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Author(s): Michael V. Plummer
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MUSEUM OF NATURAL HISTORY, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045. PRESENT ADDRESS: DEPARTMENT OF BIOLOGY, HARDING COLLEGE, SEARCY, ARKANSAS 72143. Accepted 19 Aug. 1976.

Reproduction and Growth in the Turtle *Trionyx muticus*

MICHAEL V. PLUMMER

Major aspects of reproduction and growth in a population of *Trionyx muticus* from the Kansas River were determined from 448 recaptures of 423 turtles and from 206 dissections. Males mature in their fourth year at a plastron length of 80 mm and females mature in their ninth year at 140 mm. Mature females are larger than mature males (mean plastron length ♀♀ = 154.2 mm; ♂♂ = 98.2 mm), have shorter tails, and they develop distinctive blotched carapacial patterns. Testes are largest in late fall and smallest in early summer. Females may lay two or more clutches per season. Clutch size (averaging about 11 eggs) and number of clutches per season are related to body size. Hatchlings have a mean plastron length of 24.5 mm and double in length by the end of their first year. Young males grow about 2 mm per month. Growth abruptly decreases at maturity. Females grow 2–3 mm per month until maturity. Growth rate then decreases but remains higher than in males. Growth in *T. muticus* is individually variable and changes from month to month and year to year.

BIOLOGY of trionychid turtles has not been studied in depth. Webb (1962) summarized the biology of North American species, mainly from short reports. Aspects of reproduction and growth in *Trionyx muticus* have been reported by Muller (1921), Cahn (1937), Goldsmith (1944), Anderson (1958), Webb (1962), Fitch and Plummer (1975) and Plummer (1977). I studied reproduction and growth in a population of *T. muticus* in the Kansas River near Lawrence, Douglas County, Kansas, approximately 39°N from July 1972 to May 1975. Fitch and Plummer (1975) reported preliminary observations from the years 1970–1972. Descriptions of the area and habitat have been recorded in other reports (Fitch and Plummer, 1975; Plummer and Shirer, 1975).

METHODS

Turtles were captured by hand or in wire mesh funnel traps, marked and released, or preserved for dissection. Approximately 3,700 captures were made of 2,700 turtles; 104 males and 102 females were dissected. The length of the plastron (PL) was measured midventrally with a plastic ruler to the nearest millimeter from the posterior edge to the anterior edge, including the marginal cartilaginous portion. The posterior edge of the carapace is subject to mutilation and its flexibility and curvature render it less suitable for precise measurement than the plastron. Mean carapace length/plastron length (CL/PL) remains relatively constant (1.34–1.40) throughout ontogeny (Fitch and Plummer, 1975), so that either length of carapace or length of plastron is an accurate indicator of body size. Turtles were weighed on spring scales to the nearest 5 g.

In dissected females, number and size of ovarian follicles, number of shelled oviducal eggs and corpora lutea, and widths of oviducts were noted; in males, size and condition of testes, and appearance of vasa deferentia were determined. All measurements in the laboratory were made with dial calipers. Volume of testes was computed from the formula for an ellipsoid. The probabilities of differences between means were determined by *t*-tests.

RESULTS

Size at sexual maturity.—Criteria used for determining sexual maturity in males were coiling of vasa deferentia, extension of cloaca beyond the posterior edge of the carapace, or testes volumes greater than 100 mm^3. All mature males met the 3 criteria except for a male of 91 mm which had the cloaca 4 mm short of the carapacial edge because of an unusually large CL/PL ratio. Criteria for females were presence of oviducal eggs, corpora lutea, or follicles with diameters greater than 15 mm. Mature females have thick, convoluted oviducts 12–15 mm wide; two subadults approaching maturity (148, 151 mm) had straighter, membranous oviducts 7–8 mm wide.

Males mature at plastron lengths of 80–85 mm (Table 1). The largest immature was 90 mm whereas the smallest mature was 79 mm. Females mature at 140–150 mm (Table 1). The largest immature was 151 whereas the smallest mature was 131 mm.

