

## Growth dynamics in the American alligator (*Alligator mississippiensis*)

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The growth dynamics of the American alligator (*Alligator mississippiensis*) were studied in the subtropical Florida Everglades using extensive mark-recapture data from over 2000 recaptures of known-aged and unknown-aged animals. A model based on the power curve best describes growth of Everglades alligators. The nonasymptotic character of this curve leads to rejection of the hypothesis that alligator growth is determinate. A model consisting of piece-wise linear equations better described growth in the first year, and suggested a period of arrested growth occurred in the first winter. A comparison of predictions from growth models derived from several populations indicated that Everglades alligators grew more slowly than did those in more temperate areas, leading to the rejection of the hypothesis that growth rates in subtropical Florida would be elevated because of the long growing season. We attribute this result to a combination of increased maintenance costs and a limited resource base in the Everglades.

Analyses considered the extent to which growth model evaluation and use can be affected by data selection. Mathematical constraints posed by negative growth data can be alleviated by including growth records over combined recapture intervals to achieve a positive growth increment. However, periods of no to negative growth may be real, and such deviations are obscured by fitting growth data to monotonically increasing models.

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### Introduction

The dynamics of body growth in organisms are crucially intertwined with many aspects of their evolutionary ecology and life history strategies (Van Valen, 1973; Ricklefs, 1979, 1984; Peters, 1983; O'Connor, 1984; Calder, 1984). In altricial birds, growth rates have been related to physiological restrictions on growth, mortality and food supply (Lack, 1968; Ricklefs, 1969a, b; Case, 1978). The relative importance of genetic and environmental constraints and growth dynamics appears to differ among species. For some, growth appears to proceed at a physiological maximum; for others, especially those having long growth periods, it appears that external constraints can be crucial determinants of growth dynamics (Dunn, 1975; Fendley & Brisbin, 1977; Zach & Mayoh, 1984; Ricklefs, 1984). Among poikilotherms, temperature and energetics seem important factors controlling growth (Hawkins, 1986; Sweeney & Vannote, 1986). Growth rates of poikilotherms tend to increase with increasing temperatures to some physiological limit (Precht *et al.*, 1973). However, higher temperatures entail greater metabolic costs, especially for animals of relatively large mass (Peters, 1983). Food availability, as mediated by competitive interactions, may also affect growth rates in poikilotherms (Petranka & Sih, 1986; Southerland, 1986). However, a fundamental adaptation of such organisms is their ability to use available resources efficiently and to survive periods of resource stress through variable metabolic rates.

Many poikilotherms, including colonial invertebrates and fishes, have indeterminate growth dynamics and the ability to arrest growth intermittently or even to shrink (Weatherley, 1972; Sebens, 1982). Sebens (1987) recently discussed models of indeterminate growth, but many previous studies fit growth data to asymptotic sigmoid models, which imply determinate growth, and most vertebrates studied conform to sigmoid asymptotic models (e.g. logistic or Gompertz growth models), although some lack an inflection point (e.g. Von Bertalanffy model) (Laird, 1965; Ricklefs, 1967; Kaufmann, 1981; Parks, 1983). Non-asymptotic growth dynamics can range from linear to negative exponential.

Comparisons of growth processes among species, times or locations are facilitated by such mathematical models (Ricklefs, 1967, 1969a; Kaufmann, 1981). They may be used to estimate such population parameters as maximum size, age or size at maturity, or environmentally-related variability in growth rates. However, many models can fit a data set, and comparisons among populations have been hampered by a priori choice of model and by a failure to evaluate objectively goodness of fit relative to alternative models (Zach & Mayoh, 1984). If all populations of a species were to grow according to the same theoretical model, model parameters could be compared among populations to detect localized effects of environmental conditions. However, no one model might be appropriate for all populations, if environmental conditions or ecotypic adaptations affect the shape of the growth curve (White & Brisbin, 1980). Empirical models, which are less theoretically restrictive, permit comparisons only of the quantitative predictions of the equations. Thus, the use of theoretical models is the more powerful approach because of the potential for interpreting both fundamental growth processes and quantitative predictions. But it is not yet clear which model, if any, would describe appropriately the growth of a large-sized, slow-growing poikilotherm.

Crocodylians are the largest, and among the most slowly growing, living poikilotherms (Dodson, 1975; Chabreck & Joanen, 1979). Thus they are useful organisms in which to study growth dynamics and environmental constraints on growth. Investigations of large, slow-growing animals such as crocodylians are usually severely constrained by small sample size, which decreases further with the exclusion of data for various reasons. To overcome and investigate the effects of

this constraint, we conducted an intensive capture-recapture study of the American alligator (*Alligator mississippiensis*) in the southern Florida Everglades, and had available for analyses over 2000 recapture records from nearly 5000 captures.

The American alligator is atypical among crocodylians because of its temperate, rather than tropical, distribution. None the less, alligators require relatively high temperatures for body growth and physiological functioning (Colbert, Cowles & Bogert, 1946; Hernandez & Coulson, 1957; Brattstrom, 1965; Ferguson & Joanen, 1983). Food consumption decreases in winter, stopping growth; in fact, Coulson, Coulson & Hernandez (1973) found that growth rates of captive alligators decreased in winter despite warm temperatures and unlimited food. The southernmost population of alligators is in the Everglades of southern Florida. Using this population, we tested the hypothesis that annual growth rates in subtropical southern Florida, with longer growing periods, are greater than those of more temperate populations.

Previous studies of crocodylian growth have been based on arbitrarily chosen models (Cott, 1961; Nichols *et al.*, 1976; Chabreck & Joanen, 1979; Murphy, 1981; Fuller, 1981) or curve-fitting by multiple regression techniques (Webb *et al.*, 1978, 1983; Magnusson & Taylor, 1981). These previous studies fit sigmoid growth models that are asymptotic. The question arises as to whether the theoretical implications of such models are congruent with the actual growth dynamics of a slow-growing poikilotherm. In this study, following the results of these previous findings, we tested the hypothesis that a deterministic growth pattern would provide the best model of alligator growth.

Of more general concern is the role of investigator selection of growth models and of the data used in evaluating them. To study these effects, we examined the fits of several standard models and an empirically derived segmented linear model. Investigator selection of data often involves the elimination of apparently negative or zero growth data, which are undefined in certain transformations and are not modelled by monotonically increasing functions. The disposition of records showing negative growth and which of several growth measurements are used may affect the analytical result. We therefore investigated the effect of data transformations and growth variable selection.

