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GROWTH RATES OF AMERICAN ALLIGATORS IN LOUISIANA

Robert H. Chabreck and Ted Joanen

Abstract: A capture–recapture technique was used to determine growth rates of American alligators (*Alligator mississippiensis*) in Louisiana. A strong relationship was found between total length and both snout–vent length and weight. Comparisons between small alligators showed that growth rates of males and females are not different until animals attain a total length of 1.0 m, after which growth of females declines sharply. Growth rates during different periods of the year are greatest during mid-summer and less during the spring and fall; no growth occurs during winter (Oct–Mar). A mathematical model indicates that males grow fairly rapidly for 20 years (until they are ≈3.50 m long) and that they reach a projected total length of 4.20 m at age 80. Growth of females declines considerably after age 10, and individuals are only about 2.55 m long at age 20. The maximum projected length of females is 2.73 m at age 45.

Key words: *Alligator*; Growth; Louisiana

The American alligator (*Alligator mississippiensis*) occurs in lakes, streams, and marshes of southeastern North America and is a long-lived reptile varying considerably in size. Various authors have reported growth rates, maximum sizes, and longevity (Bara, 1972; Hines et al., 1968; Kellogg, 1929; McIlhenny, 1934; Whitworth, 1971). Reported growth rates were obtained using captive animals or were based upon observations represented by limited sample size and genetic variation.

The best information available is from a single brood of 38 newly hatched young in Louisiana that were captured, marked, and released at the nest by McIlhenny (1934). Individuals were recaptured and measured over a period of 11 yr and provided 63 observations. Hines et al. (1968) presented information on growth of 33 immature alligators in Florida, and Bara (1972) reported growth rates of 26 immature animals in South Carolina. Nichols et al. (1976) used the sizes of alligators of known age recovered by McIlhenny (1934) to construct growth curves, but stated that more information is needed on age–size relationships in the species.

A life history study was begun on the American alligator in Louisiana in 1959, and more than 2,500 animals have been captured, marked, and released. Recovery of marked alligators over a period of 17 yr provides information on growth rates of animals under natural conditions. Most recoveries were of alligators from smaller size classes during the early years of the study; but a commercial harvest program was initiated in 1972, and additional recoveries were made of marked adults. During the study, 218 marked alligators were recovered (Table 1). Of these, 163 were 2 m or less in length and 55 were more than 2 m long (including 16 which were more than 3 m long).

Kellogg (1929) reported that alligators are inactive during the winter months, and observations by Joanen and McNease (1971) indicated that captive alligators feed only about 8 mo of the year. Alligators stop accepting food in mid-October and do not resume feeding until March. Therefore, as a segment of this study, we compared growth of small alligators at different times of the year.

Methods

The study was conducted in southwestern Louisiana, and most alligators were captured on the Rockefeller Wildlife Ref-

TABLE 1.—Number of alligators recovered between 1959 and 1976.

Size class (m) when recovered	Sex	n
<.50	♂	3
	♀	2
	Unknown	15
.51–1.00	♂	21
	♀	19
	Unknown	26
1.01–1.50	♂	24
	♀	22
1.51–2.00	♂	12
	♀	19
2.01–2.50	♂	15
	♀	9
2.51–3.00	♂	14
	♀	1
3.01–3.50	♂	16
	♀	0
Subtotal	♂	105
	♀	72
	Unknown	41
Total		218

uge. The Refuge is composed of coastal marshland; contains numerous bayous, canals, and shallow ponds; and lies adjacent to the Gulf of Mexico. Marked individuals dispersed widely after release (Chabreck, 1965; Joanen and McNease, 1970, 1972; McNease and Joanen, 1974), but most recoveries were made on the refuge and on adjacent marshlands. Water salinities ranged from 0 to 18 ppt, but most alligators were located in areas with salinity less than 5 ppt (Chabreck, 1971).