TABLE 1. NUMBER OF MATURE TURTLES IN VARIOUS SIZE CLASSES.

	Plastron length (mm)	N	Mature (N)	% Mature
MALES	>85	78	77	99.0
	81–85	11	8	73.0
	76–80	4	2	50.0
	<76	11	0	0
FEMALES	>150	39	38	97.0
	146–150	6	3	50.0
	141–145	9	6*	67.0
	136–140	3	0	0
	131–135	4	1	25.0
	<131	41	0	0

* Four of 6 collected in Aug.–early Sep. Corpora lutea and enlarged ova are absent in mature females at this time (Table 2); these animals were designated mature on the basis of a large number of follicles in the 11–15 mm class and the presence of thick oviducts. They possibly had oviposited that year.

Sexual dimorphism.—Mean plastron length for mature males was 98.2 ± 0.24 mm (N = 1,162), and for mature females it was 154.2 ± 0.66 mm (N = 173). In most mature females a blotched or mottled carapacial pattern has replaced the juvenile pattern of small dots and short streaks (Fitch and Plummer, 1975). Development of blotched patterns is not usually synchronized with attainment of sexual maturity; the majority of females 90–100 mm had blotched patterns as well as did one of only 59 mm. All male *T. muticus* captured retained the juvenile pattern. In most mature females the cloaca does not approach the posterior edge of the carapace, but it is even with the edge in some large individuals.

Juvenile males 60 mm or larger had slimmer tails than females. This difference permits fairly accurate sexing of juveniles; 7 of 8 dissected turtles between 60–65 mm had been correctly sexed by this character.

Reproductive cycle of males.—Mature testes are whitish, elongate ellipsoidal organs with maximum widths 3–10 mm, lengths 12–31 mm and volumes 100–1,600 mm^3, depending upon season and turtle size. Immature testes vary with size of turtle but generally are less than 2 mm wide and 10 mm long, and are flatter and more translucent than mature testes.

The volume of mature testes varies seasonally (Fig. 1). They are at maximum size before hibernation, decrease in spring and increase in midsummer. In April–May all of 23 male turtles examined had vasa deferentia about 2 mm in diameter, highly convoluted and turgid with a milky white fluid. In June vasa deferentia began to appear flaccid and translucent with several apparently empty. Six of 20 June turtles had this appearance as did 14 of 19 in July and 10 of 11 in August, but only 4 of 12 in September–October.

Reproductive cycle of females.—In 27 shelled oviducal eggs from 5 females, yolks averaged 17.3 ± 0.18 mm (range 16.0–19.0) in diameter. Thus, enlarged ovarian ova in the 16–20 mm class evidently are ready for ovulation. Number of ova in different size classes varies seasonally (Table 2). Enlarged ova progressively decrease in number as they are ovulated. The number increases in September because of proliferation

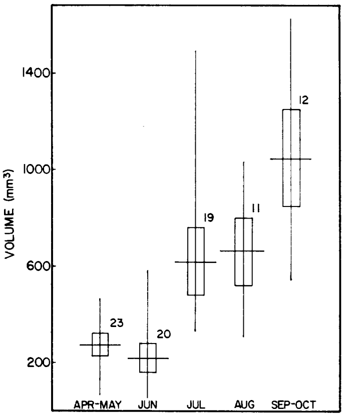

Fig. 1. Volumetric changes in mature testes of *T. muticus* throughout the season. Horizontal lines are means; vertical lines are ranges; rectangles delimit 95% confidence limits; numbers are sample sizes.

and growth of ova in the smaller size categories which began in July. Follicles 1–5 mm in diameter were present throughout the season. Atretic follicles, dark orangish-brown and firm, were found occasionally in all follicular size classes throughout the season.

