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### GROWTH AND MATURITY OF THE GOPHER TORTOISE IN SOUTHWESTERN GEORGIA

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# GROWTH AND MATURITY OF THE GOPHER TORTOISE IN SOUTHWESTERN GEORGIA

J. LARRY LANDERS, W. ALAN McRAE,  
AND JAMES A. GARNER<sup>1</sup>

**SYNOPSIS:** Growth rates of gopher tortoises (*Gopherus polyphemus*) were determined by measuring individuals during two consecutive years and by correlating plastral annuli counts and measurements with shell dimensions. Ninety-three percent of growth occurred from April-October. The annual increment in carapace length (CL) for immatures was 11-12 mm; this varied by CL class. Growth increments were greatest for specimens 100-190 mm CL (about 4-11 yr of age), and gradually decreased thereafter. However, body volume increments peaked as tortoises grew from 220-230 mm CL, shortly before attainment of somatic maturity. Sexual maturity typically occurred at age 16-18 years (230-240 mm CL) in males and at 19-21 years (250-265 mm CL) in females. Thereafter, growth in both sexes was reduced, but females grew at greater rates and became significantly larger. Development of tortoises living in sand ridge habitats in southwestern Georgia was much slower than in Florida: maturity was delayed about 7 years. Growth was influenced by habitat quality, ambient temperature, and length of the annual activity season. The extended period of time required for attainment of maturity is potentially a limiting factor in population growth, and becomes more important in the northern portions of the species' range.

## TABLE OF CONTENTS

INTRODUCTION .....	82
ACKNOWLEDGEMENTS .....	82
METHODS .....	83
Study Area .....	83
Data Collection and Analysis .....	83
SEASONAL GROWTH CYCLE .....	85
ANNUAL GROWTH RATE .....	87
Carapacial Increment .....	87
Allometric Relations .....	92
Volumetric Increment .....	97
SIZE IN RELATION TO LIFE HISTORY .....	98
Immature Stages .....	98
Size at Sexual Maturity .....	101
Age at Sexual Maturity .....	102
Post Maturity .....	103
SURVIVAL AND ADAPTIVE IMPLICATIONS .....	104
APPENDIX .....	108
Synopsis of Methods Used to Estimate Growth .....	108
LITERATURE CITED .....	109

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## INTRODUCTION

The gopher tortoise is one of four extant species of the genus *Gopherus* and the only tortoise now indigenous to the southeastern United States. In recent years this species has drawn much attention, due both to the ecological significance of its burrows (Landers and Speake 1980) and its questionable population status (Auffenberg and Franz 1975). Gopher tortoise populations have declined steadily over much of the range, due largely to habitat alteration and human predation (Franz and Auffenberg 1978). Few data exist on factors that influence the capacity of depleted populations to return to their former levels. A major aspect of population dynamics is the growth rate of individuals, especially in relation to sexual maturity. In reference to terrestrial turtles, Auffenberg and Iverson (1979) stated that the span of time between the reproductive period and prereproductive period is most important: it determines the amount of energy required and the length of time an individual is exposed to impinging factors (e.g., predation and disease) before entering the breeding population.

Unfortunately, no growth data are available on known-age gopher tortoises living in the wild. Growth has been estimated in only two areas. In central Florida, Goin and Goff (1941) determined annual growth increments of 33 specimens captured at approximately one-year intervals. In north-central Florida, Auffenberg and Iverson (1979) correlated plastron lengths of 168 gopher tortoises with ages estimated from shield annuli counts. Iverson (1980) utilized these two data sets to predict the age at sexual maturity of necropsied females collected from north-central Florida. No comparable data have been contributed from other portions of the range, and environmental factors that influence growth have not been determined.

This study includes samples from southwestern Georgia and north-central Florida and employs several methods commonly used for growth analysis of turtles. Major objectives were: (1) to determine annual growth increments in relation to age and size, (2) to estimate age at sexual maturity, and (3) to determine the influence of selected environmental factors on growth. Information on geographic variations in growth parameters and comparisons with certain other turtle species are also included.

## ACKNOWLEDGMENTS

This work is part of a study on gopher tortoise ecology sponsored by International Paper Company. It was partially financed with grant-in-aid funds under Section 6 of the Endangered Species Act of 1973 (PL 93-205) administered through the Georgia Department of Natural Resources (Project No. 8-933). W. Auffenberg and R. Franz provided specimens for study from the Florida State Museum and contributed additional data from Marion County, Florida. Without their assistance, parts of this study would never have been completed.

J. Iverson provided data on maturity of females in the FSM sample, and L. Hunt kindly brought in many specimens from various locations in southwestern Georgia. J. Douglass and J. Iverson reviewed the manuscript and offered many helpful suggestions. We especially appreciate the interest of members of the Gopher Tortoise Council; their efforts to conserve the remaining populations of gopher tortoises provided the impetus for this study.

## METHODS

### STUDY AREA

Most data used in this study were collected on Silver Lake Station, a 1400-ha tract of International Paper Company's Southlands Experiment Forest, and on adjacent lands in Decatur County, Georgia. The forested area was dominated by natural stands of longleaf pine (*Pinus palustris*) (965 ha). Sand ridges with scrub oaks (*Quercus incana*, *Q. margareta*, and *Q. laevis*) and scattered longleaf pines comprised approximately 210 ha.

A dense groundstory of wiregrass (*Aristida stricta*), bracken fern (*Pteridium aquilinum*), and running oak (*Q. pumila*) grew beneath the longleaf pine stands, but these plants were sparse on sand ridges. Open habitat conditions have been maintained by late-winter burning, and fire swept through sand ridge habitats once every 2-4 years. Large colonies of gopher tortoises were found only on xeric sites characterized by Lakeland and Troup soils. Sites with pure stands of longleaf pine were more mesic (Orangeburg and Norfolk soil series) and supported relatively few tortoises. On cultivated sites adjacent to the forested tract, isolated individuals or small groups of tortoises were located along fence-rows and field borders.

Elevations in the study area range from 24-31 m above mean sea level. The average maximum and minimum temperatures for the summer months are 32°C and 21°C, respectively; annual rainfall averages 1270 mm.

### DATA COLLECTION AND ANALYSIS

From March 1978-March 1980, gopher tortoises were captured by hand or in pit-fall traps placed in front of dens. Hatchlings from nests in the area were included, and data were collected on tortoises found dead along roadsides. Several specimens in the Florida State Museum collection were examined, and data on tortoises from Marion County, Florida, were also utilized.

When possible, the age, sex, reproductive status, shell dimensions, and body weight of tortoises were recorded. Prior to release, tortoises were marked by notching the marginal scutes according to a numbering scheme.

Age was estimated by counting annuli where they were most distinct, usually on the abdominal shields (Fig. 1). This technique has been used to estimate age in *G. polyphemus* (Auffenberg and Iverson 1979), in *Geochelone gigantea* (Grubb 1971), and in several species of water turtles (Sexton 1959, Moll 1976). False rings, formed occasionally by decreased growth during an activity season, were discounted; these were usually discontinuous and were bounded by relatively shallow marginal grooves. The ability to discern false rings was developed from observations of many specimens inspected seasonally and annually.

The sex and reproductive status of tortoises found dead were determined during necropsy; otherwise, the sex of larger specimens was determined by monitoring sexual behavior in the field and by measuring dimorphic characteristics (McRae *et al.* 1980). Subdentary glands, which function in courtship (Auffenberg 1966), were inspected each time a tortoise was examined. These glands were recorded as active if they were enlarged and contained copious fluid. Observations of courtship and mating of marked tortoises provided additional data on reproductive status.

Measurements taken were straight-line dimensions of plastron length (PL), carapace

length (CL), and (at a point near the middle of the body) maximum width (W) and thickness (TH). The carapace was chosen as the primary parameter because it is most commonly used in linear growth analysis. Also, in *G. polyphemus*, the carapace is less variable than the plastron: the latter is sexually dimorphic in length and the anterior portion (gulars) becomes reduced by abrasion with age.

Tortoises were weighed as soon as possible after capture on a triple-beam balance. Many individuals excreted profusely before they could be weighed, and this loss coupled with that which occurs during winter dormancy made weight change data too variable for accurate analysis. A box-model volume ( $CL \times W \times TH$ ) was calculated as an indicator of total size; this parameter has been used effectively as a size index in water turtles (Mosimann 1958).

Three methods were employed to determine growth rates: (1) capture-recapture analysis; (2) age-dimension correlations; (3) annuli measurement-dimension predictions. These three approaches were undertaken to allow comparisons with the findings of various other studies. When possible, growth parameters were calculated by more than one method to provide comparative checks of results.