### Methods

#### Field data

The alligator population in the southern Everglades of Florida, USA, was studied in a 10-km<sup>2</sup> area of marsh. The climate of the Everglades is subtropical, having average minimum and maximum annual temperatures of 21 and 29 °C, respectively. Frosts occur on only a few days of the year and freezing temperatures are infrequent. Rainfall does vary seasonally leading to alternating periods of high (June–December) and falling (January–May) water levels.

Alligators were captured during a mark-recapture study conducted monthly from 1977 to 1981, and annually in 1982 and 1983. Each sampling period required 3 or 4 nights, using an airboat. Alligators were measured and released at the site of their capture. Larger alligators (1.5 m total length) were captured using a pole snare, and smaller alligators by hand. Traps also were used to capture some large alligators (Murphy & Fendley, 1973). Capture-recapture records of animals of unknown age provided most of the data available for growth analysis. Hatchlings captured and tagged at nest sites provided a pool of individuals whose ages were known to within 4 days.

Uniquely-numbered Monel metal tags inserted through the middle web of the left rear foot were used to identify individuals in hand. The date of capture and sex were recorded for each captured individual. Sex of

larger animals was determined by cloacal examination (Joanen & McNease, 1978). Measurements taken to the nearest mm were total length (measured from the tip of the snout to the tip of the tail) and snout-vent length (measured from the tip of the snout to the posterior of the cloaca). Snout-vent length (SVL) was used in the present study because it could be measured with less error and was not affected by loss of pieces of the tail.

#### Growth models

For mark-recapture data of animals of unknown age, an appropriate growth model can be fitted by evaluating the relationship between size and a measure of growth rate over the interval between captures. The absolute rate of growth (GR), or the increase in size per unit of an animal of size  $S$  at time  $T$  is given by:

$$GR = dS/dT.$$

The specific (or relative) growth rate (SGR) at time  $T$  is defined as the proportion of increase in size per unit time, as given by:

$$SGR = (1/S) (dS/dT)$$

with units of (1/time). SGR is often used as a 'growth rate index' (Radford, 1967; Gurnell & Rennolls, 1983), and with appropriate transformations changes in SGR may be described linearly (Kaufmann, 1981). Parameters of certain nonlinear functions can be estimated by fitting the constants of the respective 'linear generating laws' (Causton & Venus, 1981). Such linearizing transformations allow differential equations for growth to be fitted using simple linear regression (Elliott, 1975; Causton & Venus, 1981; Kaufmann, 1981), and allows records of animals of unknown age to be used in deriving a growth model. The first step in using the linear transformations of nonlinear growth curves is to estimate the SGR using the mean SGR between times  $T_1$  and  $T_2$ , given by the integrated form:

$$SGR = 1/(T_2 - T_1) \left( \int_{T_1}^{T_2} 1/S dS/dT dT \right)$$

which can be approximated for ease of calculation as:

$$SGR = (\log_e S_2 - \log_e S_1)/(T_2 - T_1),$$

where  $S_1$  and  $S_2$  (SVL1 and SVL2 in our study) are the sizes at  $T_1$  and  $T_2$ , respectively. Estimates of SGR are then plotted against size, which is used as the independent variable rather than age, because it is expected that size is the more important determinant of growth rate of slow-growing reptiles than is age. One theoretical difficulty with the method is the nonindependence of SGR and  $S$ , but it remains of heuristic value in assessing fit.

Using linearizing functions, we tested the fit of our data to 5 growth curves:

$$\begin{aligned} \text{logistic, } S &= S_{\infty} (1 + \exp -b(T + T_0))^{-1} \\ \text{power, } S &= ab (T + T_0)^{1/a} \\ \text{Von Bertalanffy, } S &= S_{\infty} (1 - \exp -b(T + T_0)) \\ \text{log-normal, } S &= \exp (b (T + T_0)) \\ \text{Gompertz, } S &= S_{\infty} \exp (-\exp -a (T + T_0)) \end{aligned}$$

where  $S_{\infty}$  = asymptotic size,  $T$  is time of interest,  $a$  and  $b$  are constants. We also fit the data to the Richards' (1959) curve:

$$S = S_{\infty} (1 \pm \exp -a (T + T_0))^{-1/c}$$

which is a generalization of the Von Bertalanffy equation in which shape ( $c$ ) is a fourth unknown parameter (White & Brisbin, 1980; Brisbin *et al.*, 1987) that may reflect adaptive strategies or the effects of stress (Brisbin *et al.*, 1986). The Richards' function is evaluated using a range of values (over  $-1.0$ ) for the constant ' $c$ ' in the transformed equation relating SGR to initial size raised to the ' $c$ ' power (Causton & Venus, 1981). We

evaluated the Richards' function over a range of values of ' $c$ '; here we report on the best results, using  $c = 1.0$  and  $c = 0.9$ .

Model selection was made on the basis of the best least squares fit (highest  $R^2$ ,  $T$  test). We could not use the mean square error to select a model (Schoener & Schoener, 1978) because the different variable transformations for various models resulted in noncomparable mean square error units. Once a model was chosen, the parameters for the nonlinear curve were estimated from the parameters of the linearized functions (Kaufmann, 1981).

We also modelled the growth of known-aged individuals using a 'running-fit' method of identifying piecewise linear functions (Hunt, 1982). The method involved cumulative addition of progressively older animals to a regression set. At each step, mean square error and  $R^2$  were calculated, and linear functions were delineated by segments showing maximum  $R^2$ 's.

#### Data selection

Records that show zero or negative growth typically must be dealt with by the investigator, because they are not amenable to transformations involved in logarithmic or inverse functions. As a result of such records, all available data are seldom used, and the procedures used for data selection could affect the results in unappreciated ways. We evaluated the effects of such selection by fitting growth models to several sets of data.