Three females collected 10 May contained only enlarged ova, but one collected on 22 May and all those collected in early June contained both enlarged ova and corpora lutea indicating that ovulation probably occurred in mid-May. A female collected 22 May apparently had recently ovulated and had reddish-brown corpora lutea, 9–10 mm in diameter. Corpora lutea were whitish and 6–8 mm in diameter in females collected immediately after oviposition and in those with shelled oviducal eggs. In 5 females collected 27–28 June, there were 2 sets of corpora lutea; those of the larger set apparently corresponded with recently ovulated ova (in 3 individuals) or in recently oviposited eggs (in 2). Those of the smaller set, translucent and 3–5 mm in diameter, apparently corresponded to previous clutches. One female, collected 26 July, had colorless corpora lutea 4–5 mm in diameter. Females collected in August and September did not have corpora lutea discernable by gross inspection.

Migration of ova to the contralateral oviduct was indicated in 10 of 15 turtles by noncorrespondence between number of corpora lutea and number of oviducal eggs on their respective sides.

TABLE 2. NUMBER OF OVARIAN FOLLICLES IN FEMALES DISSECTED THROUGHOUT THE ACTIVITY SEASON.

	Diameter of ova (mm)		
Dates	6–10	11–15	16–20
May (N = 5)	2.0 ± 2.0	4.8 ± 2.21	18.0 ± 2.44
Jun. (N = 29)	3.3 ± 0.76	1.3 ± 0.29	10.9 ± 1.39
Late Jul.–Aug. (N = 7)	9.4 ± 1.61	8.1 ± 3.43	1*
Sep. (N = 5)	8.4 ± 1.50	9.8 ± 2.59	9.8 ± 4.07

* Atretic.

Clutch size.—From 102 nests examined in the field, clutch size averaged 10.4 ± 0.31 (range 3–26). The shelled oviducal eggs present at one time presumably represent a clutch. The oviducal complement in 22 June females dissected was 11.8 ± 0.76 (range 3–23). Clutch size in 53 natural nests constructed in June was 11.1 ± 0.48 whereas in July it was 9.3 ± 0.65 (N = 24).

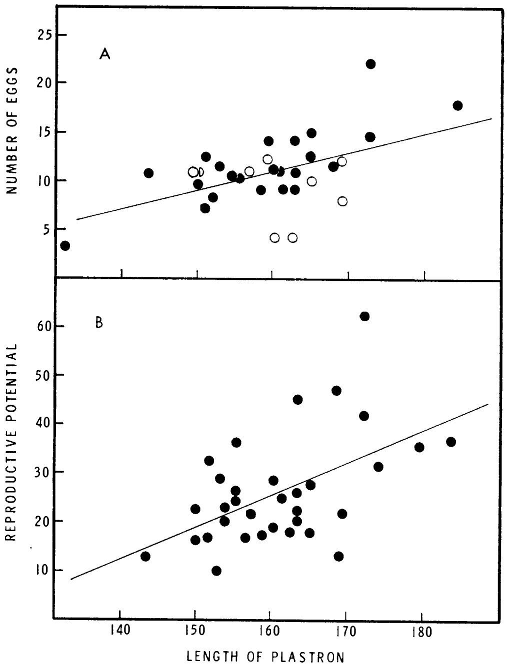

Fig. 2. A) Relationship of clutch size to plastron length. The regression equation is $\hat{Y} = -21.5 + 0.20x$ ($P < 0.001$). Closed circles are data determined by dissection; open circles are data gained through examining natural nests. B) Relationship of reproductive potential (number of eggs that a female is capable of producing in 1 year) to plastron length. The regression equation is $\hat{Y} = -81.1 + 0.67x$ ($P < 0.001$).

TABLE 3. EXAMPLES OF FEMALES POTENTIALLY CAPABLE OF PRODUCING MORE THAN 1 CLUTCH IN A SEASON.