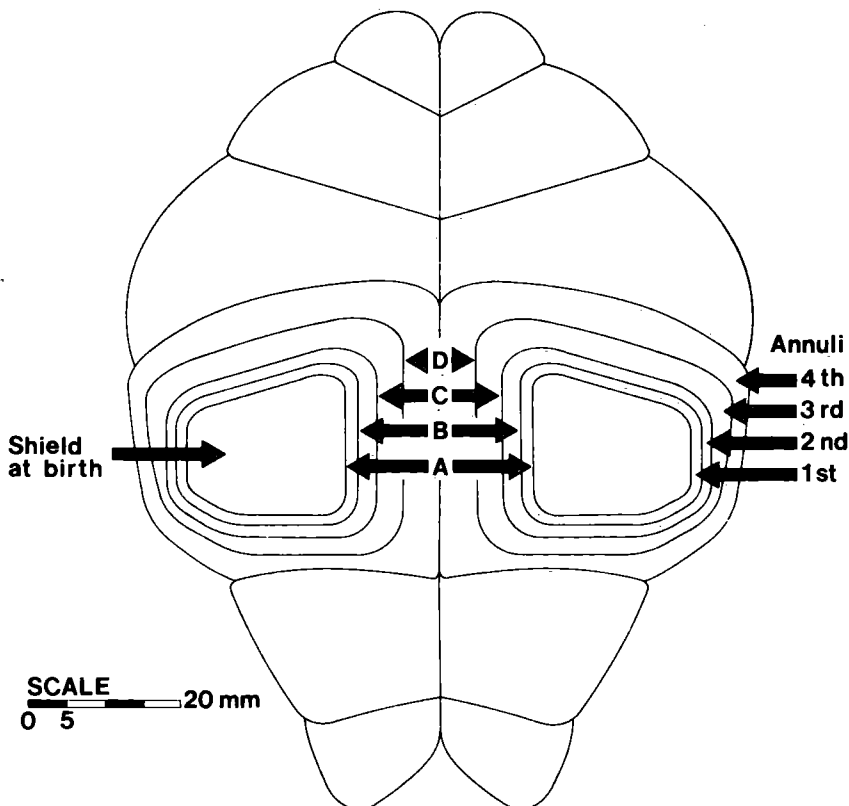


FIGURE 1. Measurements of abdominal annuli used to estimate carapace length in previous years. Total annuli width (A) was correlated with CL at present age (here,  $N = 4$  yr) to form regression equation (Fig. 2). CL for first previous year ( $N-1$ ) was calculated using distance A minus D, for second previous year ( $N-2$ ) using A-C, etc.

**Capture-recapture method:** A total of 106 tortoises were caught in corresponding months of two consecutive years. The annual growth increment was taken as the difference in measurements from one year to the next (cf. Goin and Goff 1941).

**Age-dimension correlations:** These included measurements regressed against estimated age at the time of each capture ( $N = 579$ ). Only tortoises with distinct plastral annuli were included in this analysis (cf. Auffenberg and Iverson 1979).

**Annuli measurement-dimension predictions:** These were made to discern the growth history of selected tortoises. A regression equation was developed to predict carapace length from a measurement of cumulative annuli width on abdominal scutes (Figs. 1 and 2) for all previous years of an individual's life. Growth of 72 tortoises from sand ridge habitats was compared to that of 12 others living nearby in cultivated fields. Comparisons were also made with samples from Florida (15 from Alachua County, 30 from Marion County). Studies of various species of water turtles (Sexton 1959, Gibbons 1968, Moll 1976) and a giant tortoise (*Geochelone gigantea*) (Grubb 1971) have shown the utility of body dimension-annuli measurement relationships in growth analysis. Unless otherwise stated, differences in means were assessed using t-tests.

### SEASONAL GROWTH CYCLE

During this study it was noted that tortoises of all sizes were essentially dormant during winter (December-March). In early spring they showed increased activity, especially on warm days; they were most active during summer (late May-August). Tortoises were seen more infrequently as fall progressed.

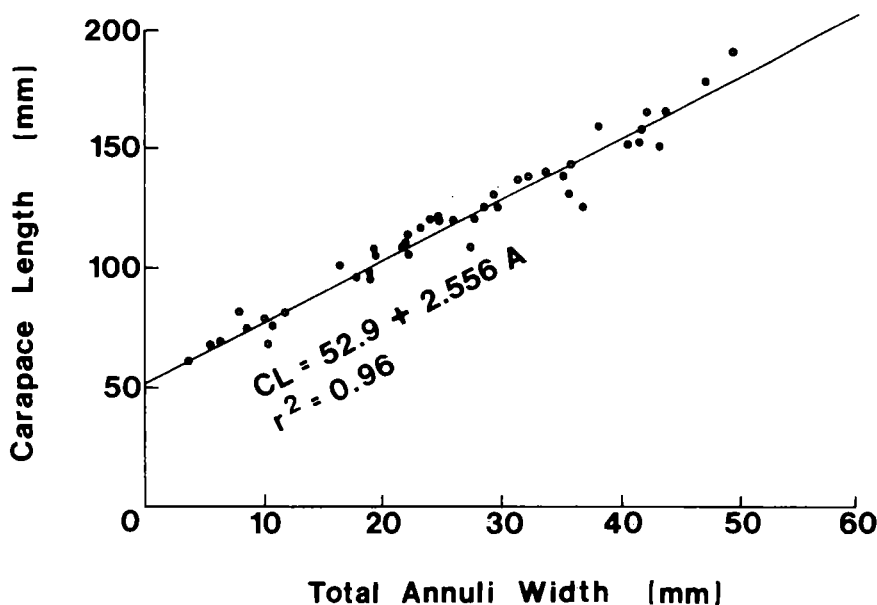


FIGURE 2. Relationship between carapace length and an abdominal annuli measurement; total annuli width (A) as in Figure 1.

In an attempt to determine the relationship between seasonal activity and growth, young tortoises were chosen because they appeared to grow at a rapid, fairly uniform rate from year to year. Mean monthly CL plotted against age indicated that growth occurred from spring through fall and ceased during winter (Fig. 3). Mean bimonthly CL increments were averaged through the first five years of life and expressed as a percentage of annual growth (Fig. 4). There was slight growth during early spring, a rapid increase to a constant rate (34% bimonthly) during late spring and summer, and a gradual decrease through fall to zero growth during winter dormancy. Ninety-three percent of total growth occurred from April-October. Growth was negligible when mean maximum temperature was 18-20°C (December-February). It increased slightly at temperatures of 21-27°C (March-April, October-November), peaked when the mean maximum temperature was fairly stable at 32°C during the warmer months (May-August). Eighty percent of growth occurred during May-September, the peak growth period noted in north-central Florida by Auffenberg and Iverson (1979).

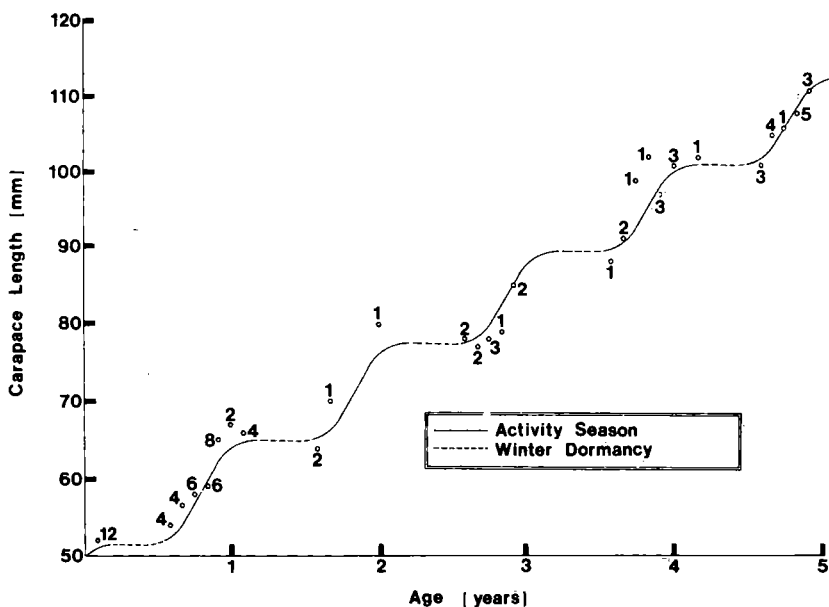


FIGURE 3. Seasonal variation in growth as indicated by CL of young tortoises during various months of the year. Numerals indicate sample sizes by month of capture.



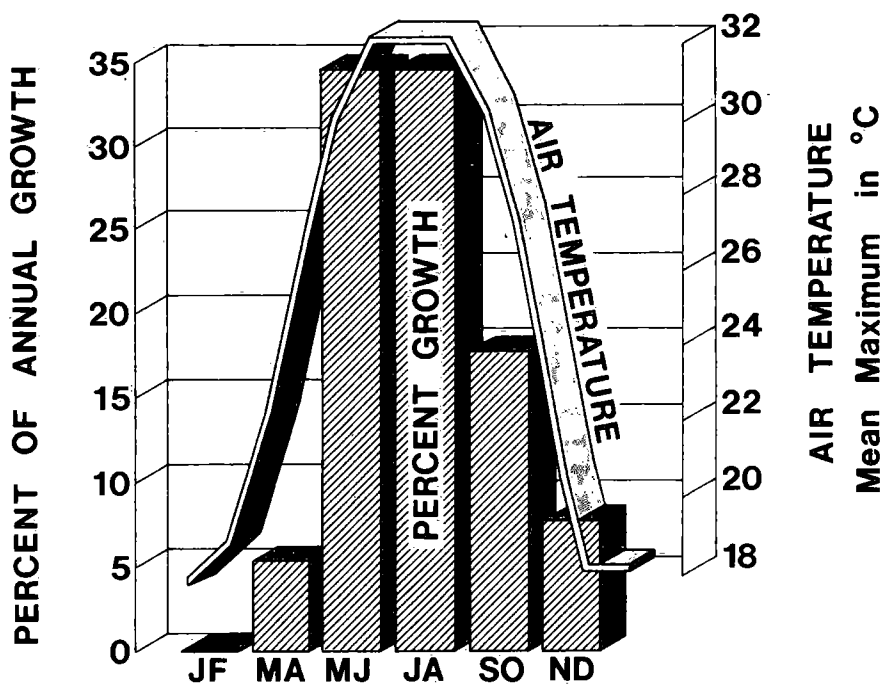


FIGURE 4. Percent of total annual growth by 2-month intervals in relation to mean maximum ambient temperature. Bars represent the mean bimonthly CL increment averaged through the first 5 years of life and expressed as percentage of annual growth.

