

## Efficacy of Using Scute Annuli to Determine Growth Histories and Age of *Gopherus polyphemus* in Southern Alabama

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Complete demographic studies require an accurate determination of age and age-specific growth rates of individuals in a population. Life-history studies of reptiles have shown that individual growth rates influence key traits such as age at maturity and survivorship (Cagle, 1946; Tinkle et al., 1970; Iverson, 1991). Long-lived reptiles, such as the gopher tortoise, *Gopherus polyphemus*, often require 10–20 yr to reach reproductive maturity. The growth interval required for tortoises to attain maturity varies among populations with such factors as climate and habitat quality (Landers et al., 1982; Mushinsky et al., 1994; Aresco, 1998). Life-history traits such as delayed sexual maturity must be considered in the design and implementation of conservation plans for long-lived organisms (Congdon et al., 1993). Because of habitat loss and habitat degradation, gopher tortoise populations have suffered a dramatic decline and are legally protected over much of their range (Landers and Speake, 1980; Diemer, 1986). A reliable method of assessing growth rates and age is necessary to determine population structure and age at maturity and is therefore vital to the management and recovery of gopher tortoise populations.

Growth and age in turtles have been studied primarily using either external scute annuli or recapture of marked individuals. Mark-recapture studies of known-age turtles provide the most reliable data on age-specific growth rates. This method requires a long-term capture-recapture program (often at least 20 yr) to follow individuals from the hatchling stage through sexual maturity (Gibbons, 1987; Frazer et al., 1990). However, many chelonians display growth annuli on epidermal scutes that allow an estimation of age and growth rates (Gibbons, 1987; Zug, 1991). To be useful for age determination, it must be demonstrated that growth lines are formed annually. Galbraith and Brooks (1987) cautioned that the accuracy of using scute annuli to estimate age must be established before using the method in a study population. Annulus counting also has been shown to be age-limited in its usefulness (Brooks et al., 1997). Extremely slow growth of older individuals causes growth lines to overlap with one another and appear indistinct (Germano, 1992; Mushinsky et al., 1994). Woodbury and Hardy

(1948) reported that number of scute annuli did not correlate well with age of the desert tortoise (*G. agassizii*). Legler (1960) and Germano (1988) concluded that this discrepancy was caused by the inclusion of old tortoises which were past the age of regular growth.

Sergeev (1937) devised a method for estimating a series of previous carapace lengths from measurements of the length of growth lines on the plastral scutes. This method has been modified to estimate annual growth rates in ornate box turtles (*Terrapene ornata*; Legler, 1960) and desert tortoises (*G. agassizii*; Germano, 1988, 1994). Landers et al. (1982) developed a similar method based on the width of each growth annulus. These methods may be used to supplement or replace mark-recapture data for calculating growth rates and generating growth curves.

In this study, we assessed the accuracy of using scute annuli to determine growth histories and age of gopher tortoises in south-central Alabama. This information should be beneficial to biologists or land managers who need to estimate growth rates and ages of gopher tortoises in areas where a long-term mark-recapture program is not feasible. Growth rates calculated from measurements of scute annuli were compared to growth rates determined from mark-recapture data. We used nonlinear regression to describe tortoise growth patterns and compared parameter estimates of asymptotic size ( $a$ ) and intrinsic growth rate ( $r$ ) derived by the von Bertalanffy model using scute annuli and mark-recapture datasets. In addition, we compared von Bertalanffy model estimates of  $r$  derived using both known-age and growth-interval forms of the equation based on a specified value for asymptotic size.

### MATERIALS AND METHODS

Data used in this study were collected from 1991–1996 during a mark-recapture study of gopher tortoise populations on the Conecuh National Forest in south-central Alabama. Tortoise capture methods, measurements, sex determination, and marking techniques were described elsewhere (Aresco, 1998). To use scute annuli to determine tortoise age and growth histories, we had to establish that growth lines were pro-

duced annually. We tested whether plastral scute lines were produced annually by comparing annulus counts of each tortoise (< 15 yr) captured two or more times ( $n = 72$  recaptures of 39 tortoises) to the actual number of years of the capture interval. False annuli are caused by periods of inactivity during the growing season and were not counted. These annuli were identified by the shallow depth and discontinuity of the grooves bounding the annulus when compared to true annuli (Moll and Legler, 1971; Landers et al., 1982).