Date	Plastron length (mm)	Oviducal eggs (N)	Corpora lutea (N)	Enlarged ova (N)	Eggs laid (N)
22 May	165	15	15	14	—
5 June	179	14	14	21	—
15 June	168	0	12	35	12
20 June	155	10	10	26	—
27 June	163	0	12	13	4

The difference is significant ($P < 0.05$). Unfortunately, females collected in July for dissection did not contain shelled oviducal eggs or corpora lutea of sufficient size to determine the ovarian complement, but mean oviducal complement from dissected turtles in June (11.8) was similar to the estimate of June clutch size in natural nests (11.1).

Reproductive potential.—Reproductive potential is the number of eggs a female is capable of producing in 1 year (Gibbons, 1968). Ova of 16–20 mm, plus the eggs actually laid, and the shelled oviducal eggs (or the corpora lutea representing the last 2 categories) provide a total count of eggs produced. This procedure assumes that few enlarged ova become atretic, which seems to be true in *T. muticus*. Reproductive potential in 33 turtles averaged 25.7 ± 2.01 (range 10–62), or the equivalent of a little over 2 clutches. Reproductive potential is positively correlated with body size (Fig. 2); probably small adults produce 1 clutch per year whereas larger adults produce more than one (Table 3).

In 1974 ovulation probably began in mid-May and oviposition began in late May, suggesting retention of eggs for about 2 weeks. The nesting season extended approximately 1.5 months, long enough for 2 or more clutches to be laid by an individual turtle. Every mature female dissected during the nesting season contained eggs and/or corpora lutea. Thus, each mature female in the population probably breeds annually.

Growth.—Growth was studied by examining size classes in hatchlings and yearlings and by direct measurement of growth in individually marked turtles. Except in some rapidly growing small individuals in midseason, a minimum of 2 months between captures was required for sufficient growth to occur to overcome random errors in measurement. Some 365 recaptures of 348 males and 83 recaptures of 75 females were used in growth analyses. When a turtle was recaptured more than once at intervals of several months the growth rates for each period were considered individually. However, such instances were rare, so that usually an individual yielded only 1 record of growth rate. Turtles were grouped into 10 mm size classes (5 mm classes for adult males in which sample sizes were large). If an individual growth record involved progression from 1 size class to another, the record was used only for the class of the original capture. Growth rates decreased with size of

TABLE 4. AVERAGE SIZE OF YEARLINGS IN COHORTS COLLECTED AT VARIOUS TIMES OF THE ACTIVITY SEASON.

Date	Plastron length (mm)	N
Late May	30.1 ± 0.50	24
Mid-June	35.1 ± 0.58	54
Mid-July	38.5 ± 3.00	2
Early Aug.	44.6 ± 1.01	9
Late Aug.	45.4 ± 0.64	18
Mid-Sep.	47.1 ± 1.32	5

TABLE 5. STATISTICS OF GROWTH RATE EXPRESSED AS MILLIMETERS OF GROWTH PER MONTH FOR MALE *T. muticus*.

Plastron length (mm)	N	$\bar{x}$	Range
61–65	10	1.95 ± .40	0.67–2.33
66–70	16	2.17 ± .45	0–6.67
71–75	20	2.48 ± .27	0.50–5.71
76–80	20	1.92 ± .28	0.29–4.52
81–85	35	1.03 ± .13	0.09–3.08
86–90	41	1.18 ± .20	0–6.67
91–95	46	0.73 ± .09	0–3.00
96–100	56	0.37 ± .05	0–1.67
101–105	65	0.20 ± .02	0–1.00
106–110	37	0.30 ± .12	0–4.17
111–115	19	0.09 ± .04	0–0.77