Alligators were located by traveling waterways at night in a boat and shining their eyes with a headlight. Animals were captured by placing a wire noose mounted on a heavy pole around the neck. The noose was then tightened, and the alligator was pulled into the boat or towed to the nearest shore where it was measured and marked and its sex was determined.

Alligators were marked by toe-clipping and by notching dorsal tail-scutes. A monel tag was attached to the tail scutes. Capturing, marking, and sexing techniques were described in detail by Chabreck (1963).

Total length (TL) was measured along the dorsal surface of each animal from the tip of the snout to the tip of the tail. Snout–vent length (SVL) was measured along the ventral surface from the tip of the snout to the posterior edge of the vent. Regression analysis was used to develop predictive models for relating TL measurements to both SVL and weight as described by Snedecor and Cochran (1967). A stepwise regression technique was used to select the "best" model for predicting weight from known TL. The technique used 6 powers of TL ($\sqrt{TL}$, TL, $\sqrt{TL^3}$, TL^2, $\sqrt{TL^5}$, and TL^3) as independent variables, which were tested individually and in various combinations. The technique employs the maximum R^2 improvement procedure, as developed by Goodnight (Barr et al., 1976). This procedure selects the "best" one-variable model, the "best" two-variable model, and so on; and the variables added to the model at each step are those producing the largest increase in R^2. Models considered in the selection process had all independent variables significant at $P \leqslant .05$. The model finally selected includes as many independent variables as necessary for accuracy but no more than are necessary for a good fit. The data set contained 321 observations and included weight and total length measurements from both male and female alligators.

To compare growth rates of small alligators, individuals of both sexes were grouped into four classes based upon TL: class 1 (<50 cm), class 2 (50–75 cm), class 3 (76–100 cm), and class 4 (101–125 cm). Four males in each size class were paired with 4 females for testing. Pairing was done with animals of almost identical size over similar periods of time, and under similar habitat and seasonal conditions. A paired *t*-test (Steel and Torre, 1960) was used to test for differences between sexes in each class.

Monthly growth rates of small alligators (20–125 cm long) during different times of the year were compared by dividing the year into 4 periods: period 1 (Apr–May), period 2 (Jun–Jul), period 3 (Aug–Sep), and period 4 (Oct–Mar). Although alligators normally feed during 8 mo of the year (Joanen and McNease, 1971), the months at the beginning (Mar) and end (Oct) of the feeding period were considered to be marginal and therefore were included in the fasting period. Growth rates were recorded on seven different individuals of various sizes during each period, using males and females taken randomly. Differences between periods were tested using analysis of variance with a completely randomized design. Orthogonal comparisons were used to locate differences (Snedecor and Cochran, 1967). No growth was noted during period 4; consequently, that period was not included in the statistical analysis.

Growth in TL with time was computed from capture–recapture data using the von Bertalanffy growth curve as described by Fabens (1965). This method is particularly valuable for incorporating growth data for animals of known sizes for which information on age is not available. Growth curves were developed for both male ($n = 167$) and female alligators ($n = 137$). No difference was found ($P > 0.05$) between growth rates of males and females less than 1.0 m TL (see Table 2), and data from these individuals ($n = 86$) were pooled and used in developing growth curves for both males and females. Only data from the 8 mo of the year when alligators feed were included in the analysis.

Fabens (1965) has reviewed a procedure for fitting capture–recapture data with a growth curve of the form

$$x = a(1 - be^{-kt}) \qquad (1)$$

where x is size expressed as TL, t is age of the animal in months (8 mo = 1 yr), a is an upper bound of x (to be estimated), b is a parameter (to be estimated), k is a parameter (to be estimated), and e is the base of natural logarithms.

Fabens (1965) also presented a computer program written in FORTRAN that permits estimation of the aforementioned parameters. The computer program estimated those data in two parts. The first part was done with the capture–recapture data. Fabens (1965) noted that the parameters a and k can be estimated from a relationship derived from equation (1):

$$y = x + (a - x)(1 - e^{-kd}) \qquad (2)$$

where x is the size measurement at the first capture (time t), y is the size measurement at the second capture (time t + d), d is the elapsed time between captures, and a and k are parameters described above which were calculated by an iterated least squares method.