We evaluated 4931 records of alligators captured, recaptured, or identified without being recaptured. The data set of 'all' records included 2015 recaptures for which length was available on both capture and recapture. 'Positive' records ( $n = 1713$ ) were those showing positive growth. Fifteen percent of our records (302) showed zero or negative growth. These were assigned a very small non-zero value ( $10^{-8}$ ) to create an 'adjusted' data base ( $n = 2015$ ). Because such negative or zero growth may be due to measurement error, we created a 'pooled' data set that minimized potential error. First, we skipped recapture intervals showing

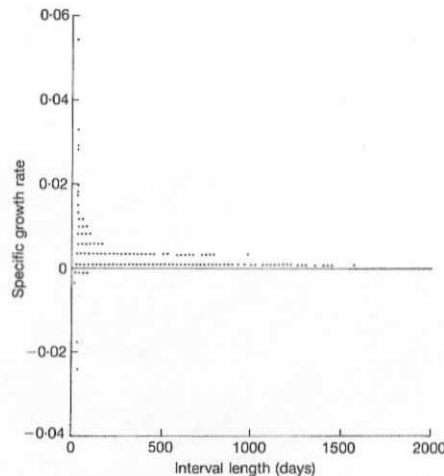


FIG. 1. Variability of specific growth rate (change in SVL/time/GMSL) in relation to capture interval (time in days since last capture). 1848 records plotted, some hidden.

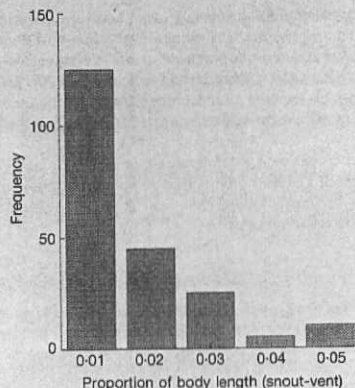


FIG. 2. Frequency of non-positive growth records as a percentage of body length.

negative growth, combining them with the next recapture showing positive growth. In cases where the final available record for an animal remained negative or zero, the capture history was eliminated from the data set. The rationale for skipping periods of apparent non-positive growth is that longer intervals between captures allowed the growth increment to overcome measurement error. We also eliminated other data that had a high probability of being in error. The highest variability in specific growth rates occurred when recaptures were made in fewer than 18 days (Fig. 1). Because this short-term variation is most likely due to measurement error, we eliminated recaptures within 18 days. Similarly, most negative growth records occurred when the growth increment was between 0.5 and 1.5% of body length (Fig. 2), so we also excluded growth records of less than 1.5% of initial size. Thus, the 'pooled data base' contained 1326 records, derived from consolidating adjacent records if possible (eliminating 121 non-positive changes in growth and 65 non-positive records that could not be so pooled), eliminating 129 growth records taken over recapture intervals less than 18 days, and eliminating 374 records with apparent changes in size of less than 1.5% of initial size.

Another aspect of data selection is the choice of the growth measurement itself. Although size varies over a growth interval, a point estimate of size must be used in developing a growth model. We tested the use of 3 size measures: the initial size, SVL1, (Causton, 1969); the geometric mean of initial and subsequent sizes,  $GMSVL = [(SVL1)(SVL2)]^{-1/2}$  (Kaufmann, 1981); and the arithmetic mean size,  $AMSVL = (SVL1 + SVL2)/2$  (Van Devender, 1978).

### Results

The descriptive statistics for allometric measurements, specific growth rates, and recapture intervals are shown in Table I. Three data subsets and three size measures were analysed to examine the potential effects of data selection on seven models of growth (Table II).

#### Model evaluation

##### Data set effect

On comparing the regression results for the positive, adjusted and pooled data sets (Table II),

TABLE I  
Summary statistics for three data sets used to evaluate growth models for Everglades alligators

Variable <sup>1</sup>	Statistic <sup>2</sup>						
	Mean	S.D.	Max.	Q <sup>3</sup>	Med.	Q <sup>1</sup>	Min.
<b>Adjusted Records (n = 2015)</b>							
SVL1 (cm)	23.3	19.36	166.5	24.5	16.1	14.1	11.0
GMSVL (cm)	24.6	19.76	164.9	25.8	17.1	14.6	11.2
AMSVL (cm)	24.6	17.79	165.0	26.0	17.2	14.6	11.2
SGR (day <sup>-1</sup> )	0.0014	0.00273	0.0558	0.00184	0.000767	0.000219	-0.00239
TIME (days)	147.5	200.2	1865	163	70	35	1
<b>Positive Records (n = 1713)</b>							
SVL1 (cm)	23.0	18.03	160.5	24.5	16.0	14.0	11.0
GMSVL (cm)	24.4	18.65	164.9	26.0	17.2	14.6	11.4
AMSVL (cm)	24.5	28.69	165.0	26.2	17.3	14.6	11.4
SGR (day <sup>-1</sup> )	0.0017	0.00268	0.0558	0.0021	0.0010	0.00044	0.000046
TIME (days)	158.5	210.20	1865	182	77	35	1
<b>Pooled Records (n = 1326)</b>							
SVL1 (cm)	22.6	17.9	160.5	24.4	16.0	14.0	11.3
GMSVL (cm)	23.9	17.07	163.2	25.7	17.4	14.8	12.1
AMSVL (cm)	24.2	17.84	165.0	26.2	17.4	14.7	11.4
SGR (day <sup>-1</sup> )	0.0016	0.00141	0.0079	0.0022	0.0012	0.00055	0.000040
TIME (days)	166.9	213.5	1865	194	91	9	19

<sup>1</sup> Variables are initial snout-vent length (SVL1), geometric mean snout-vent length (GMSVL), arithmetic mean snout-vent length (AMSVL), specific growth rate (SGR), and length of capture interval (TIME). For meaning of record subsets see text.

<sup>2</sup> Statistics include standard deviation (S.D.), maximum value observed (Max.), upper (Q<sup>3</sup>) and lower (Q<sup>1</sup>) quartiles, median (Med.), and minimum (Min.) values.

the R<sup>2</sup> values, slopes and intercepts were increased by eliminating or pooling negative and zero growth records compared with adjusting these records to a minimum non-zero positive growth value. The effect of the choice of data set used differed depending on the model being evaluated, owing in part to the nature of the differing transformations. Only a small data set effect was apparent on the fit and parameter estimates of the logistic, Von Bertalanffy, Richards or Gompertz models. The greatest effects were observed with the power and log-normal models.