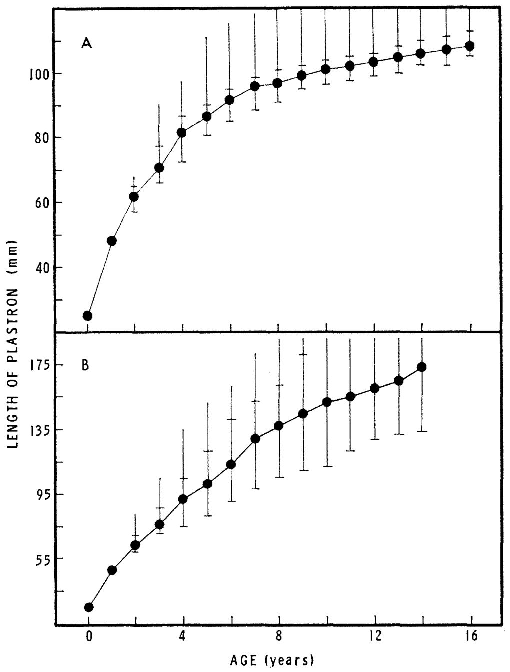

Fig. 3. The relationship of plastron length and age in *T. muticus*. A) Males. B) Females. Dots are means; vertical lines are ranges; horizontal lines delimit 95% confidence limits. Plots were obtained by cumulative addition of monthly growth at yearly (5 growth months) intervals. For example, at the end of its first year a turtle averages 48 mm, and one in its second year would grow 2.9 mm/month to 60 mm in early September. Then the turtle could be sexed and assigned to the appropriate growth rate for the remainder of September. The plastron lengths at the end of successive years in September are plotted. This procedure was employed 4 separate times in each graph to plot means, upper and lower confidence limits, and upper ranges using the respective growth rate values in Tables 5 and 6. For some size classes minimum growth rate was zero preventing calculation of lower range plastron length–age relationships.

turtle, therefore this procedure slightly decreases the mean growth rate recorded for the original class. However, records of this sort were relatively few. Activity was concentrated from May through September, and this coincided with the period of growth observed in individuals.

TABLE 6. STATISTICS OF GROWTH RATE EXPRESSED AS MILLIMETERS OF GROWTH PER MONTH FOR FEMALE *T. muticus*.

Plastron length (mm)	N	x̄	Range
61–70	7	2.79 ± .59	0.33– 5.00
71–80	12	3.20 ± .85	0–10.86
81–90	14	2.23 ± .42	0.44– 5.00
91–100	12	2.75 ± .57	0.36– 6.76
101–110	10	2.09 ± .65	0.24– 5.56
111–120	9	2.46 ± .39	1.14– 5.20
121–130	4	3.98 ± 1.27	1.64– 7.33
131–140	4	1.37 ± .64	0.17– 3.10
141–150	4	1.70 ± .67	0.46– 3.60
151–160	4	0.70 ± .39	0– 1.76
161–170	3	1.71 ± 1.22	0– 4.07

Growth of juveniles.—Plastron lengths of 142 hatchlings measured in the laboratory averaged 24.5 ± 0.17 mm (range 19.5–28.8). Emergence of hatchlings extended from August through September. Turtles hatching early in the season could grow several weeks before hibernation whereas turtles hatching in late September would make little or no growth before entering into hibernation. Size at hatching and time of hatching therefore are important in determining the size at which a turtle enters its first full season of growth the following May.

Several hundred hatchlings were marked during the course of the study, but none was recaptured after periods long enough to reveal growth. Samples of small turtles which seemed to be yearlings were grouped at different times of the season in order to show the increasing size of cohorts (Table 4). Average size increased as the season progressed, but range of sizes was great in all groups, and young as small as 26 mm could be found as late as mid-June. There probably was little growth during late September; size of yearlings at the end of the first full season of growth was about 48 mm. Fourteen juveniles in the 48–60 mm class were recaptured after intervals of 1.3 to 5.3 months. Their mean monthly growth rate was 2.9 ± 0.32 mm (range 1.0–5.38). At a length of 60 mm or more turtles may be sexed; separate analyses reveal different growth patterns for the 2 sexes.