The second part estimated the parameter b. A second set of data taken from field measurements of newly hatched alligators (TL = 0.23 m) was included in the data and established the size at age 0.

After both sets of data had been used to secure estimates of a, b, and k, the program automatically calculated a number of points and plotted eq. (1).

RESULTS AND DISCUSSION

Relationship of SVL to TL.—SVL is the standard measurement normally used in describing sizes of most reptiles and amphibians. However, TL is the standard upon which regulations for harvest of alligators are based (Palmisano et al., 1973) and was used during this investigation, although SVL was recorded on a number of animals. In order to determine the relationship between these two variables, regression analysis was used with TL considered as the independent variable. Data from male ($n = 63$) and female ($n = 48$) alligators were analyzed separately to test for differences between the sexes.

Regression analysis (Fig. 1) disclosed that SVL of both male and female alligators is almost exactly one-half of the TL. Correlation coefficients (r) indicated that the measurements are highly correlated in both males (0.9987) and females (0.9957). SVL of small males is similar to that of small females, but SVL of males increases more rapidly with increasing TL than that of females ($t = 3.34$, df $= 107$, $P < .01$).

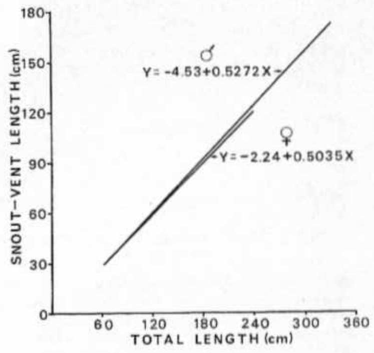

FIG. 1.—Relationship between snout–vent length and total length in American alligators.

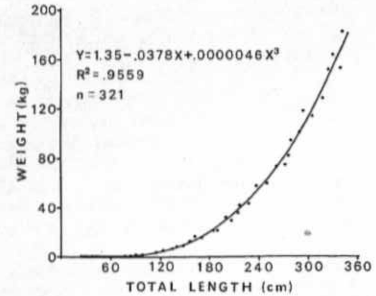

FIG. 2.—Relationship between weight and total length in American alligators. The data were partitioned into 25 cm length classes, and three observations were drawn at random from each class and plotted (solid circles) for comparison with predicted values shown by the curve.

Relationship of weight to TL.—The main reason for using TL as an index of body size was the ease with which measurements were made. Weighing animals required special equipment, and when a marked alligator was recovered, this equipment often was not available. Nevertheless, TL and weight measurements were made on enough individuals to determine the relationship between these two variables.

Data on weight by TL were partitioned in 25 cm TL groups, and three observations were randomly selected from each group and plotted in Figure 2 for comparison with weights predicted by the model. The model tends slightly to overestimate weight in newly hatched young and to underestimate weight of other young up to 1 m in TL. Above 1 m TL the model provides a very reliable estimate of weight. The coefficient of determination (R^2) indicates that 95.6% of the variation in weight was accounted for by the regression of weight on TL.

Growth rates of small alligators.—Monthly growth rates of small male and female alligators of four size classes were compared (Table 2). No difference was noted between sexes in classes 1, 2, and 3, which included individuals less than 100 cm TL. However, the same comparison between sexes in class 4 (101–125 cm) disclosed that males were growing at over twice the rate of females. The difference between sexes in class 4 apparently resulted from a reduction in growth of females at that size.

This segment of the investigation used

TABLE 2.—A comparison of monthly TL growth rates (cm) of small male and female alligators by size classes. The symbol $\bar{d}$ denotes the mean of differences in growth rates (♂ − ♀) within each size class ($n = 4$).