In these models, when negative and zero records were eliminated or pooled, the R<sup>2</sup> values increased 8–15 times over those obtained using adjusted data. The use of adjusted records especially affected the power model because the mathematics require a declining function set above the y-axis, where the zero records fall. Thus, the negative and zero growth records (Fig. 3a) are widely separated from the bulk of data that otherwise tend to support the selection of the power model. As in any least-squares model, the fit is extremely sensitive to such extreme values. These records are not part of the general trend of the data, and they are not linked by transitional records. In contrast, in curves such as the Von Bertalanffy (Fig. 3b), the small positive slope incorporates points along the y-axis which do not much affect the relatively poor fit. The omission of zero growth data in the pooled and positive data sets proved more useful in developing a generalized growth model of alligators that were actually growing. Of the two data sets (pooled

TABLE II

Linear regression parameters for evaluation of growth model for Everglades alligators using three data sets

Model	Size <sup>1</sup>	MSE	R <sup>2</sup>	Slope	Intercept	MSE	R <sup>2</sup>	Slope	Intercept
Positive Records <i>n</i> = 1713									
Logistic	GMSVL	0.000067	0.069	-0.000038	0.0027	0.000062	0.051	-0.000029	0.0022
	AMSVL	0.000067	0.069	-0.000038	0.0027	0.000062	0.051	-0.000029	0.0022
	SVL1	0.000067	0.067	-0.000039	0.0026	0.000062	0.052	-0.000030	0.0022
Power	GMSVL	1.0446	0.300	-1.346	-2.912	11.619	0.021	-1.000	-5.333
	AMSVL	1.0497	0.297	-1.336	-2.937	11.632	0.020	-0.973	-5.412
	SVL1	0.987	0.339	-1.430	-2.749	11.381	0.041	-1.388	-4.230
Von Bertalanffy	GMSVL	0.000060	0.173	0.0579	-0.00131	0.000056	0.132	0.0482	-0.00107
	AMSVL	0.000060	0.172	0.0578	-0.00129	0.000057	0.131	0.0479	-0.00105
	SVL1	0.000059	0.179	0.0562	-0.00142	0.000055	0.152	0.0496	-0.00129
Log-Normal	GMSVL	1.112	0.256	-0.033	-6.191	11.576	0.025	-0.0276	-7.688
	AMSVL	1.114	0.254	-0.033	-6.191	11.585	0.024	-0.0272	-7.696
	SVL1	1.088	0.271	-0.035	-6.189	11.444	0.036	-0.0339	-7.575
Richards <i>c</i> = 1.0	GMSVL	0.000060	0.173	0.0579	-0.00131	0.000056	0.132	0.0482	-0.00107
	AMSVL	0.000060	0.172	0.0578	-0.00129	0.000057	0.131	0.0479	-0.00105
	SVL1	0.000059	0.179	0.0562	-0.00140	0.000055	0.152	0.0496	-0.00129
Richards <i>c</i> = 0.9	GMSVL	0.000060	0.168	0.0465	-0.00152	0.000057	0.129	0.0386	-0.00124
	AMSVL	0.000060	0.168	0.0464	-0.00150	0.000057	0.128	0.0384	-0.00122
	SVL1	0.000060	0.175	0.0453	-0.00163	0.000056	0.148	0.0398	-0.00147
Gompertz	GMSVL	0.000063	0.123	0.0075	-0.00189	0.000059	0.093	0.00616	-0.00154
	AMSVL	0.000063	0.123	0.0075	-0.00189	0.000059	0.093	0.00615	-0.00153
	SVL1	0.000063	0.126	0.0074	-0.00190	0.000058	0.102	0.00630	-0.00161

<sup>1</sup> Three size measures (snout-vent length) are tested—geometric mean (GMSVL), arithmetic mean (AMSVL), and initial (SVL1). Mean square errors (MSE) result from regressions of transformed data and are thus not comparable among models.

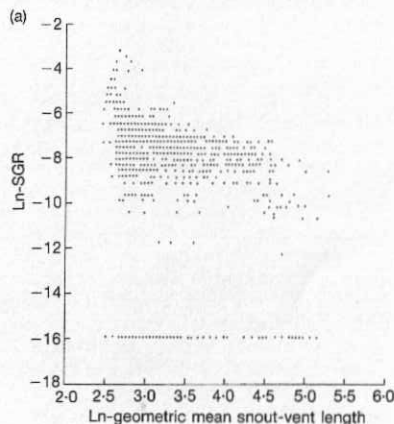


FIG. 3. Scatter plots of the relationship between specific growth rate (SGR) and length (transformed) according to the model being tested. (a) Power curve using all data, showing the departure of no growth data from linear relationship.

TABLE II (cont.)

MSE	R <sup>2</sup>	Slope	Intercept
Pooled Records <i>n</i> = 1326			
0.0000066	0.061	-0.000036	0.00251
0.0000066	0.061	-0.000036	0.00251
0.0000066	0.060	-0.000038	0.00248
1.222	0.251	-1.319	-3.123
1.228	0.248	-1.307	-3.154
1.153	0.294	-1.427	-2.887
0.0000059	0.152	0.0542	-0.00124
0.0000059	0.151	0.0541	-0.00122
0.0000059	0.160	0.0530	-0.00136
1.259	0.229	-0.0343	-6.296
1.262	0.226	-0.0341	-6.298
1.226	0.249	-0.0371	-6.283
0.0000059	0.160	0.0530	-0.00136
0.0000059	0.152	0.0542	-0.00124
0.0000059	0.151	0.0541	-0.00122
0.0000059	0.156	0.0428	-0.00156
0.0000059	0.148	0.0435	-0.00144
0.0000060	0.148	0.0434	-0.00142
0.0000062	0.109	-0.0018	0.00708
0.0000062	0.109	-0.0018	0.00707
0.0000062	0.112	-0.0018	0.00705

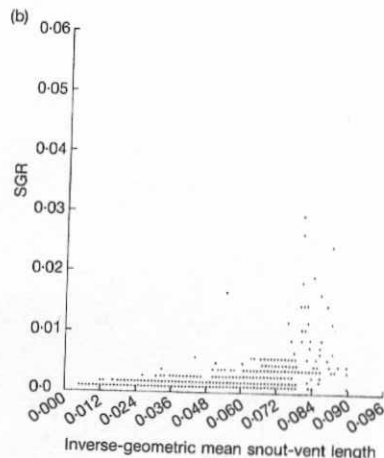


FIG. 3. Scatter plots of the relationship between specific growth rate (SGR) and length (transformed) according to the model being tested. (b) Von Bertalanffy curve, showing poor linearity.

and positive), the model derived from pooled data was less arbitrary because it allows more accurate growth measures of larger alligators, which have a strong effect on the ultimate shape of the growth curve.