Measurements of abdominal scute length at the midline suture were recorded from 44 tortoises. The proportional relationship of scute length and carapace length could allow for the length of any growth line on the abdominal scute to be used to determine the approximate length of the carapace at the time the growth line was formed (Sergeev, 1937; Legler, 1960; Moll and Legler, 1971). The formula is defined as

$$\frac{AB}{CL} = \frac{AB^1}{X}, \quad (1)$$

where AB is the abdominal scute length at the midline suture, CL is the present carapace length,  $AB^1$  is the length of any given growth line, and X is the carapace length at the time  $AB^1$  was formed. This proportion assumes that the length of the abdominal scute remains constant relative to carapace length through time (Cagle, 1946; Moll and Legler, 1971). The validity of this assumption was tested by examining the relationship of the ratio of abdominal scute length to carapace length with the actual carapace length (Jones and Hartfield, 1995). If the assumption is valid, then the slope of the resulting regression equation should not be significantly different from zero. However, the slope of the regression equation was significantly different from zero ( $n = 44$ ;  $t = -6.89$ ;  $P < 0.0001$ ; slope =  $-2.3$ ) for tortoises ranging from 63 to 271 mm CL. The regression plot indicated that abdominal scute length decreased relative to carapace length as carapace length increased beginning at approximately 120 mm CL. Therefore, Sergeev's formula using annulus length measurements to calculate past carapace lengths could not be used to accurately reconstruct growth histories of gopher tortoises in this study.

During the 1996 trapping period, width of each growth annulus was measured on an abdominal scute, and a full set of annular width measurements was recorded from 35 tortoises (size range 63–271 mm CL). The width of an annulus was measured from its lateral edge to

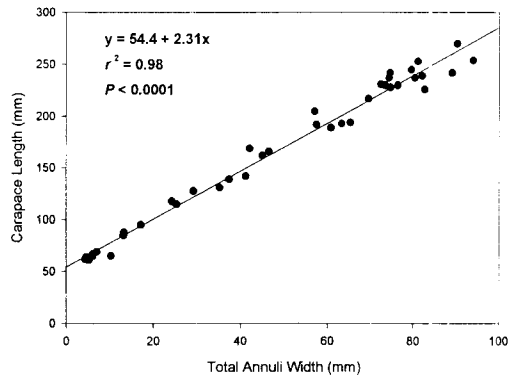


Fig. 1. Relationship between total width of abdominal scute annuli and carapace length in *Gopherus polyphemus* ( $n = 39$ ).

the lateral edge of the preceding annulus (Landers et al., 1982; Germano, 1988, 1994). A regression equation was determined from the relationship of total annular width to carapace length (Fig. 1). The regression equation was used to calculate past carapace lengths from measurements of cumulative annular width on an abdominal scute (Landers et al., 1982). Growth histories for 35 tortoises were reconstructed using calculated carapace lengths.

Growth rate was calculated as the change in carapace length divided by the time interval between captures using the equation for "instantaneous relative growth rate" ( $K_x$ ) devised by Brody (1945) as

$$K_x = \frac{(\log_e X_2 - \log_e X_1)}{t_2 - t_1}, \quad (2)$$

where X represents carapace length (mm) and  $t_2 - t_1$  represents the time interval (yr) between consecutive captures. This measure allows for comparison of growth rates of tortoises of varying sizes (Jackson, 1970; Cox et al., 1991; Lindeman, 1997). In the capture-recapture dataset, each tortoise was included only once, using data from the first recapture interval (i.e., first and second capture). To reduce variation associated with animals recaptured over short time intervals, we imposed a minimum interval of 0.7 yr (8 months) between captures. In the annulus width (AW) dataset, we included only one annulus measurement from each tortoise so that data points represented independent observations. Instantaneous relative growth rates ( $K_x$ ) calculated by the AW method were compared to  $K_x$ -values determined from recapture data. Tortoises were separated into 4-yr age classes for ages 0–16, and significant differences in  $K_x$ -values among the two methods were examined us-

ing  $t$ -tests. Significance was accepted when  $P < 0.05$ .