Class	Size (cm)	Mean monthly growth (± SD) ♂♂	♀♀	$\bar{d}$ ± SD	Paired t	P
1	<50	4.97 ± 3.32	4.76 ± 3.09	0.21 ± 0.61	0.70	>.10
2	50–75	2.97 ± 0.43	2.93 ± 0.53	0.04 ± 0.13	0.67	>.10
3	76–100	1.52 ± 0.68	1.75 ± 1.10	−0.23 ± 0.50	−0.90	>.10
4	101–125	2.35 ± 0.24	1.01 ± 0.44	1.34 ± 0.75	3.56	<.05

paired observations and was conducted solely to test for differences between individually paired groups; therefore, comparisons among classes of one sex group were subject to considerable error. Nevertheless, females showed a progressive and rapid decline in growth from class 1 (4.76 cm/mo) to class 4 (1.01 cm/mo). Male growth also indicated a decline (4.97 cm/mo to 2.35 cm/mo) but at a somewhat lower rate and with some irregularity. The greater growth rate in males in class 4 (2.35 cm/mo) than in class 3 (1.52 cm/mo) apparently resulted from experimental error.

This test suggested that the growth rate of immature American alligators declines as size increases and that individuals of both sexes grow at similar rates until they are approximately 100 cm long. Beyond that size, the growth of the female declines at a greater rate than growth of the male.

Growth by period of the year.—Rates of growth in TL of small alligators (20–125 cm long) during three periods of the year were compared using mean monthly growth, and differences were noted among periods ($F = 9.36$; df = 2,18; $P < 0.01$). Mean growth rate in the group measured during period 1 was 2.1 cm/mo (Fig. 3). Growth rates increased during period 2 and averaged 6.0 cm/mo ($F = 15.66$; df = 1,18; $P < 0.01$). Mean growth declined to 2.7 cm/mo during period 3 ($F = 12.20$; df = 1,18; $P < 0.01$), or to about the same rate as in period 1, and continued to decline into period 4. In fact, no growth was noted during period 4, and shrinkage ranging from 0.1 to 0.4 cm/mo was recorded in 5 of the 7 alligators measured.

Coulson and Hernandez (1964) noted seasonal differences in metabolic rates of captive alligators and related these to blood glucose levels. Even when environmental temperature was maintained at 28°C, blood glucose levels in summer exceeded those recorded in winter. Lowest levels were recorded in the fall, and seasonal variation in mean plasma glucose concentrations followed patterns similar to those of animals subjected to natural seasonal conditions.

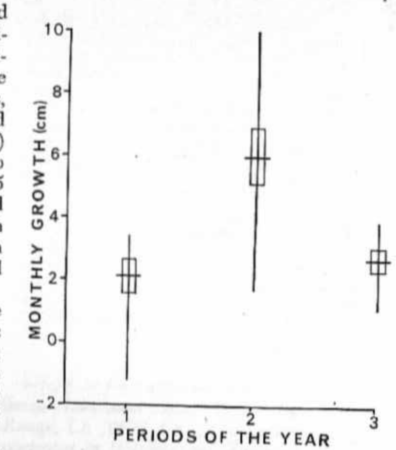

FIG. 3.—Growth in total length per month during three periods of the year. Vertical line = range ($n = 7$); open box = ±1 SE; horizontal line = mean. Period 1 = Apr–May; period 2 = Jun–Jul; period 3 = Aug–Sep.

They reported that blood glucose is low during the winter when appetite is decreased and high in summer when the alligator is hungry.

Coulson and Hernandez (1964) also attempted to identify the mechanism affecting food consumption and seasonal growth by holding two groups of 24 small alligators in tanks at constant temperature for 14 mo. One group was given 14 h of light daily (summer) and the other 10 h of light daily (winter) as observed in New Orleans. Day length had no effect on rates of food consumption, and when fall arrived, both groups responded by losing their appetites and decreasing the glucose level of the blood. No changes in body temperature, activity, or demeanor were noted.