#### Size measure effect

We evaluated the effect on model estimates of three size measures—geometric mean (GMSVL), arithmetic mean (AMSVL) and initial (SVL1) snout-vent length (Table II). The use of SVL1 provided slightly higher  $R^2$  values across models and across data sets. However, as might be expected, SVL1 underestimated size (Fig. 4), and becomes an increasingly inappropriate measurement as capture intervals (i.e. total growth in the interval) become large (Van Devender, 1978). The arithmetic mean and geometric mean gave equivalent predictions (Fig. 4) and similar  $R^2$  values (Table II). The choice between the two therefore becomes a theoretical and practical matter. GMSVL reflects better the variable growth rate that actually occurs within capture intervals and has been used in critical studies of growth curve analysis (Kaufmann, 1981; Zach & Mayoh, 1984). Other measures of central tendency might also be used (e.g. median, harmonic mean) but, given the similarity of results using arithmetic and geometric means, there is little reason to use intermediate measures. Thus the geometric mean appears to be an appropriate size measure for mark-recapture data obtained from unequal capture intervals.

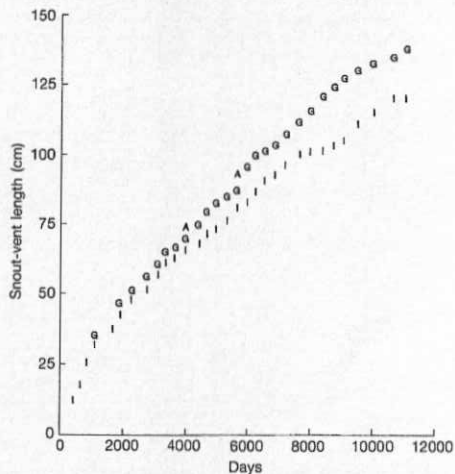


FIG. 4. Differences in growth estimates by the power curve model using three measures of length. I = Initial Snout-vent Length. G = Geometric Mean Length. A = Arithmetic Mean Length. Most 'A's are hidden by 'G's; both 'A's and 'G's are hidden by 'I's at early points in curves.

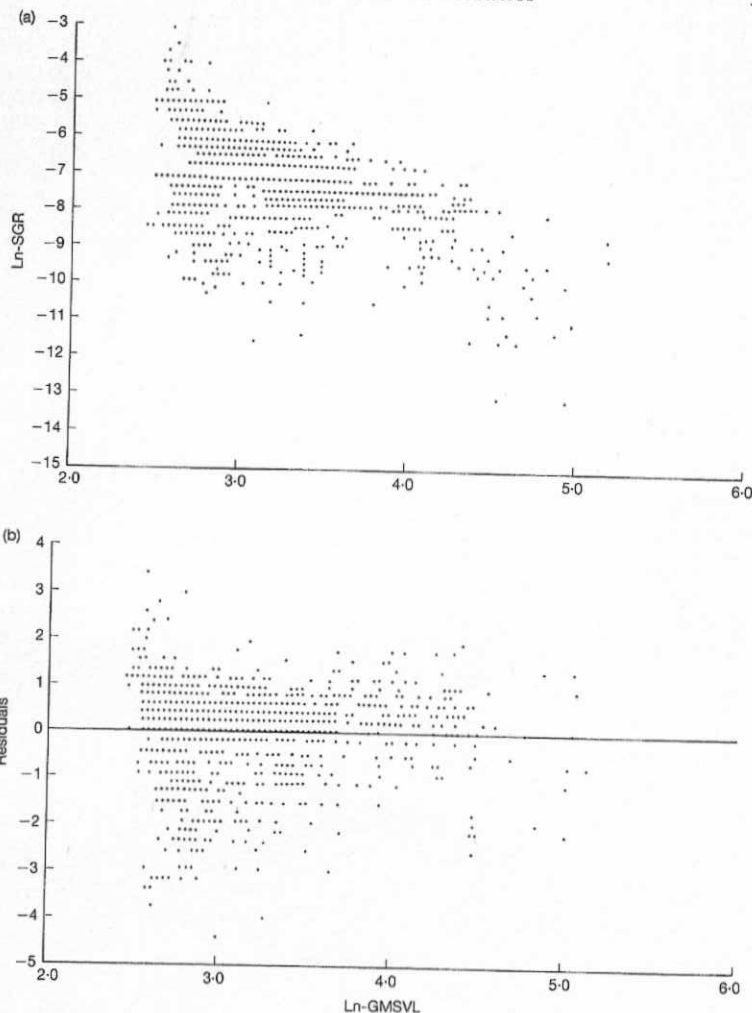


FIG. 5. (a) Linear relationship between specific growth rate (SGR) and geometric mean length (GMSVL), and (b) the corresponding residual plot.

### Model effect

The decision as to which of several growth models was most appropriate depended to a certain extent on the data set used. Using 'adjusted' data, the highest  $R^2$  values were for the Von Bertalanffy and Richards' curves. Using the 'positive' and 'pooled' data, the power model was the best fitting, significantly better than the model with the next highest  $R^2$  value, the Von Bertalanffy ( $T=4.977$ ,  $P<0.001$ ,  $df=1704$ ). Because of the better fit using positive and pooled data, we concluded that the power curve represented the generalized growth of Everglades alligators more precisely than did the other models.

The linear relationship for the power curve model, using pooled data and GMSVL, is shown in Fig. 5. Evaluating the linear parameters described by Kaufmann (1981):

$$S = [ab(t + t_0)]^{1/a}$$

the growth model of Everglades alligators takes the form:

$$SVL = 12.3 [1.319 (0.0016) (A + 473.844)]^{0.758}$$

where SVL is the predicted snout-vent length in cm and A is the age in days. The size (SVL) at age = 0 (hatching) is 12.3 cm for Everglades alligators.

In deriving this model, the frequency with which individual alligators contribute more than one data point are: 207 captured twice; 82 three times; 26 four times; 10 five times; 2 six times; and 1 seven times. Characteristics of data eliminated to arrive at the final model indicate that a larger percentage of small than large alligators were dropped because the capture interval did not exceed 18 days, while a larger percentage of large than small alligators were dropped because the growth recorded was less than 1.5% of the initial size.