## ANNUAL GROWTH RATE

### CARAPACIAL INCREMENT

Measurements of tortoises captured during corresponding months of two consecutive years were initially used to determine growth increments. Capture-recapture data for tortoises of CL < 240 mm were compared with those obtained by Goin and Goff (1941) in central Florida (one of the specimens in the latter sample (*i.e.*, number 13) was deleted because it showed no growth). For purposes of comparison, Goin and Goff's (1941) data were adjusted to a growth interval of 12 months based on the calculated percentage growth per month for each individual (Fig. 4). In both Goin and Goff's (1941) sample and our own, the mean CL increment was about 12 mm per year (Table 1). The Florida sample included only three individuals in smaller size classes (initial CL < 130 mm), and these represent the stages of most rapid development. Larger tortoises grew at a mean rate of 11.1 mm per year, while those in our sample grew

TABLE 1. Annual carapacial increments of gopher tortoises from southwestern Georgia and central Florida. Data were obtained by capture-recapture.

First year CL class (mm)	Mean CL increment (mm)					
	Southwestern Georgia			Central Florida <sup>a</sup>		
	Range	$\bar{x}$	N	Range	$\bar{x}$	N
50-59	7-20	13	15	—	10	1
60-69	—	13	1	—	—	—
80-89	7-15	12	4	—	—	—
90-99	8-22	14	4	—	13	1
100-109	—	18	2	—	—	—
110-119	15-20	17	2	—	17	1
120-129	10-16	13	4	—	—	—
130-139	7-9	8	3	3-19	13	4
140-149	4-19	11	2	13-60	37	2
150-159	—	11	1	—	4	1
160-169	8-19	13	2	3-18	11	4
170-179	—	—	—	4-16	10	4
180-189	—	14	1	4-14	8	4
190-199	—	7	1	1-9	6	4
200-209	—	8	1	6-9	8	3
210-219	5-9	7	2	—	—	—
220-229	—	11	1	—	4	1
230-239	4-24	10	4	3-18	10	2
All classes	7-18	11.8	16	4-37	11.6	13
All individuals	4-24	12.5	50	1-60	11.2	32

<sup>a</sup>Data adapted from Goin and Goff (1941).

9.8 mm annually (about 12% less). The greater potential for growth in the Florida sample was evidenced by specimen number 9, which grew 42 mm in 9 months, or about 60 mm per year (our estimate). This rate is approximately twice that of our fastest-growing specimen. Douglass and Layne (1978) presented information that also indicates more rapid growth in more southerly populations: in an area near Lake Placid, Florida, they found tortoises to exceed 100 mm in PL by age 3-4 years; this size was attained (on the average) after 4-5 years in our part of Georgia.

A second approach to determining relative carapacial growth was derived by estimating CL in previous years from annuli width measurements (see METHODS). The difference between reconstructed CL from one year to the next was plotted against CL class.

Figure 5 depicts an increment curve in relation to initial size based on two methods. Small individuals with CL of about 50 mm grew rapidly, but at 60-90 mm CL experienced below average (< 12 mm per year) development. This trough was followed by a growth surge at about 100-120 mm CL, following which tortoises grew regularly at above average rates

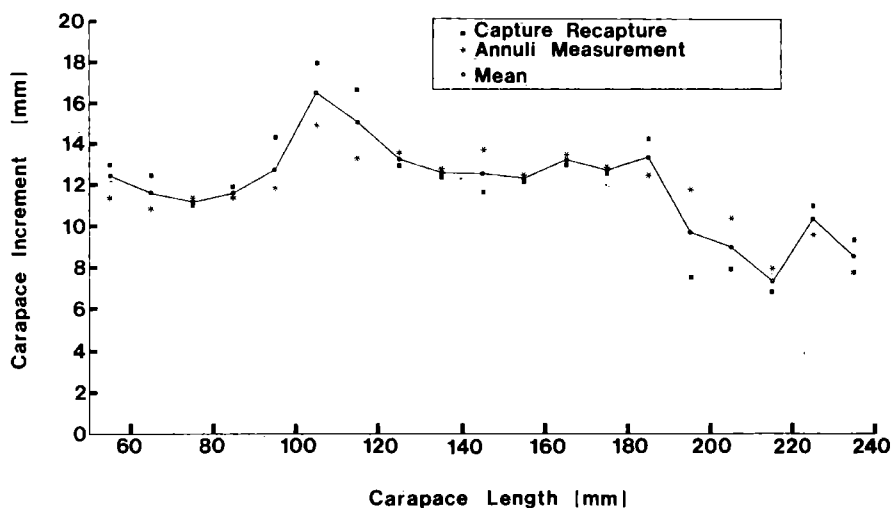


FIGURE 5. Annual carapacial increments in relation to carapace length. Data points are mean increments of individuals in 10-mm CL classes, plotted over class midpoints.

until they reached 180-190 mm CL. Growth generally decreased beyond that point, but a slight surge was noted in tortoises 220-230 mm CL.

A comparison of growth increments in relation to age, as estimated by three methods (Table 2), shows most rapid development to occur in younger age classes, followed by sharply decreasing increments in later years. The similarity in results of these methods indicates that any of the three methods can be used to estimate growth.

A summary of CL growth per 4-year class as estimated from annuli measurements is given in Table 3; only individuals in wiregrass habitats were used in this analysis. Of 599 annuli measurements for growing seasons 1-12, over 67% represented CL increases of at least 10 mm. During these years of immaturity, annual growth was characteristically 5-20

TABLE 2. Annual growth in CL in 4-year groups of *G. polyphemus* as determined by each of three methods. Specimens are from natural habitats in southwestern Georgia.

Age	Capture-recapture		CL-age correlation		Inter-annuli Measurement	
	N	$\bar{x}$	N	$\bar{x}$	N	$\bar{x}$
1-4	23	12.6	82	11.8	271	12.0
5-8	15	12.3	36	12.0	210	12.1
9-12	2	11.8	25	11.6	118	11.5
13-16	5	9.3	24	9.8	70	9.5
17-20	5	5.7	37	6.2	35	7.8

mm ( $\bar{x}$  = 12.0 mm) (Table 3). Auffenberg and Weaver (1969) suggested that growth in CL in immature *G. berlandieri* averaged 16-18 mm per year. Giant tortoises grow 15-20 mm per year in CL early in life, then steadily decline in growth rate to about 5 mm annually by age 15-20 years, depending upon population density (Grubb 1971). Occasionally, annual increments of 20 mm or more were detected in our study area; only rarely did tortoises <20 years of age grow <5 mm per season. Growth in the 17-20 year age class was typically only 5-10 mm per year (80%), and was occasionally 10-15 mm per year (13%).

Most tortoises (55 of 69) grew in an intermittent pattern, with peak CL increases typically occurring at 3 to 6 year intervals. Grubb (1971) found that giant tortoises grew intermittently, often exhibiting sudden increases in growth rates after several years of very slow growth. In our study, the most rapid growth usually occurred during 1 to 3 year periods within the 6th-10th growing seasons of an animal's life. Carapace length increases of  $\geq 15$  mm occurred on the average once every 5 years in the life of an individual; increments of 10-15 mm were twice as common, occurring an average of once every 2.5 years in the lives of individuals. Growth surges of >15 mm per season were manifested by individuals for periods of 1-4 years only; 44 such surges were confined to a single year, 12 occurred in two successive years, and only three each occurred during 3 and 4 consecutive years.

Fourteen of 69 individuals (20.3%) grew at fairly uniform rates throughout life (*i.e.*, variation in CL growth was not significant [ $P > 0.10$ ] among years). These individuals generally grew at rapid rates ( $\bar{x}$  = 13.3 mm/yr,  $N = 6$ ) or at comparatively reduced rates ( $\bar{x}$  = 8.8 mm/yr,  $N = 8$ ). Varying nutritional regimes are possible determinants of these unusual growth patterns.

Of 52 tortoises living in wiregrass habitats, 13 experienced growth of >20 mm CL in a single season; five of these grew at least 20 mm during

TABLE 3. Increases in CL, per 4-year period, of 72 tortoises living in natural habitats. Increments were estimated from annuli measurements using regression equation (see METHODS). Numbers in the body of the table are percentages of total annuli ( $N$ ) measured that represent an estimated CL increase falling within each increment class.