Values of  $K_r$  calculated from recapture data ( $n = 87$ ; 31 males, 20 females, 36 nonadults) and the AW method ( $n = 35$ ; 11 males, 5 females, 19 nonadults) were fitted to the von Bertalanffy growth-interval equation using nonlinear least-squares regression with the Marquardt algorithm in Statistical Analysis Systems PROC NLIN (Cary, NC, 1989, unpubl.). We chose the von Bertalanffy model because it fit our dataset better than the logistic model (Aresco, 1998). The growth-interval form of the von Bertalanffy equation assumes that ages are not known and is based only on carapace length measurements taken at capture and at recapture and the time interval between captures. The growth-interval form of this equation is

$$GR = ar[1 - (CL/a)], \quad (3)$$

where GR is instantaneous relative growth rate ( $K_r$ )  $\times 100$ ,  $a$  is asymptotic body size,  $r$  is intrinsic growth rate, and CL is carapace length at the midpoint of the growth interval (Fabens, 1965; Schoener and Schoener, 1978). Parameter estimates for asymptotic size ( $a$ ) and intrinsic growth rate ( $r$ ) were compared between the two calculation methods and were considered significantly different if the 95% "support-plane" confidence intervals did not overlap (Schoener and Schoener, 1978).

Growth was also modeled using carapace lengths and known ages obtained from both the actual capture data and the AW method fitted to the general von Bertalanffy equation with Statistical Analysis Systems PROC NLIN. The general (known-age) form of the von Bertalanffy equation is

$$CL = a(1 - be^{-rt}), \quad (4)$$

where CL is carapace length at age  $t$ ,  $a$  is mean asymptotic size in the population,  $b$  is a variable related to size at hatching,  $e$  is the base of the natural logarithm,  $r$  is intrinsic growth rate, and  $t$  is age (yr). Age was based on number of growth rings on an abdominal scute. Variable  $b$  can be calculated using the estimate for asymptotic length ( $a$ ) if mean size at some age is known (Fabens, 1965). Mean size at hatching (age = 0) has been used to calculate this constant in other turtle growth studies (Frazer et al., 1990; Kennett, 1996). We used mean carapace length of 17 hatchling *G. polyphemus* captured during this study ( $\bar{x} = 51$  mm CL; SE = 0.5 mm).

Parameter estimates for intrinsic growth rate ( $r$ ) were derived from both known-age and growth-interval forms of the von Bertalanffy

equation (eqs. 3 and 4) based on a specified value for asymptotic size ( $a$ ). Approximate asymptotic size ( $a$ ) was calculated as the mean carapace length of the 10 largest tortoises captured during this study (Frazer et al., 1990; Lindeman, 1997). Parameter estimates for  $r$  were compared using 95% support-plane confidence intervals. We used mean-square residual values ( $MS_{res}$ ) to judge which form of the von Bertalanffy equation best fit the data (Schoener and Schoener, 1978).

## RESULTS

The number of abdominal scute annuli produced during capture intervals ( $n = 72$ ) matched the actual number of years of the interval in all tortoises ( $n = 39$ ) less than 15 yr (Table 1). Plastral wear and slow growth prevented accurate annulus measurements on most tortoises 15 yr or older. False annuli were detected on 27% of the juvenile and subadult tortoises captured in 1996. Twenty percent of these were formed in 1995 when southern Alabama experienced lower than average rainfall during the growing season (2.67 cm below normal June–Sept.; Agricultural Weather Services, Inc., unpubl.).

Annulus counts were used to determine the actual relationship between age and carapace length (Fig. 2). Variation in growth rates produced marked variation in the size attained by each age class. Because of plastral wear and slow growth, very few mature individuals ( $> 15$  yr) were represented in the scute annuli dataset, and this prevented an accurate determination of the age-size relationship of these tortoises.

Measurements of AW were used to calculate carapace length in past years for 35 tortoises. Instantaneous relative growth rates ( $K_r$ ) calculated using this method were not significantly different from the recapture data for all 4-yr age classes (Table 2).  $K_r$ -values calculated using recapture data and the AW method were fitted to the von Bertalanffy growth-interval model. Estimates of intrinsic growth rate ( $r$ ) were identical for the two calculation methods (Table 3). The 95% support-plane confidence intervals for asymptotic size ( $a$ ) overlapped between the two methods and, therefore, were not significantly different. Values of  $MS_{res}$  were virtually identical for the two methods, indicating that model fit did not differ between the methods. Low  $MS_{res}$  values ( $< 1.5$ ) demonstrated that both datasets fit the model quite well.

Asymptotic size ( $a$ ) in both the known-age and growth-interval equations was set as mean carapace length of the 10 largest tortoises cap-

TABLE 1. ACTUAL TIME ELAPSED (YR) VERSUS NUMBER OF RINGS FORMED ON ABDOMINAL SCUTES OF *Gopherus polyphemus* RECAPTURED ONE OR MORE TIMES ( $N = 39$ ). Tortoise age (yr) is estimated from annulus counts at first capture. Number in parentheses is number of years each tortoise was recaptured. CL is the range of carapace lengths (mm) recorded for each tortoise during the time interval.