### Model verification

To examine further the accuracy of the model, we modelled growth using 451 records of

TABLE III

Linear regression parameters of specific growth rate versus the geometric mean snout-vent length between captures, for growth data of known-age Everglades alligators

Model	MSE	$R^2$	F	df.	a	b
Logistic	0.0016	0.087	48.5	1,510	0.0070	-0.00032
Power	0.691	0.051	27.5	1,510	-1.99	-1.599
Gompertz	0.0016	0.088	49.1	1,510	0.0154	-0.0049
Ln-normal	0.691	0.053	28.3	1,510	-4.716	-0.106
Von Bertalanffy	0.0016	0.088	48.9	1,510	-0.0027	0.073

TABLE IV

Regression statistics for linear regression models fitted to four age segments

Section	Time interval	MSE	$R^2$	F	df.	a (at x=0)	b	Significance
A	18-110 days	1.00	0.347	153.83	1,290	13.24	0.028	<0.05
B	110-190 days	1.90	0.132	13.53	1,89	17.84	-0.018	<0.05
C	190-360 days	1.22	0.767	237.30	1,72	7.87	0.038	<0.05
D	Over 360 days	2.81	0.643	98.97	1,55	15.47	0.016	<0.05

alligators for whom hatching date was known. The oldest known-age alligator included was 1460 days old. The mean size of these animals at hatching was 12.3 cm (S.D. = 1.252,  $n=451$ ).

None of the curvilinear models fits the known-aged data well, over the entire growth curve (Table III). We therefore fitted a succession of linear regressions, which revealed four distinct growth periods during the first year (Table IV). The age-size scatterplot of the known-age data (Fig. 6) shows an early slowing (and perhaps reversal) of growth that was not modelled by the continuous functions. This is shown in Fig. 7, which compares the piece-wise linear model with the power curve model. Early growth was initially rapid, until four months after hatching (in late August). From age 110 to 190 days, or December to March, there was a retardation of growth, which is actually fitted with a negatively sloping line, although the fit was not tight (Table IV, section B). The coldest temperatures of the year occurred during this period. Growth resumed in April, as indicated by the third regression, section C. A small but positive slope in section D indicated that the effect of the second winter was less severe than that of the first winter. The empirical curve cycles around the power curve before paralleling it. Thus the models differed in year one, but were similar thereafter, over the period compared.

### Comparative growth

Previous studies of the growth of American alligators did not use a power model. Thus we cannot compare model parameters among existing studies. However, we can compare predictions of the models selected, for whatever reasons, by the various authors. (Because other authors used total length, we converted our SVL for this comparison.) The age-size relationship based on the power function can be used to generate the predicted mean size of Everglades alligators at any age, which can be compared with sizes of alligators generated using models of populations in other geographic areas.

In such a comparison (Table V) we find that Everglades alligators grow relatively slowly, reaching just 1.26 m in total length in 10 years. Alligators in Louisiana and in an artificially heated lake in South Carolina are estimated to reach this size in just 3-4 years, growing from 2.5 to 3.3

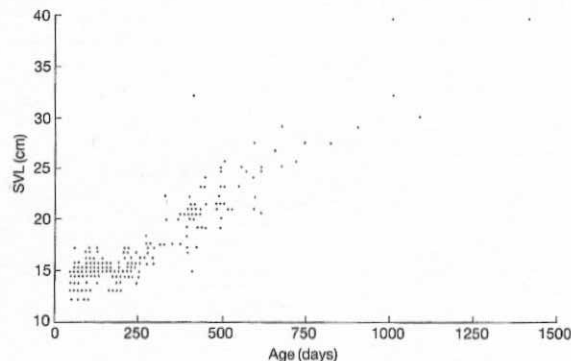


FIG. 6. Scatter plot of the growth of known-aged alligators (615 observations plotted, some hidden).

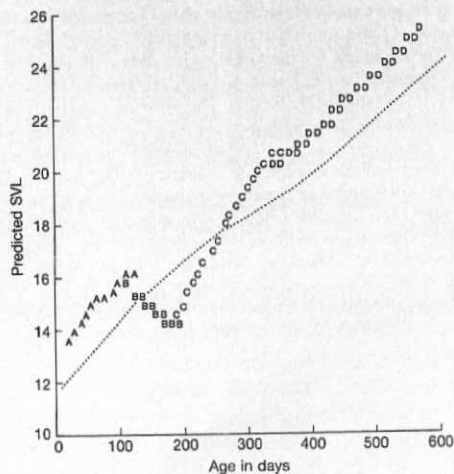


FIG. 7. Comparison of the power curve model of alligator growth to a model using sequential linear equations. Linear segments identified by number.

TABLE V

Comparison of predicted total length of alligators of different ages in several localities

Age (years)	Predicted total length (cm)					
	Louisiana McIlhenny <sup>1</sup>	Louisiana Chabreck <sup>2</sup>	S. Carolina Hot Arm <sup>3</sup>	S. Carolina North Arm <sup>3</sup>	Everglades <sup>4</sup>	N. Carolina <sup>5</sup>
1	60.5	55.6	51.4	43.1	37.9	38.3
2	95.9	84.7	76.7	62.2	49.9	51.8
3	131.2	110.8	101.9	81.2	65.2	64.4
4	166.6	134.1	127.1	100.3	76.4	76.7
5	201.9	155.0	152.3	119.4	86.9	88.0
6	237.3	173.8	177.6	138.5	97.0	98.8
7	272.6	190.6	202.8	157.6	106.6	108.8
8	308.0	205.8	228.1	176.6	116.0	118.4
9	343.3	219.4	253.3	195.7	125.0	127.3
10	378.7	231.6	278.6	214.8	126.8	135.7

<sup>1</sup> McIlhenny, 1934

<sup>2</sup> Chabreck & Joanen, 1979

<sup>3</sup> Murphy, 1981

<sup>4</sup> This study, power curves

<sup>5</sup> Fuller, 1981

times faster than alligators in the Everglades. Alligators can grow even faster in captivity (Coulson *et al.*, 1973).

The predicted sizes for Everglades alligators using a power function are similar to sizes predicted for alligators in North Carolina. At an age of 30 years, the Von Bertalanffy model for North Carolina predicts that females will reach an asymptotic size of 2.39 m total length, with males reaching 2.55 m total length, giving an average prediction of 2.47 m total length. For 30-year-old Everglades alligators, the size reached is estimated to be 2.27 m total length. Thus, Everglades alligators grow relatively slowly and reach full maturity at a small size.