Growth of males.—Growth in male turtles (Table 5) is slower than in hatchlings or juveniles, with monthly increments of approximately 2 mm until maturity is reached at about 80 mm. Growth decreases abruptly after maturity and apparently ceases in old males. Figure 3 shows the relationship between body size and age indicated by growth rates.

Growth of females.—Females grow faster than males (Table 6). Rate of growth declines as maturity is approached at 135–140 mm, but

TABLE 7. VARIATION IN MEAN GROWTH RATE IN *T. muticus*. Early–late season extends from 1 Sep. to 15 Jun. Midseason extends from 16 Jun. to 31 Aug.

Sex	Time	Mean rate (mm/month)	N	*t*
Males	Early–late season	0.56 ± 0.10	25	7.08 ($P < 0.001$)
	Midseason	2.73 ± 0.30	22	
Females	Early–late season	0.57 ± 0.16	5	2.42 ($P < 0.05$)
	Midseason	3.68 ± 0.78	13	
Males	1973	2.17 ± 0.32	44	1.67 ($P < 0.10$)
	1974	2.84 ± 0.65	19	
Females	1973	2.51 ± 0.34	20	4.47 ($P < 0.001$)
	1974	5.57 ± 0.70	11	

mature females continue to grow at rates greater than those in males. Confidence intervals are greater in females because of greater variation (10.86 mm per month maximum compared to 6.67 mm per month maximum in males), and to smaller sample sizes. Figure 3 shows the relationship between body size and age indicated by growth rates.

Variation in growth rates.—If yearly growth is divided into two 2.5 month segments (16 Jun.–31 Aug. and 1 Sep.–15 Jun.), growth rates are higher for midseason than they are for early–late season (Table 7). In 1974, females grew more than twice as fast as in 1973, and males grew slightly faster in 1974 (Table 7). In the case of males the difference is not significant but the probability is only about 6 or 7% that it resulted solely from chance.

DISCUSSION

Cagle (1946) was one of the first to emphasize the extremely variable growth rates of individual turtles, geographical differences in growth rates, and the sensitivity of growth to ecological factors. Gibbons and Tinkle (1969) demonstrated that in 3 populations in the same geographic area reproductive parameters were strikingly different because of different growth patterns.

The various aspects of reproduction and growth in *T. muticus* are similar to those in other groups of freshwater turtles, and these aspects also demonstrate temporal and spatial variability.

My estimate of average clutch size in natural nests (10.4) from 1973–1974 is significantly different ($P < 0.001$) from the 12.6 average clutch size from 1970–1972 reported by Fitch and Plummer (1975). This unexpected difference is at present inexplicable, except as a result of fluctuating environmental conditions from year to year. The larger clutches in June than in July also was reported by Fitch and Plummer (1975) and probably means that for a given female, the first clutch is larger than succeeding clutches.

To account for the unusually small number of eggs occasionally found in nests, Fitch and Plummer (1975) suggested that possibly *T. muticus* distributes a clutch in more than 1 nest. One female (163 mm) found near her recently completed nest which contained 4 eggs, later revealed 12 corpora lutea of approximately the same size, and 13 ova in the 16–20 mm class. Another female (131 mm) contained 3 shelled oviducal eggs and 3 corpora lutea. Because clutch size is positively correlated with body size (Fig. 2), unusually small numbers of eggs in nests may also represent small females in their first nesting season.

Various authors have recorded clutch size in *T. muticus*: 22 from Iowa (Muller, 1921), 18–22 from Illinois (Cahn, 1937), 18.6 from Iowa (Goldsmith, 1944) and 20 from Missouri (Anderson, 1965). From more southern localities Webb (1962) found an average clutch size of 7.7. Webb suggested a latitudinal gradient in clutch size and number of clutches similar to that found in other turtles (e.g., *Sternotherus*; Tinkle, 1961), but he perceptively cautioned that there may be great variation within a given area. In my study clutch size was notably smaller than those previously reported for the same general geographic area. Inasmuch as both clutch size and reproductive potential are correlated with body size and apparently female body size is potentially much larger than in my study, perhaps clutch size was smaller because the population was young or because growth rates were unusually slow. No indications of reproductive senility were found in any turtle dissected.

