 306–310.
- Eberhardt, L. L. 1977. Optimum policies for conservation of large mammals with special reference to marine ecosystems. – *Environ. Conserv.* 4: 205–212.
- Eberhardt, L. L. 1987. Population projections from simple models. – *J. Appl. Ecol.* 24: 103–118.
- Eberhardt, L. L. 1992. An analysis of procedures for implementing the dynamic response method. – *Mar. Mamm. Sci.* 8: 201–212.
- Eberhardt, L. L. 2003. What should we do about hypothesis testing? – *J. Wildlife Manage.* 67: 241–247.
- Eberhardt, L. L. and Siniff, D. B. 1977. Population dynamics and marine mammal management policies. – *J. Fish. Res. Board Can.* 34: 183–190.
- Eberhardt, L. L. and Simmons, M. A. 1992. Assessing rates of increase from trend data. – *J. Wildlife Manage.* 56: 603–610.
- Fowler, C. W. 1981. Density dependence as related to life history strategy. – *Ecology* 62: 602–610.
- Freckleton, R. P. et al. 2006. Census error and the detection of density dependence. – *J. Anim. Ecol.* 75: 837–851.
- Fredin, R. A. 1984. Levels of maximum net productivity in populations of large terrestrial mammals. – In: Perrin, W. F. et al. (eds), *Reproduction in whales, dolphins and porpoises*. Rep. Int. Whaling Commission. Spec. Iss. 6, Cambridge, UK, pp. 381–387.
- Hesselton, W. T. et al. 1965. Population dynamics of deer in the Seneca army depot. – *N. Y. Fish Game J.* 12: 17–30.
- Jeffries, S. et al. 2003. Trends and status of harbor seals in Washington State; 1978–1999. – *J. Wildlife Manage.* 67: 207–218.
- Lubow, B. C. et al. 2002. Dynamics of interacting elk populations within and adjacent to Rocky Mountain National Park. – *J. Wildlife Manage.* 66: 757–775.
- Nelder, J. A. 1961. The fitting of a generalization of the logistic curve. – *Biometrics* 17: 89–110.
- Pella, J. J. and Tomlinson, P. K. 1969. A generalized stock production model. – *Bull. Inter-Am. Trop. Tuna Commission* 13: 419–496.
- Ricker, W. E. 1954. Stock and recruitment. – *J. Fish. Res. Board Can.* 11: 559–623.
- Rugh, D. J. et al. 2005. Estimates of abundance of the eastern North Pacific stock of gray whales (*Eschrichtius robustus*) 1997–2002. – *J. Cetacean Res. Manage.* 7: 12.
- Sæther, B.-E. et al. 2006. Climate and spatio-temporal variation in the population dynamics of a long distant migrant, the white stork. – *J. Anim. Ecol.* 75: 80–90.
- Sibly, R. M. et al. 2005. On the regulation of populations of mammals, birds fish and insects. – *Science* 309: 607–610.
- Stewart, B. S. et al. 1994. History and present status of the northern elephant seal population. – In: LeBouef, B. J. and Laws, R. M. (eds), *Elephant seals, population ecology, behavior and physiology*. Univ. of California Press, pp. 29–48.
- Thomas, W. R. et al. 1980. Chaos, asymmetric growth and group selection for dynamic stability. – *Ecology* 61: 1312–1320.
- Watt, K. E. F. 1964. Density dependence in population fluctuations. – *Can. Entomol.* 96: 1147–1148.
- Watt, K. E. F. 1968. Ecology and resource management. – McGraw-Hill.
- White, G. C. and Lubow, B. C. 2002. Fitting population models to multiple sources of observed data. – *J. Wildlife Manage.* 66: 300–309.