## Discussion

### Factors affecting model selection

The selection of a growth model may be influenced by the choice of variables, the analytical procedures employed, and by the character and quality of the data. As suggested by our results, insufficient consideration to implicit or explicit assumptions may strongly bias the biological interpretation of the growth model selected.

There are, broadly, two types of data that can be collected in growth studies. In the classical mark-recapture study, the growth process may be followed over infrequent but intensive, well-replicated recaptures of animals of all ages, providing 'cross-sectional' data. Recaptures may alternatively be made such that the growth curve can be fitted to fewer individuals, usually of known age followed intensively over time, providing 'longitudinal' or 'functional' data. In practice, many mark-recapture studies are intermediate between cross-sectional and longitudinal approaches. In dealing with a long-lived species with high mortality rates, such as crocodylians, mark-recapture studies such as the one presented here must inevitably be more of the cross-sectional type if a comprehensive growth model is the objective.

Use of such a study design requires the assumption that the growth of all individuals approximate the mean trajectory that is characteristic of the population under study. Thus when we use the observed sizes of an individual at different times, we are assuming that each record represents the growth of a 'representative individual' in the population. We also assume that neither capture interval differences nor seasonality will cause large deviations from the 'average' growth curve. Neither of these assumptions is true (Ricklefs & Peters, 1979; Zach & Mayoh, 1982), and deviations from such assumptions may cause difficulties in determining the most appropriate form of the growth curve.

The use of discrete growth intervals to approximate a continuous growth process often requires a number of assumptions among which are, constancy of rate within the growth interval, minimization of measurement error, and representativeness of the model over the chosen interval. In mark-recapture studies, there is little freedom to choose the growth interval, which is frequently variable among individuals in the data set. Ford-Walford plots, which are used in fisheries studies (Ricker, 1975), require that time intervals for all data points be the same, and data taken over different time intervals cannot be pooled. Other problems with variable interval lengths are that long intervals confound seasonal, annual, or age-dependent differences in growth and may inhibit detection of the approach to asymptotic size. Short intervals may result in greater residuals because the growth increment is small relative to measurement error (Fig. 1). We feel that variable interval length is such an inherent feature of mark-recapture data that its effect must be accepted as an error component in any growth model.



In our data, measurement interval length varied, as probably did the growth rate within that interval. We concluded that the geometric mean size was the most acceptable point estimate of size within the interval. However, any mean estimate involves error associated with both measurements rather than a single measurement, as is the case with using initial length.

Growth records can be partitioned into components representing: (1) the mean increase in size; (2) a deviation from the mean response due to seasonal and individual variability; and (3) potentially size-variant measurement errors that occur at both measurement events. The potential for error is size-varying because any associated error would represent a larger proportion of measured length of smaller than of larger animals, which could lead to an unequal variance distribution in the final growth curve. This assumes that large alligators are as accurately measured as small alligators, but field workers (and anyone watching an alligator wrestling match) would agree that the potential is greater for measuring large crocodilians inaccurately. Thus, it may be that the error variance is evened out across the range of data used in the model.

There are two ways of dealing mathematically with error in growth records, described as 'sampling error' and 'process error' models. Least squares estimation techniques, used in sampling-error growth models, represent the growth process by incorporating stochastic variation or error as part of each growth measurement (White & Brisbin, 1980). Basic assumptions for fitting the sampling error model may not be met often in practice. Autocorrelation of errors may be significant, especially in that the optimal sampling interval over which errors can be assumed to be independent is generally not evaluated and not incorporated into planning. Process error models are recommended in such situations. Assumptions of independence, however, are more likely to be violated when a model is based strongly on few individuals contributing many data points. In our study situation, we were able to use data on many individuals with a low percentage of recaptures, thereby diminishing autocorrelation. Thus, while acknowledging the potential usefulness of process error models for describing the stochastic component of growth, we believe that the use of the traditional sampling error approach is appropriate for three reasons: the estimates are unbiased (and identical) regardless of the error method used (White & Brisbin, 1980); the method is straightforward using standard linear least square estimation techniques; little autocorrelation is anticipated owing to limited repetition of individuals in the data set.

We had hoped to treat all sources of error, including zero and negative growth records, as residuals. However, it is usually the case in such studies that apparent negative or zero growth records are ignored in order to increase the goodness of fit of the model or even to be able to use a particular model at all, in that some models require transformation by logarithms or calculating the inverse ratio of the growth rate, making these variables undefined for some models. Because of this, some authors have eliminated up to 70% of their records (e.g. van Devender, 1978). Unfortunately, to evaluate growth models, some selection from or adjustment to the data set appears to be required.

In evaluating the effect of data choice, we examined several data sets, each having certain assumptions. Our primary data set contained all records, some of which could not be used in all models. An 'adjusted' set, approximating zero growth by a small non-zero positive growth rate, implicitly assumes that growth occurs in all intervals. A third approach that eliminated all negative or zero growth records from a 'positive' data set assumed such records to be in error. A fourth approach attempted to account for various sources of error by 'pooling' negative or zero growth intervals with adjacent positive intervals and also by setting detection limits, using a procedure partly analogous to the 'fixed' data used by Schoener & Schoener (1978). The strength of using such pooled data is in minimizing the exclusion of data while meeting the mathematical

requirements of the monotonically increasing growth models. Non-growing animals provide no information on the pattern of growth, and are best considered outliers to the growth data base (Fig. 3a). It should be remembered, however, that the model plots the growth of growing animals to address questions of growth patterns. For other applications, such as to address questions of individual variation, it might be quite useful to identify the residual nongrowth data for additional analysis.

In our selection of the power curve, we used the pooled data set because it was more accurate and because it provided the best fit. Use of pooled data may have especially important implications when a choice is being made between an asymptotic and non-asymptotic model, because small growth increments were not included in the model. Obtaining accurate growth records of large alligators should be of special concern in the future.