Year	N	Carapace growth/yr (mm classes)						
		<5	5-9.9	10-14.9	15-19.9	20-24.9	25-29.9	$\geq 30$
1-4	271	6.2	28.1	41.0	19.1	5.6	0.0	0.0
5-8	210	3.8	28.6	38.1	20.9	4.8	3.3	0.5
9-12	118	1.7	30.5	35.6	20.3	6.8	4.3	0.8
13-16	70	9.1	42.4	30.3	15.2	3.0	0.0	0.0
17-20	35	6.7	80.0	13.3	0.0	0.0	0.0	0.0

two or more years. All of these atypical growth surges were experienced during growing seasons 2, 6-11, or 13, and usually during 7-8. Only one of 25 tortoises aged 13 and older grew more than 20 mm per year in CL after the 12th growing season. Only two single-year increases were over 30 mm; one occurred in the 8th year, the other in the 9th year of life. It appeared that surges of above-average growth ( $> 12$  mm/yr) did not occur in any specific year of life, but tended to occur during the 6th-10th growing seasons.

To determine if there was significant variation in growth in relation to rainfall or other environmental factors, annual carapacial increments were estimated for the years 1967-1978 (Fig. 6). Two 5-year age cohorts, 2-6 and 7-11, were used in the analysis; these groups were chosen because of the insignificant ( $P > 0.20$ ) variation in annual growth within each group. There were no significant differences in growth rates among the 12 years in either of the two samples ( $P > 0.20$ ). Nor were annual increments in growth correlated with rainfall in the spring, summer, or preceding fall, although seasonal rainfall was quite variable among these years. Annual growth of *G. polyphemus* in this area is determined to a greater extent by the age and growth potential of the individual and by food quality (see below) than by seasonal rainfall. This is to be expected as rainfall in this area, especially in spring and early summer, is typically sufficient for adequate plant development.

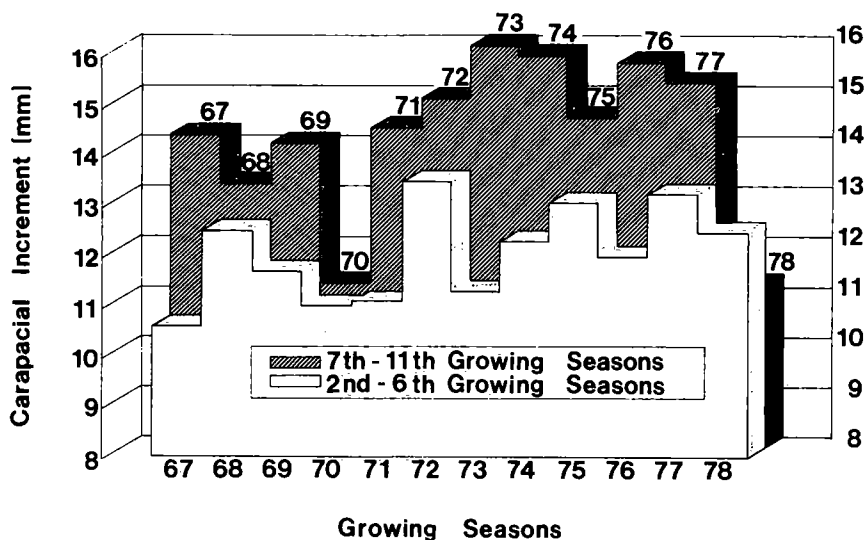


FIGURE 6. Estimated annual growth in carapace length for two age-groups (2-6 and 7-11 yr) by calendar year: Sample sizes were 16-50 ( $\bar{x} = 32$ ) per year.

Annual growth rates thus did not vary significantly with rainfall; the effects of nutrition and geographic location on growth were then examined. Depicted in Fig. 7 are CL growth rates estimated for years 1-10 for *G. polyphemus* from north-central Florida and from sand ridge and agricultural habitats in southwestern Georgia. Individuals in natural habitats in Georgia were significantly ( $P < 0.01$ ) more likely to grow 10 mm per year than were individuals in Florida or in fertilized Georgia sites.

The influence of improved nutrition was evident: tortoises in agricultural situations consistently grew about 4 mm more per year ( $\bar{x}$  increment = 16.2 mm) than those in natural communities ( $\bar{x}$  = 12.0 mm). This was to be expected: for example, Jackson *et al.* (1978) reported CLs of 236 mm at 4 years in *G. agassizii* captives on highly nutritious diets, while those living in natural habitats require 15-20 years to reach this size (Woodbury and Hardy 1948). Nearly 20% of the gopher tortoises in a colony in a ruderal habitat in Florida exceeded 318 mm CL, while less than 7% of the individuals in each of 11 other colonies were this large (Alford 1980). Significant differences in growth rates of *Chrysemys picta* on diets differing in nutritional quality are well documented (Gibbons 1967; Ernst 1971; Christiansen and Moll 1973). Giant tortoises in two low-density populations grew much more rapidly (Swingland 1977) and reached sizes over 2.4 times larger (Coe *et al.* 1979) than those in a food-limited, high-density population.

That the warmer climate and longer growing season in north-central Florida led to a greater annual CL increment ( $\bar{x}$  = 17.7 mm) seems clear (Fig. 7); this increment is identical to that determined from data presented by Auffenberg and Iverson (1979). The growing season at the Florida locality was 295 days, approximately 12% longer than that in southwestern Georgia (259 days). Over 75% of Georgia *G. polyphemus*, regardless of habitat, were in increment classes of less than 20 mm; individuals in Florida were significantly ( $P < 0.01$ ) more likely to grow more than 20 mm per year. In an additional sample of 30 tortoises from Marion County, Florida (provided by W. Auffenberg), projected CL increase exceeded 13 mm annually during the first 17 years of life and was 15-16 mm at ages 1-8 years. These values also are significantly greater than corresponding data in our samples ( $P < 0.01$ ). Earlier maturity, faster growth rates, and larger body size of southern versus northern *Kinosternon subrubrum* (Ernst *et al.* 1973) and *Chrysemys picta* (Christiansen and Moll 1973) have been attributed to longer annual growing seasons in the south. Jackson *et al.* (1978) felt that year-round activity was a significant factor, in addition to nutrition, in the rapid growth of *G. agassizii* captives.

#### ALLOMETRIC RELATIONS

Proportional changes in various body dimensions are important com-

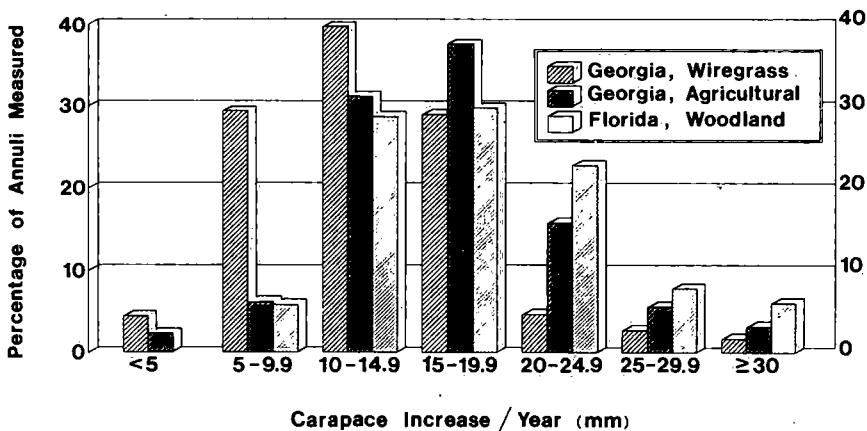


FIGURE 7. Comparison of mean annual carapacial increment during growing seasons 1-10 for gopher tortoises in Georgia (wiregrass and agricultural habitats) and Florida (woodland habitat).

ponents of shape and development (Mosimann 1958). In this section, allometry is utilized to depict changes from the juvenile to subadult to fully mature form in *G. polyphemus*. The relative rates of increase in CL, width (W), and thickness (TH) are apparent in Fig. 8. As has been noted for CL increase, mean body widths and thicknesses for age cohorts 0-17 were not significantly different from values predicted from the linear regression lines ( $P > 0.20$ ). Thus it is assumed that deviations about the line (Fig. 8, notably at age 9) are due to small sample sizes in some age cohorts.

Mean annual increments for various dimensions are given in Table 4. The major axis of growth through age 17 was antero-posterior, width and thickness increasing at only 73 and 41 % of the CL rate of increase, respectively. The annual increase in CL is a larger percentage of carapace length (compared to relative growth in W and TH) for 4-5 years after hatching. Mosimann (1958) noted dissimilarity between hatchlings and later forms and suggested that this reflected selection for "form-changing" types, *i.e.*, the advantageous form is produced mainly just after hatching through differential growth. This also seems to characterize the relative growth relations in *G. polyphemus*.

From about age 5 to just before maturity, growth is linear with age at the same relative rate in all 3 dimensions. Grubb (1971) reported isometry between CL and width in giant tortoises. Beginning at about age 17, as individuals reached adult form, annual increments in all body dimensions decreased sharply (Fig. 8). Growth rates in linear dimensions for the first 11 years as adults ranged from 23-54 % of rates for the younger group (Table 4).