Age at first capture	Actual time elapsed	Number of rings formed	CL
1	1(1)	1	58-66
1	2(2)	2	61-84
1	4(3)	4	64-128
2	3(2)	3	74-117
3	1(1)	1	85-93
3	1(1)	1	88-94
3	1(1)	1	94-106
3	2(1)	2	75-95
3	2(1)	2	87-118
3	2(2)	2	88-109
3	4(3)	4	89-162
3	5(3)	5	101-205
4	2(2)	2	98-106
4	3(2)	3	86-134
4	3(2)	3	91-112
4	3(2)	3	95-119
4	3(2)	3	98-106
4	3(2)	3	105-131
4	5(5)	5	98-139
5	1(1)	1	94-107
5	2(2)	2	110-124
6	4(2)	4	118-170
7	1(1)	1	130-135
7	2(1)	2	120-149
7	2(2)	2	123-141
7	2(2)	2	129-146
7	2(2)	2	130-150
8	1(1)	1	116-125
8	1(1)	1	138-146
9	1(1)	1	130-138
9	3(3)	3	168-192
9	5(4)	5	154-192
10	1(1)	1	145-162
10	2(2)	2	140-149
10	2(2)	2	158-169
10	4(2)	4	162-192
12	1(1)	1	148-157
12	3(2)	3	166-195
14	1(1)	1	182-189

tured ( $\bar{x} = 273.7$ ,  $SD = 12.1$ , range 260-298). The 95% support-plane confidence intervals for  $r$  did not overlap between the two forms of the von Bertalanffy model (Table 4). The value of  $r$  estimated by the known-age model was significantly greater than that estimated by the growth-interval model. The growth-interval form of the von Bertalanffy model provided bet-

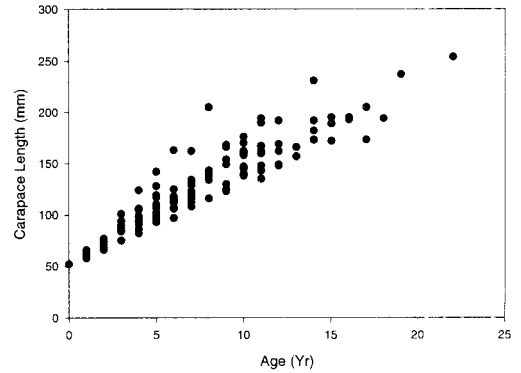


Fig. 2. Age-size relationship of *Gopherus polyphemus* in the Conecuh National Forest, south-central Alabama using counts of abdominal scute annulus to age tortoises.

ter fit compared to the known-age model as judged by the much lower  $MS_{res}$ -values.

#### DISCUSSION

Scute annuli have been used in several studies both to determine the age of tortoises and calculate growth rates by predicting past carapace lengths (Landers et al., 1982; Germano, 1988, 1994). These methods can be important in determining the demography of populations where data from a long-term mark-recapture program are not available. Mushinsky et al. (1994) reported that scute annuli could be used to accurately determine ages of gopher tortoises up to 11-13 yr in central Florida. Germano (1988) used scute annuli on the second costal scute of the carapace to age desert tortoises (*G. agassizii*). He found a significant positive correlation between age and number of scute rings in tortoises with up to 20-25 growth rings. In

TABLE 2. MEAN INSTANTANEOUS RELATIVE GROWTH RATES ( $K_c$ ) BY AGE CLASS OF *Gopherus polyphemus* USING CAPTURE-RECAPTURE DATA AND ANNULUS WIDTH MEASUREMENTS WITH  $t$ -TEST RESULTS. Standard deviations are shown in parentheses.

Age-class	Capture-recapture		Annulus width method		P-value
	n	$K_c$	n	$K_c$	
0-4	11	0.065 (0.018)	11	0.068 (0.008)	0.55
4-8	10	0.039 (0.012)	8	0.037 (0.014)	0.81
8-12	10	0.027 (0.010)	7	0.032 (0.009)	0.30
12-16	9	0.014 (0.014)	9	0.019 (0.005)	0.40

TABLE 3. PARAMETER ESTIMATES WITH 95% SUPPORT PLANE CONFIDENCE INTERVALS DERIVED FROM THE VON BERTALANFFY GROWTH-INTERVAL EQUATION FOR *Gopherus polyphemus* IN THE CONECUH NATIONAL FOREST, ALABAMA. Estimates of  $a$  and  $r$  resulted from nonlinear least-squares regression (Statistical Analysis Systems PROC NLIN) of both capture-recapture data and scute annulus width data fitted to the growth-interval equation under the assumption that ages were not known. Variable  $a$  is asymptotic carapace length (mm), variable  $r$  is intrinsic growth rate, and  $MS_{res}$  is mean-square residual error. The 95% support-plane confidence intervals are indicated in brackets and standard errors in parentheses.