#### *Growth dynamics*

Our analysis indicates that the growth of Everglades alligators is best modelled by the exponential power curve. The non-asymptotic shape of the power curve implies that the growth of Everglades alligators is indeterminate. Thus we reject the hypothesis, based on previous modelling studies, that growth is asymptotic. Among vertebrates, such indeterminate growth is primarily characteristic of fishes, and has a strong environmental component (Weatherley, 1972). Temperature and food availability influence growth rates and final size (Brett, 1979). Because growth depends on energy intake minus energy costs, decreasing food availability or increasing costs (expenditures and metabolic costs) could retard growth. Species having asymptotic growth dynamics are subjected to selective pressures to maximize growth within physiological limits, whereas indeterminate growth accommodates additional flexibility to vary not only the rate but also the trajectory of growth. Thus it becomes possible to delay growth or alter size at maturity under environmentally restrictive conditions. For a large, slow-growing poikilotherm, indeterminate growth should permit optimal responses to environmental constraints.

Our confidence in the use of any growth function to describe the indeterminate growth of Everglades alligators is, of course, constrained to the range of sizes observed in this study. Beyond this point an asymptote may exist. None the less, indeterminate growth is not inconsistent with morphological evidence from skeletal growth dynamics. Unlike most vertebrates, the ends of crocodilian long bones do not fully ossify allowing continuous growth in bone length (de Ricqlès, 1975).

One purpose in deriving a theoretically based model of growth was to compare the growth of alligators in the Everglades to those elsewhere, living under different environmental conditions. Unfortunately, comparative interpretations of current models of crocodilian growth are limited because the models chosen by various authors differed and did not involve an objective evaluation of alternative indeterminate models. Our selection of the power model based upon best fit did not correspond to any previously chosen model of alligator growth. Thus differences in model parameters cannot be evaluated.

On the other hand, it may be that a universally applicable growth model does not exist. There seems little reason to expect growth to follow a particular mathematical model in different populations, and the best fit in one location may not be so in another. In fact, it has been suggested that the growth curve shape may be more likely to change in response to environmental stress than would other curve parameters (Brisbin *et al.*, 1986, 1987). Forcing a fit without evaluating other models provides no assurance of its appropriateness. Thus it may be both feasible and desirable to

compare the outcomes of the growth processes, rather than the model parameters, irrespective of the models chosen, (Zach, 1988).

The low metabolic rate characteristic of reptiles can permit limitation of their growth potential in the wild below that which might theoretically occur under ideal environmental conditions. Our initial hypothesis was that Everglades alligators would grow relatively fast in the subtropical Everglades because of the relatively long growing season and their metabolic efficiency (Burton & Likens, 1975). However, our results did not support this hypothesis in that Everglades alligators grew at a rate comparable to alligators in the much cooler and more seasonal North Carolina, where the growing season is limited to 8 months per year (Fuller, 1981). Thus factors other than climate are limiting growth in this population.

We hypothesize that two factors are involved in the slow growth of Everglades alligators, lowered energy availability and higher costs. It is possible that food is limited in the Everglades, in that it lacks substantial populations of large prey, such as water fowl and mammals that make up much of the diet of adult alligators elsewhere (McNease & Joanen, 1977, 1981). This limited resource availability may inhibit growth. The second factor may be metabolic costs, which would be higher in warmer environments (Parks, 1983). Thus we suggest that the increased costs that cannot be offset by increased energy intake account for the lowered growth rates of Everglades alligators.

Homeotherms can achieve growth rates an order of magnitude greater than poikilotherms and thereby achieve adult size relatively rapidly (Case, 1978). Among the relatively slow-growing poikilotherms, large size can only be achieved by a long growth period, requiring longevity (de Rieqlès, 1975). The consequences of slow growth in Everglades alligators would have far reaching life history implications. A longer time required to reach sexual maturity increases susceptibility to predation, disease and cannibalism. When combined with a low survivorship rate, a long maturation period would thus require a large annual output of hatchlings. However, the clutch size of Everglades alligators is less than that in other populations and mortality is high (Kushlan & Jacobsen, In prep.). Because the slow growth of Everglades alligators is not compensated by increased reproductive output, the overall life history strategy of Everglades alligators must be constrained by its growth dynamics.

#### Summary

Our results suggest that the growth of alligators in the Florida Everglades is indeterminate, with body size continuing to increase through adulthood. Determining whether other populations grow similarly will require re-evaluation of previous studies to determine if a non-asymptotic model better fits the growth data available. Information on the growth of large alligators is also desirable.

Southern Florida alligators grow more slowly than do alligators from more northern populations having shorter growing seasons. We suggest that higher metabolic costs and a lower food base in the Everglades is responsible for the retarded growth.

Studies of body growth, using pre-existing theoretical models, require comparative fitting rather than a priori choice. Growth dynamics of different populations may best be evaluated using predictions of the growth models for comparable ages rather than comparative model parameters or shapes.

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## Life history differences among the eutherian radiations

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(With 3 figures in the text)

In this paper, we critically evaluate the view that eutherian life history diversity arises because of constraints imposed by the allometric consequences of body size, rather than selection acting on a broad array of possible life histories. Using life history data from over 700 species of eutherians, we examine covariation of life history variables across the 18 orders represented. Eutherian orders can be arranged from those characterized by small rapidly reproducing, rapidly developing, short-lived species, such as lagomorphs, to large, slowly developing, slowly reproducing, long lived species, such as elephants. When the effect of body weight is controlled for, this pattern remains, but the relative positions of the orders on the new fast-slow continuum are very different. There is a trade-off between the weight and number of offspring in a litter which is independent of adult body weight. Maximum recorded lifespan is the best identified predictor of annual fecundity: high fecundity is associated with short lives. This is not easily explained as a cost of reproduction, because it is a function of the whole lifetime, rather than just the maximum reproductive lifespan. Those mechanisms said to underlie the allometric scaling of life histories, and which make testable predictions—growth constraints imposed by basal metabolic rate, brain weight and the rate of neuronal tissue growth—are not associated with life history variation once the effects of body weight are removed. Thus these variables have no greater explanatory power than body weight itself, since they cannot explain the variation in life histories which is not correlated with weight. Rates of litter growth rate are associated with life history variation independent of body weight, but until we understand why litter growth rates vary, they are unable, on their own, to explain considerable amounts of life history diversity. Differences in life histories among orders, whether or not the effect of body weight is controlled for, are associated with differences in mortality rates. We suggest that eutherian life histories are better thought of as adaptive strategies, and that mortality patterns offer considerably more promise in the understanding of eutherian life history diversity than loosely defined ideas about scaling principles and the allometric consequences of body size.

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