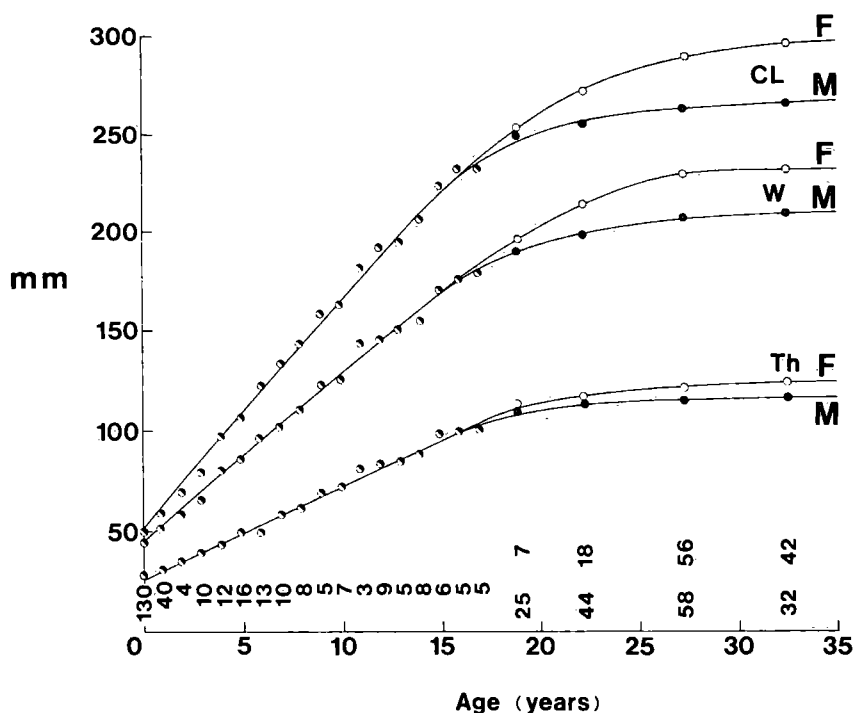


FIGURE 8. Relative growth in carapace length (CL), body width (W), and body thickness (TH) in relation to age estimated from annuli counts for male (M) and female (F) tortoises. Symbols are mean values for tortoises in 1-year age classes; sample sizes are indicated above the age axis. Through age 15, regression lines are used; thereafter, lines are fitted to the points by hand.

TABLE 4. Mean annual increments in body dimensions of young (0-17 yr) and older (18-28 yr) gopher tortoises. Increments for the first group are the slopes of regression equations (see text); for the older group, increments are values for the 26-30 age-cohort ( $\bar{x} = 28$ ) minus values at age 18 divided by 11 yr. Sample sizes in parentheses.

Dimension	Group 1 0-17 yr			Group 2 18-28 yr	
	(298)	Males (63)		Females (61)	
	$\bar{x}$	$\bar{x}$	% Group 1	$\bar{x}$	% Group 1
Carapace length (mm)	11.3	2.7	23.9	5.2	46.0
Width (mm)	8.3	2.5	30.1	4.5	54.2
Thickness (mm)	4.7	1.3	27.7	1.8	38.3
Volume (cc)	210.6	181.8	86.3	345.5	164.1



Allometric relations of older tortoises were clearly sexually dimorphic (Table 4). Width increases of males were almost equal to CL increments, and growth in thickness, although greatly reduced from the rate for the smaller group, was more rapid relative to CL increase. In females, however, CL and W continued to increase at approximately half the rates in the younger cohort, contrasted to rates in males of less than 1/3 those in the younger cohort (Table 4). The thickness of females increased at a much lower rate (38%). As a result of these allometric changes, mature females were longer and wider relative to their thickness than they had been during the latter stage of rapid growth (ages 12-17 yr). Increase in TH of both sexes and increase in CL and W of males typically was asymptotic soon after maturity was reached; CL and W of females usually increased substantially for several more years. Relative growth in the three dimensions is depicted in Figure 9.

Box-model volume ( $CL \times W \times TH$ ) was a curvilinear function of both CL and age (Fig. 10). As weight data were too variable for accurate analysis, volume was employed as an index to size. Regression analysis using 605 individuals demonstrated that weight and volume ( $V$ ) of gopher tortoises were linearly correlated ( $r^2 = 0.95$ ). It was found that patterns of development of secondary sex characters (e.g., plastral concavity) were

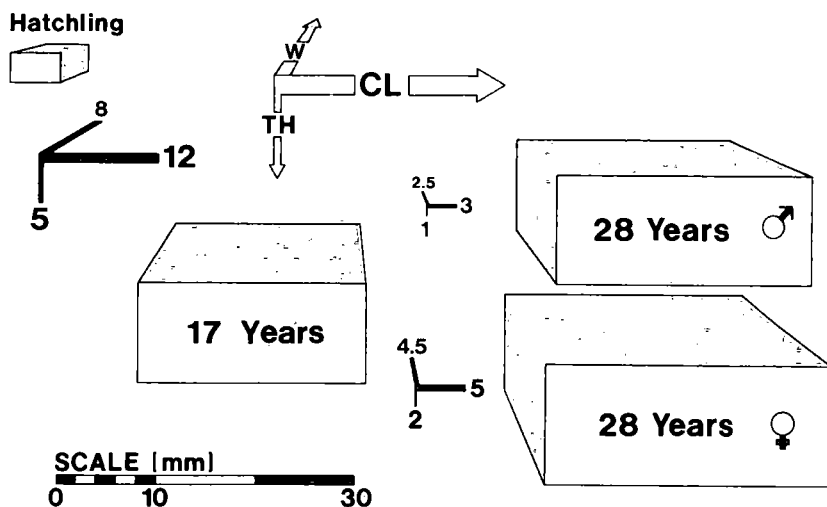


FIGURE 9. Three-dimensional growth models of *Gopherus polyphemus* in the hatchling, subadult, and mature stages of development. Arrows represent growth vectors of the three body dimensions, expressed in terms of mean annual increments (mm) between developmental stages.

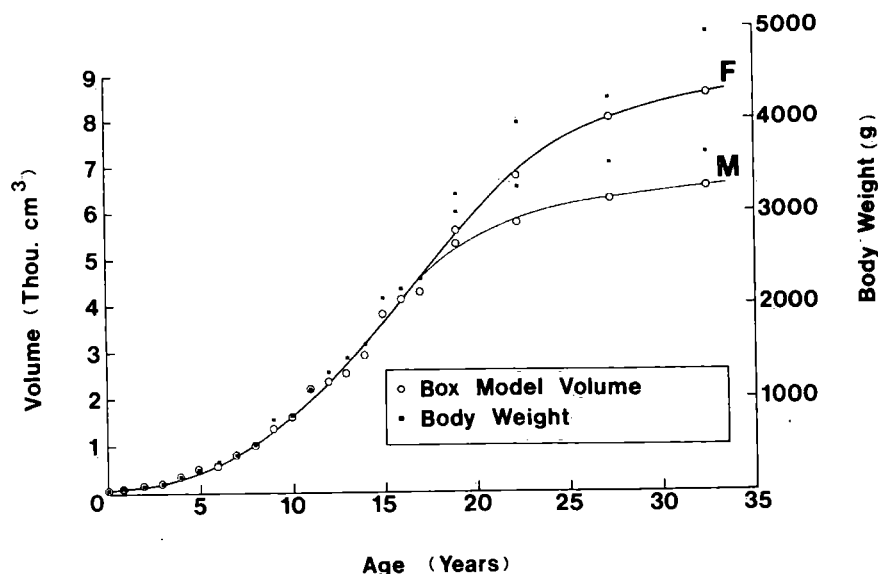


FIGURE 10. Volumetric growth and body weight in relation to age. Data were obtained using the volume-age correlation method, and the line for volume was fitted by eye.

highly correlated with body volume in linear relationships (McRae *et al.* 1980).

Since volume is a quadratic of three dimensions (CL, W, TH), all of which increase linearly with age (through 17 yr), its exponential increase (Fig. 10) is expected. The 90% greater rate of volumetric increase in 18 to 28 year old females (Table 4) relative to males was due mainly to continued growth in CL and W of females. Older females almost doubled in body volume during this 11-year span (Fig. 10), while males began to approach terminal size.

The exponential increase in total body size demonstrates a pronounced change that is not clearly reflected in linear dimensions taken separately. Volumetric change is a more meaningful indicator of growth; it best reflects the rapid development that is apparent in weight change with age (Table 5). A very close relationship exists between the box-model estimate of volume and body mass from age 0-17 years; the carapace in this age cohort is characteristically dome-shaped. In older, larger tortoises, the carapace becomes more dorsoventrally compressed and the body conforms more closely to the box model. This change in shape has also been noted in certain aquatic turtle species (Mosimann 1958). The body mass per cubic unit of box-model volume consequently increases greatly in older individuals (Fig. 10).