The average male grows to maturity at 80 mm in its fourth year (Fig. 3), as tentatively concluded by Webb (1962). A mature male of average size (98.2 mm) would be approximately 9 years old. Large males, those over 110 mm, probably grow at rates of about 0.10 mm per month, indicating that the largest male (123 mm) was about 48 years old. Such turtles more likely represent those with accelerated growth rates. Rates ranged to 0.77 mm per month in the 111–115 mm class. Such growth would permit a turtle to reach 120 mm in as little as 8 years. Although it is unlikely that any turtle would grow that fast for an extended period, large turtles probably are younger than 48 years. Webb (1962) indicated a maximum size of 140 mm in male *T. muticus*.

Females mature at about 140 mm, typically in their ninth year (Fig. 3). Confidence limits suggest that some individuals mature as early as their sixth year. For example, the smallest mature female (131 mm) may have been in her sixth year. Mitsukuri (1905) wrote of captive *T. sinensis*: "In the sixth year they reach maturity and may begin to deposit eggs, although not fully vigorous till two or three years later." Webb (1962) predicted that some female *T. muticus* probably matured in their sixth year but most did not until their seventh. Little confidence may be placed in the extreme sizes at certain ages suggested by the ranges because of their statistical nature and because it is unlikely that any one individual would grow at such an accelerated rate for an extended period. Growth rates are sensitive to seasonal and yearly trends as well as being sporadic in other, unexplained ways. An average size mature female (154.2 mm) would be approximately 11 years old. The largest female was 186.0 mm in length and had grown from 163.0 mm in 5.5 growth months. Recorded lengths of 356 mm CL (Carr, 1952), 345 mm CL (Ernst and Barbour, 1972), and of 215 mm PL (Webb, 1962) demonstrate that individuals do grow to sizes considerably greater than those I observed.

The records of growth that were the bases for Tables 5 and 6 were obtained at various times of the year and spanned 3 years. Individual variation in growth rates was expressed in wide ranges and confidence intervals. Average growth rates also vary with ecological conditions. Rapid individual growth most often occurred in spurts. For example, a male in a size category usually characterized by slow growth (99 mm), grew only 1 mm in almost 7 growth months, but thereafter he grew 8 mm in the next 5 growth months. Most such growth spurts could be attributed to either seasonal differences or to yearly differences.

The most obvious explanation for the seasonal differences, assuming similar dietary habits, is the higher average temperature during midseason presumably involving maintainance of higher levels of metabolism.

The year to year differences in growth are not as easily explained. Turtles became active earlier in 1974 than in 1973 (Plummer, 1975), and water temperatures were higher, especially in May and early June in 1974. Also in 1973 heavy precipitation with rapidly fluctuating high water levels contrasted with the relatively dry weather in 1974 with low, stable water levels. High water levels may scour the substrate and result in less available food and retarded growth. High water levels also limit basking activity by inundating preferred basking sites on sandbars and gentle slopes on mud banks.

Some authors have correlated rainfall and water levels with growth rates in turtles. Ernst (1971) found that drought reduced growth in *Chrysemys picta* through loss of habitat and loss of feeding patches of algae. Webb (1961) thought that fluctuation in water level might be a factor influencing growth in *Chrysemys*. Moll and Legler (1971) reported cyclic growth of *Chrysemys scripta* in the relatively constant temperature and photoperiod regimes of Panamá. Rapid growth was associated with the dry season and slower growth with the wet season. They suggested that turtles became inactive and did not feed during floods.

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MUSEUM OF NATURAL HISTORY, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045. PRESENT ADDRESS: DEPARTMENT OF BIOLOGY, HARDING COLLEGE, SEARCY, ARKANSAS 72143. Accepted 7 June 1976.