Length–age relationships.—Length–age curves were derived from the capture–recapture data for both male and female alligators (Fig. 4). Values calculated for eq. (1) are:

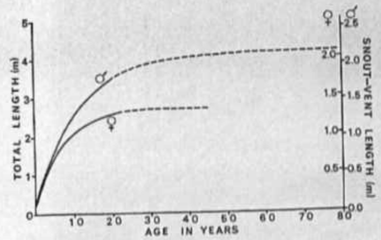

FIG. 4.—Length–age relationship derived from capture–recapture data (♂♂: $n = 167$; ♀♀: $n = 137$). Solid lines indicate the size classes included in the data. Broken lines represent the projected length–age relationship beyond the limits of the data.

$$\text{Males: } x = 4.205\,(1 - 0.9453e^{-0.01082t}).$$
$$\text{Females: } x = 2.735\,(1 - 0.9159e^{-0.01720t}).$$

The value of t in the formula represents the age of an animal in growth-months of which there are only 8 per year. Therefore, to predict length for any age (in years), the value of t should be calculated by multiplying that age (in years) by 8.

The difference in successive estimates of the parameters k and a after 20 iterations varied 0.04806% and 0.00017%, respectively, for males, and 0.12209% and 0.00036%, respectively, for females. The computed differences in k and a for males and females show that the data for females are considerably more variable and suggest greater variation in growth rates among females than males.

The length–age curve projected growth of males from age 0 to age 80 with a maximum TL of 4.20 m (Fig. 4). Growth of females was projected to age 45 with a maximum TL of 2.73 m. Both males and females grow at a fairly rapid rate during the first 10 yr with males reaching a TL of approximately 2.55 m and females 2.10 m at that time. Growth rates of females decline very rapidly beyond that point, and at age 20, they are approximately 2.55 m TL. Males, however, continue a fairly rapid growth and are approximately 3.50 m TL at age 20. Beyond that age, male growth declines rapidly, and at age 30, they approach 3.90 m TL; 4.00 m is not reached until age 40.

McIlhenny (1934) recorded the growth of alligators of known age and reported that males and females grow at equal rates (slightly greater than 30 cm/yr) until age 5. He reported that growth rates of females decline after age 5, but that males maintain the same rate of growth until about 9 yr of age.

Comparisons of small alligators during our study indicated that males grow at a greater rate than females after reaching 1.0 m TL (Table 2). The length–age curve (Fig. 4) shows that this size is reached slightly before age 3. Both males and females have greatest growth during the first year after hatching, and the rate gradually declines for both sexes beyond that time. However, the rate of decline is more gradual with males than with females. After age 3, annual growth of males exceeds that of females by almost 20%, and by age 10 males are growing at a rate 62% greater than females. The growth differential continued to widen with age. At age 15, male growth exceeds that of the female by 120% and by age 20 the differential is almost 200%.

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THE IDENTITY OF THE BLIND SNAKE *STENOSTOMA SIGNATUM* JAN, 1861 (SERPENTES: LEPTOTYPHLOPIDAE)

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ABSTRACT: The holotype of *Stenostoma signatum* Jan, 1861, is shown to be conspecific with *Leptotyphlops amazonicus* Orejas-Miranda, 1969. Accordingly the valid name for the species is *Leptotyphlops signatum* (Jan).

Key words: *Leptotyphlops*; *Stenostoma*

THE allocation of the blind snake *Stenostoma signatum*, described by Jan (1861) and figured by Jan and Sordelli (1861), has long been uncertain, largely because of the unknown type locality associated with the name. In 1864, Jan provided a more extensive description of the species, but made no attempt to discuss its relationships. Jan's descriptions and figure are reasonably good by 19th-Century standards for this group, but are typical in lacking most meristic data. Müller (1880) assigned a specimen in the Basel Museum from Rabinal, Guatemala, to *Stenostoma signatum* without any additional comment or description. Boulenger (1893) provided an English translation of the original description of the species, known then as *Glauconia signata*, and stated that the geographic range was unknown. Sternfeld