## VOLUMETRIC INCREMENTS

Estimates of annual volumetric increments were determined by calculating the mean volume of tortoises in each age class (Fig. 10) and then determining differences in volume from one year to the next. Values were plotted over CL to provide a general comparison with CL increments (Fig. 5). This curve (Fig. 11) shows a slight decrease in added size at CL of 60-70 mm, after which volume increased at an increasing rate. The inflection point occurred at 220-230 mm CL, beyond which tortoises were still growing, but at decreasing rates. This growth change occurred at the size of most rapid development of sexually dimorphic external characters (McRae *et al.* 1981).

TABLE 5. Body weights (g) of gopher tortoises, by age, in natural habitats in southwestern Georgia.

Age	N	$\bar{x}$	SD
0	130	34.4	3.1
1	40	50.1	10.4
2	4	64.1	12.4
3	10	100.1	19.1
4	12	181.4	28.8
5	16	238.1	41.8
6	13	319.3	45.2
7	10	400.2	47.4
8	8	519.7	100.2
9	5	779.1	81.6
10	7	817.6	118.3
11	3	1103.7	338.4
12	9	1272.5	303.1
13	5	1427.9	220.0
14	8	1581.2	358.6
15	6	2064.0	188.6
16	5	2165.4	366.9
17	5	2278.3	325.0
18-20 M	25	3012.3	575.9
F	7	3184.2	513.7
21-25 M	44	3287.4	688.2
F	18	3959.6	1102.0
26-30 M	58	3603.2	558.7
F	56	4205.3	958.7
31+ M	32	3651.9	573.6
F	42	4911.6	775.5

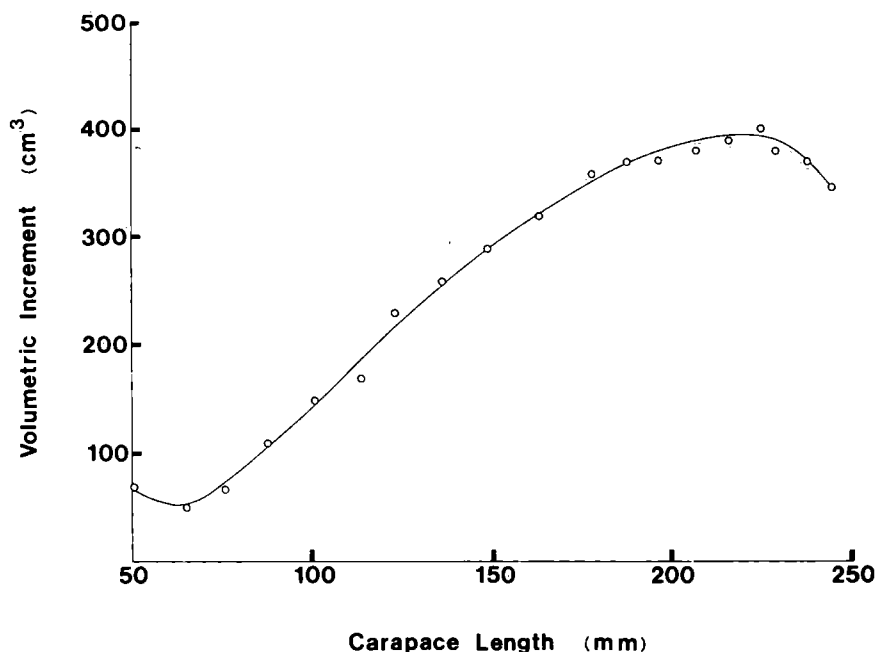


FIGURE 11. Annual volumetric increment in relation to CL. Increments are differences in mean volume between age classes, plotted over mean CL for each age class. Sample sizes as in Figure 8.

## SIZE IN RELATION TO LIFE HISTORY

### IMMATURE STAGES

As shown in previous sections, gopher tortoises develop most rapidly in early years, though not at a uniform rate. The cumulative effect of these variable rates is an overall growth curve, which is useful in depicting life history stages.

The progressive development of the carapace was estimated by three methods. Capture-recapture data from Table 1 were applied, starting at hatchling size (50 mm CL) and adding CL increments; theoretically, as a tortoise entered a new CL class, the mean annual increment for that class was added as the next year's growth. The second method was to plot CL over estimated age at the time of capture (data from Table 6). A curve was developed by connecting CL values obtained in September-October, when termination of yearly growth occurred. Carapacial increases estimated from annuli widths provided a third estimate (see Table 6).

These approaches indicate similar, curvilinear relationships (Fig. 12), beginning with a steep linear increase extending through age 11 years

(190 mm CL). This pronounced growth coincides with the above-average growth reflected in annual increments (Fig. 5). Thereafter growth gradually decreased; it was greatly reduced beyond age 17 years, especially in males.

TABLE 6. Carapace lengths of young gopher tortoises, by age, in natural habitats in southwestern Georgia. Values calculated by CL-age correlation are data for the middle of the growing season; annuli measurements provide values for the end of the growing season (winter).

Growing season	Carapace length (mm)					
	CL-age correlation			Annuli measurement		
	N	$\bar{x}$	SD	N	$\bar{x}$	SD
0	130	50.1 <sup>a</sup>	2.1	—	—	—
	40	59.4	5.5			
1	4	69.8	7.6	52	64.6	0.6
2	10	79.4	4.2	44	76.0	1.0
3	12	97.4	6.0	44	88.2	1.4
4	16	106.4	6.9	42	100.5	1.9
5	13	122.6	5.3	31	111.6	2.7
6	10	134.1	5.5	29	122.9	3.1
7	8	144.4	7.5	23	136.2	3.5
8	5	159.6	7.6	20	148.9	4.6
9	7	163.0	5.1	17	162.6	6.4
10	4	181.8	15.0	16	177.5	7.6
11	9	191.7	11.9	16	187.5	7.9
12	5	194.8	15.6	12	197.0	10.8
13	8	206.4	14.9	11	207.1	10.9
14	6	223.2	16.1	11	216.2	10.1
15	5	231.1	13.3	7	225.0	10.2
16	5	232.1	11.8	7	228.8	10.4
17				7	237.9	10.4

<sup>a</sup>Actual size during first day of life.

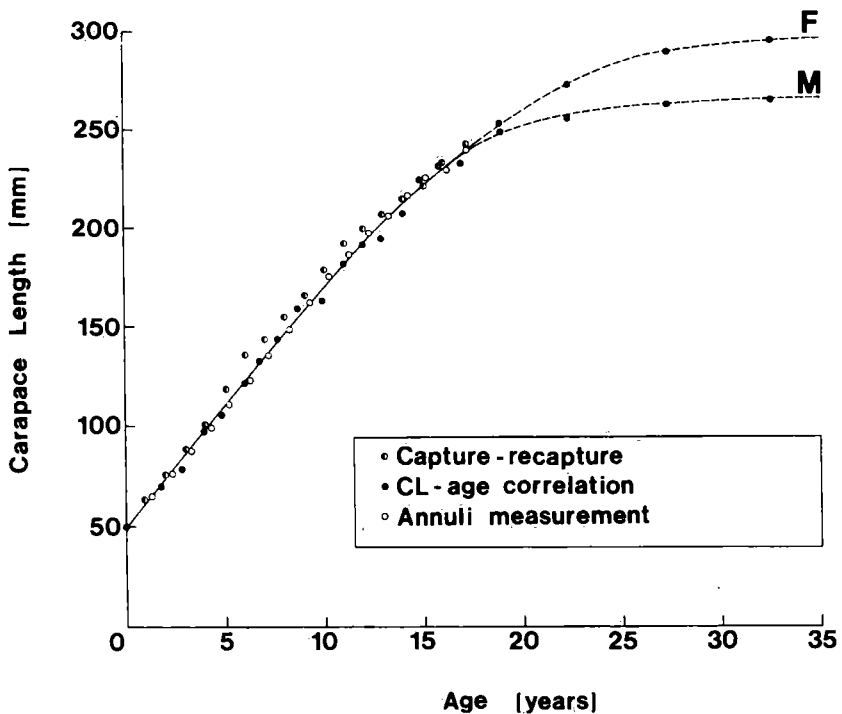


FIGURE 12. Comparison of CL-age relationships estimated by three methods of analysis. The curves are fitted to the CL-age correlation data only.

Tortoises passed through two general life history stages before reaching maturity. The juvenile stage lasted until the carapace was about 100-120 mm in length. The shells of young tortoises were very soft, and carapacial scutes usually had distinct yellow centers. Laminal spurs on the humeral and femoral shields were pronounced. During the following few years the juvenile coloration faded as tortoises entered the subadult stage. Laminal spurs became indistinct from abrasion, and the shell less compressible. During the latter portion of the subadult stage (190-220 mm CL), the shell was nearly rigid and sexual dimorphism became more apparent; body volume increased rapidly during this stage (Fig. 8). There was no evidence of social interaction (*i.e.*, visits to dens of others) in the juvenile stage, and very little interaction was observed among subadults.

Auffenberg and Iverson (1979) studied aging in relation to plastron growth in the Florida State Museum (FSM) collection. The growth curve in that sample appeared to be sigmoid, compared to the somewhat parabolic curve determined for tortoises at the southwestern Georgia locality (Fig. 13). Student's *t*-tests indicated that yearly means of PL

growth increments for the Florida tortoises 7-14 years of age were significantly larger ( $P < 0.01$ ). Means at ages 6 and 15 were different only at the 10% level, and at other ages the means were not significantly different ( $P > 0.10$ ). The Florida specimens were collected near Gainesville, approximately 140 km south of our study site. The differences in growth increments seem attributable to dissimilar yearly activity periods, as noted earlier.

#### SIZE AT SEXUAL MATURITY

Several criteria were used to determine size at maturity. Estimating the size at which males are functionally mature is a complex matter. Necropsy data showed that physiological maturity, as indicated by sperm production, occurs in individuals with a CL of 210 mm, and possibly smaller. Somatic maturity, including rapid development of secondary sex characters, usually occurs from that point up to 240 mm CL or more (McRae *et al.* 1981). Of greater importance is psychogenic maturity, which occurs when males acquire a propensity to breed. Determining that stage from field observation is difficult because large males attempt to prevent smaller ones from visiting females (Douglass 1980).

Subdentary glands were active from spring-fall in 55 males over 230 mm CL; glands of 18 others (160-235 mm CL) were inactive, but those of two males (222 and 227 mm CL) were slightly active. During a study of the mating system in southern Florida, Douglass (1980) observed seven males that visited females at their dens; plastron lengths of these males

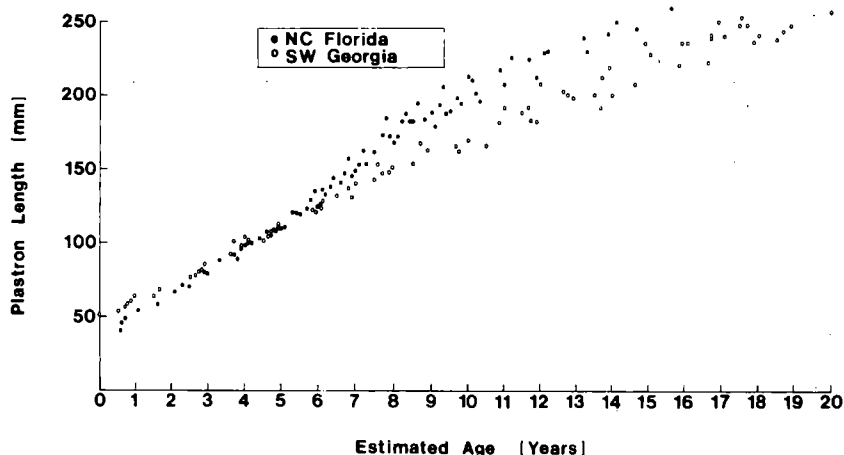


FIGURE 13. Plastral growth in relation to age in southwestern Georgia (this study) and north-central Florida (from Auffenberg and Iverson 1979). Symbols represent means for 0.1-year age classes.

were 222-256 mm (227-251 mm CL, our estimate). Of 32 males seen copulating or visiting females in our study, all were at least 240 mm CL.

Taking all factors into account, we estimate that males usually become functionally mature in this region as they reach 230-240 mm CL. The lower size limit of mature males indicated by Auffenberg and Iverson (1979) was also 230 mm CL.

Females in our study area reach somatic maturity at about 250 mm CL (McRae *et al.* 1981). The minimum CL of confirmed sexually mature females ( $N = 44$ ) was 252 mm. Ten small females (215-261 mm CL), necropsied during April and early May, contained no oviducal eggs, enlarged follicles, or corpora lutea; reproductive activity would probably have been discernible at this season (*e.g.*, Iverson 1980). Subdentry glands were active during spring for females 255 mm in length and larger, and inactive in smaller individuals.

From the FSM collection we also examined 23 females for which reproductive data were provided by J. Iverson. External sex characters in this sample were evident at smaller sizes than in our area (McRae *et al.* 1981). The smallest mature females in the FSM collection were 242, 245, and 249 mm CL. Other mature females reported from Florida have been as small as 238 mm CL (Auffenberg and Iverson 1979) and 241 mm CL (Hallinan 1923). Behavioral evidence presented by Douglass (1980) indicated that seven females 242-303 mm PL were frequently visited at their dens and often showed interest in male courtship; two of the larger individuals (245 and 303 mm PL) apparently laid eggs. Smaller females (184-240 mm PL) were rarely visited by males, and showed no interest in courtship. Based on a review of the literature and examination of the FSM and other samples, Iverson (1980) concluded that females mature at 220-230 mm PL (226-236 mm CL) in northern Florida.

We examined four immature females from our study area that were 243-261 mm CL: the smallest mature female was 252 mm CL, and all other confirmed mature individuals were 260 mm in CL or larger. From a collection made near Douglas, Georgia, Jackson *et al.* (1974) examined a female 241 mm CL that contained enlarged follicles, but this is not conclusive evidence of maturity. In turtles ovarian follicular development can occur several years prior to ovulation; this process is demonstrated in studies of *Chelydra serpentina* (Christiansen and Burken 1979) and *Geochelone gigantea* (Swingland 1977). Therefore we estimate that females in this part of Georgia reach maturity at some point between 250-265 mm CL.

#### AGE AT SEXUAL MATURITY

Growth rates of the two sexes were very similar up to about 240 mm CL, but began to diverge beyond that size. Volumetric increments peaked



at 220-230 mm CL (Fig. 8). After divergence the reduced growth rates of males and the greater rates in females led to sexual dimorphism in size beyond age 17 years (Table 7). Males attained the size of estimated sexual maturity (230-240 mm CL) at 16-18 years while females reached mature size (255-265 mm CL) at 19-21 years. The latter period is considerably greater than the 10-15 years estimated by Iverson (1980) for attainment of maturity by females in northern Florida. As stated earlier, the Florida specimens examined became mature at smaller sizes, and the minimum age was determined from faster-growing tortoises (Auffenberg and Iverson 1979).

Estimated ages at maturity in other *Gopherus* species in the wild vary considerably. *Gopherus agassizii* is said to mature at 15-20 years (Woodbury and Hardy 1948; Berry 1976). Burge and Bradley (1976) suggested that both sexes mature at 215-220 mm CL in that species, and data obtained by Medica *et al.* (in Auffenberg and Iverson 1979) indicate that this size is attained some time after 17 years of age. Miles (1953), however, stated that *G. agassizii* can reach maturity at ages as low as 10 years.

TABLE 7. Mean CL (mm) of large gopher tortoises, by sex and age group, in southwestern Georgia.

Age	Males			Females		
	N	$\bar{x}$	SD	N	$\bar{x}$	SD
18-20	25	248.2	10.0	7	251.8	8.7
21-25	44	254.9	12.7	18	271.6	7.7
26-30	58	261.9	10.5	56	288.6	12.6
31 +	32	263.7	16.1	42	294.3	15.9

In the Texas tortoise (*G. berlandieri*), attainment of breeding size has been estimated to occur at 15-20 years of age (Anonymous 1967, in Douglass 1980). However, Auffenberg and Weaver (1969) estimated that maturity in this species is reached at 105-128 mm CL, at ages of only 3-5 years.

Apparently the only information on sexual maturity in *G. flavomarginatus* is that of Legler and Webb (1961). They suggested that both sexes mature at 220-300 mm CL, and that the age of one female in this size range was about 11 years.

#### POST MATURITY

After maturity is reached, growth occurs occasionally, but at reduced rates. Unusually large size in adult *Chrysemys picta* (Gibbons 1967) and

*Geochelone gigantea* (Grubb 1971) has been attributed to exceptionally rapid growth as immatures rather than to continuing growth as adults. Auffenberg and Weaver (1969) noted a sharp decrease in growth of the Texas tortoise after attainment of sexual maturity. Abrasion of the shell of gopher tortoises over the years can hinder accurate age estimation. Males in this part of Georgia typically stop growing at some point between 250-270 mm CL. Females grow to be significantly larger; mean CL for adult females in our area was 283 mm ( $N = 102$ ); the largest captured was 335 mm CL. Sexual dimorphism in size may be related to differential energy intake and expenditure. Movement data from radio-instrumented tortoises in this area (unpublished) and data presented by Douglass (1980) show that males travel much more and spend more time in mate-seeking and courtship than do females.

By applying the mean growth rate of adults that grew measurable amounts from one year to the next (Table 8), we estimated that the age of the largest female in our sample was at least 57 years, and of the largest male (290 mm CL) was 46 years. So about 53% of recaptured adults did not grow during a one-year period, sporadic growth from year to year is indicated. Probably some tortoises at our locality live to be perhaps 80-100 years of age. Hubbard (1894) suggested that tortoises of this species may live more than 100 years.

TABLE 8. Annual growth of 56 adult gopher tortoises in southwestern Georgia, as determined by capture-recapture.

	Males <sup>a</sup>	Females <sup>a</sup>
Growing Tortoises		
N	11	15
$\bar{x}$ increment (mm)	2.1	2.3
Increment range (mm)	0.2-5.2	0.4-5.8
All Tortoises <sup>b</sup>		
N	24	32
$\bar{x}$ increment (mm)	0.9	1.1
Increment range (mm)	0.0-5.2	0.0-5.8

<sup>a</sup>CL > 240 mm for males, > 265 mm for females.

<sup>b</sup>Includes tortoises that did not show growth (13 males, 17 females).

## SURVIVAL AND ADAPTIVE IMPLICATIONS

Data gathered thus far suggest a latitudinal cline in body size in *G. polyphemus*, with a general northward increase. Notable exceptions are record-sized individuals from Florida, such as one of 368 mm CL

(Conant 1958) and another of 343 mm CL (Carr 1952). Local variations in growth due to differences in habitat quality and nutrition, documented in this study and by Gibbons (1967), Jackson *et al.* (1978), and Swingland (1977) for other species, may explain these exceptions.

The typical upper size limit for this species, according to Cochran (1952), is about 305 mm CL in Florida, and the largest reported by Ditmars (1946) and Hutt (1967) in Florida are less than 300 mm CL. Douglass and Layne (1978) noted that adults of PL greater than 300 mm were rare in a large sample ( $N = 366$ ) from south-central Florida, and Iverson (1980) reported a mean CL of 262 mm for adult females in a north-central Florida sample ( $N = 16$ ). Alford (1980) reported that only 4% of the individuals in 12 northern Florida colonies exceeded 300 mm in CL. Contrasting with these reports are: (1) in our study area in south Georgia, a mean CL for adult females of 283 mm (over 24% with CL exceeding 300 mm); and (2) observations that the largest individuals of a Florida-Georgia sample were in the fall-line hills of Georgia, at the northern limit of the range (D. Franz, pers. comm.). Further evidence that gopher tortoises in the south are generally smaller is implied by existing data on clutch size, which increases with the size of females (Iverson 1980; Landers *et al.* 1981). The mean and upper limit of clutch size in our study area (7+ and 12 eggs, respectively) exceed corresponding data from Florida (see Landers *et al.* 1981) with only two exceptions, both from Dade County (a clutch of 15 eggs and a group of 19 enlarged follicles in a female, Iverson 1980). Considerable evidence suggests a similar north-south cline in clutch size in some aquatic turtles (Cagle 1954; Tinkle 1961; Christiansen and Moll 1973).

The higher growth rates of Florida *G. polyphemus* relative to those in our study area seem attributable to longer growing seasons in the south. The reasons why females in Florida attain mature form and lay eggs at smaller sizes (McRae *et al.* 1980; Landers *et al.* 1981) and are apparently smaller on the average than those in southwestern Georgia are probably more complex. Several possible explanations are presented here for consideration.

One hypothesis is based on differential physiological age. In southwestern Georgia tortoises are dormant for 3-4 months during winter. Those in the southern portion of the range are active for much longer periods during a given year, and in extreme southern Florida are active year-round (W. Auffenberg, pers. comm.). Thus a southern specimen living the same number of calendar years as a more northerly one is physiologically older. If physiological age is a primary determinant of maturity, internal and external morphological traits accompanying maturity would be expressed in fewer calendar years and at smaller sizes in southern animals. Maturity is followed by a cessation or great reduction in growth,

and, consistent with the hypothesis, terminal sizes appear to be smaller in the south.

Another possible explanation for these size differences is based on the probable tendency of gopher tortoises to modify their habitats through grazing pressure. A longer growing season (*i.e.*, Florida vs. Georgia) results in earlier maturity and may induce more frequent additions to the population. If a high density ensues, overgrazing may reduce the more nutritious herbs in the feeding stratum and serve to limit the growth of larger individuals, which require greater quantities of food. Work on the giant tortoise (Swingland 1977; Coe *et al.* 1979) is interesting in this connection: Adults in a dense, food-limited population attained sizes only 40% as great as those attained in two low-density populations.

Additionally, environmental influences may select for terminal body size. If high-density populations have occurred more frequently and exerted stronger grazing pressure in southern portions of the range, selection for smaller, more energy-efficient tortoises could have resulted.

Selection for thermal efficiency may also be at work. Southern specimens not only tend to be smaller, they are also lighter in color on the carapace and plastron. In southwestern Georgia the carapace is dark gray and the plastron mottled black and yellow, while at the northern limits of the range (*e.g.*, the Georgia fall-line hills) the carapace is even darker and the plastron is often totally black (our observations and those of R. Franz, pers. comm.). It seems that smaller, lighter-colored tortoises may be better adapted to reflect heat (*i.e.*, in the south), while larger, darker individuals probably conserve heat more efficiently (*i.e.*, northern portions of the range).

Selection for larger females may be linked to fecundity. For example, in a study of geographic variation in size and reproduction of *Sternotherus odoratus*, Tinkle (1961) hypothesized that selection in the south must be mainly for smaller body size, while in the north, selection for both larger size and higher reproductive potential seems to exist. These selective forces may also affect gopher tortoises. The less frequent addition to colonies in southern Georgia, as indicated by longer periods of growth to sexual maturity, may be somewhat compensated by selection for larger females producing larger clutches. Growth is probably further reduced in more northerly populations, which may be even less productive. This species is distributed patchily in the fall-line hills of Georgia, and sand ridge habitats exist in many areas north of the present and known historic range of these animals. As annual temperature cycles influence growth and age at sexual maturity, it is possible that the length of the growing season is a major factor limiting the range of this species.

As Auffenberg and Iverson (1979) pointed out, growth to the age of sexual maturity is a very important parameter in population dynamics.

This period is critical, as individuals are exposed to predators and diseases before becoming reproductively active.

A study made in this area (Landers *et al.* 1981) revealed that female *G. polyphemus* nest at most once per year, and most nests (87%) are destroyed by predators. Many hatchlings are killed in the nests or shortly after emerging by predatory mammals and fire ants (*Solenopsis saevissima*) and, for at least two years after hatching by several species of snakes and mammals. In some areas, larger tortoises are preyed upon by canids (Causey and Cude 1978) and black bears (*Ursus americanus*) (D. Speake, pers. comm.). In addition, gopher tortoises are known hosts for several types of parasites (*e.g.*, Petter and Douglass 1976), but the effects of these and other possible agents of disease on populations are unknown. During this study, three immature tortoises (aged 2, 4, and 5 yr) and four adults were found dead in or near their burrows, but the causes of death could not be determined.

Low reproductive rates and the high incidence of postnatal mortality in this species no doubt greatly impede the comeback of depleted populations. The extended period of time required for hatchlings to reach maturity (*e.g.*, 10-15 yr in Florida, 16-21 yr in our study area) is an additional limiting factor, especially in more northerly parts of the range.

## APPENDIX

## SYNOPSIS OF METHODS USED TO ESTIMATE GROWTH

Results of this study are based on application of three methods commonly used in testudinid growth estimation. In using these methods, it was noted that each had its merits and shortcomings. This section is a comparison of the approaches, and is presented as an aid on future studies.

The capture-recapture method is most time-consuming. Due to varying rates of increase among and within size classes, a large sample is required (*i.e.*, at least 100 specimens). It is difficult to capture gopher tortoises at the same time in two successive years because they relocate frequently and become wary of even well-camouflaged traps. Recapture success was only 27% in this study and 25% in that of Goin and Goff (1941). If measuring seasonal growth is a study objective, this method should not be used because frequent capture may cause gopher tortoises to move to other burrows and may alter normal patterns of movement and feeding. If volumetric increments are to be studied, even larger samples are required; exponential increases make inferences from small samples of little value. The advantage of the capture-recapture method is that it yields exact measurements of linear increments over time. Its effectiveness can be improved by concentrating trapping efforts on juveniles and subadults, as adults grow very little.

The accuracy of age-dimension correlations is dependent upon the regularity of ring deposition in a given location and the ability of the observer to discern actual annuli. Both can be understood by close examination of specimens captured at various time intervals. To depict the entire aging process, a sufficient sample is needed for each 1-year class through maturity. In gopher tortoises, 5-10 per class is adequate to determine the overall pattern of growth, but not to estimate accurately increments between yearly age classes. The advantages of this method over the capture-recapture procedure are: (1) data can be gathered each time a live or dead specimen is available; (2) seasonal growth can be estimated by comparing sizes of the individuals captured during various months of the year. This method is also the most practical means of discerning trends in volumetric increase, as adequate data are easily obtained.

The utility of annuli measurement-prediction equations is also dependent upon accuracy in discerning rings. Total annuli width on the abdominal scutes was considered to be the best measurement for our purposes because (1) it takes into account the breadth of corresponding (paired) abdominal annuli; (2) it provides more precise points of measurement in comparison to other dimensions of that scute; (3) rings on the other plastral scutes are difficult to measure because of their irregular shapes and greater susceptibility to abrasion. Annuli are also deposited on the carapace, but measurements made on the convex shields are somewhat inconsistent from one tortoise to the next and false rings are not so easily detected as on the plastron. Resulting equations are valuable in estimating linear dimensions in past years, but not volume; the logarithmic relationship involved and the variable nature of the data prevent predicting volume from annuli measurements within acceptable limits. The advantages of this method are: (1) few specimens are required to obtain an adequate data set; (2) both preserved and live specimens can be utilized. Growth histories can also be used to compare the effects of differing environmental conditions over long periods of time.

Studies of growth and maturity of this and similar species are most thorough when all three methods can be employed. Capture-recapture data provide an essential check of results from other approaches. Seasonal growth and volumetric increase are most efficiently determined by age-dimension correlation, and long-term environmental effects and individual growth histories by the annuli-prediction equations.

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