Dataset	n	$a$	$r$	$MS_{res}$
Capture-recapture	87	255.3 (6.16) [243.01–267.5]	0.032 (0.002) [0.028–0.036]	1.49
Annulus width	35	265.3 (15.0) [234.9–295.8]	0.032 (0.003) [0.025–0.039]	1.36

the present study, growth annuli on the abdominal scute of the plastron were accurate in determining ages of gopher tortoises up to 15 yr. Over 15 growth rings were visible on some individuals; however, we could not determine whether these were annual rings or whether extremely slow growth in some years may have prevented one or more rings from being formed.

Landers et al. (1982) and Germano (1994) used annulus width and annulus length measurements, respectively, to back-calculate carapace lengths of tortoises to estimate growth histories. In the present study, growth rates estimated from AW measurements did not differ significantly from actual growth rates as calculated from the recapture data. This method was accurate in reconstructing growth histories of tortoises up to 15 yr. However, the maximum age at which this method is accurate may vary between populations. Maximum age at which

scute annuli are measurable may be reduced in populations where tortoises grow faster and reach adult size at earlier ages than tortoises in this study (Mushinsky et al., 1994; Aresco, 1998). In addition, investigators must ensure that growth lines are produced annually in their study populations and be able to discern false annuli.

Measurements of annulus length could not be used to calculate past carapace lengths in this study because we demonstrated that relative scute length at the midline suture decreased significantly with an increase in carapace length. We agree with Landers et al. (1982) that measurements of annulus width on the abdominal scutes of gopher tortoises provide more precise points of measurement in comparison to other dimensions of that scute (e.g., annulus length). Germano (1988) measured annuli on carapacial scutes of desert tortoises; however, we could not measure scute lines on carapacial scutes of

TABLE 4. PARAMETER ESTIMATES FOR INTRINSIC GROWTH RATE ( $r$ ) AND MEAN-SQUARE RESIDUAL VALUES ( $MS_{res}$ ) DERIVED FROM TWO FORMS OF THE VON BERTALANFFY GROWTH EQUATION FOR *Gopherus polyphemus* IN THE CONECUH NATIONAL FOREST, ALABAMA. Estimates of  $r$  resulted from nonlinear least-squared regression (Statistical Analysis Systems PROC NLIN) of both capture-recapture data and scute annulus width data. Asymptotic carapace length ( $a$ ) was set at 273.7 mm in both equations, and  $b$  is a variable in the known-age equation related to carapace length at hatching, where  $b = 1 - 51.0/a$  (see text for explanation). The 95% support-plane confidence intervals are indicated in brackets and standard errors in parentheses.

Dataset	n	$r$	$b$	$MS_{res}$
(A) Growth-interval model				
Capture-recapture	87	0.027 (0.001) [0.025–0.030]		1.59
Annulus width	35	0.031 (0.001) [0.029–0.033]		1.33
(B) Known-age model				
Capture-recapture	45	0.062 (0.003) [0.056–0.067]	0.813	307
Annulus width	35	0.078 (0.003) [0.071–0.084]	0.813	233

adult gopher tortoises because the carapace was often worn smooth by abrasion during burrowing.

Growth rates calculated by AW measurements were fitted to the von Bertalanffy growth model to determine the accuracy of using this method to generate a nonlinear growth model. Parameter estimates for asymptotic size ( $a$ ) and intrinsic growth rate ( $r$ ) were not significantly different from those generated by capture-recapture data. The AW dataset was limited to tortoise growth for years 1–15 and therefore lacked data from larger tortoises. When fitted to the growth-interval equation, the AW data generated parameter estimates similar to those for capture-recapture data, which were not truncated by lack of large tortoises. For both AW data and capture-recapture data,  $MS_{res}$ -values and estimates of intrinsic growth rate ( $r$ ) were almost identical regardless of whether asymptotic size was estimated by or specified in the growth-interval model. Frazer et al. (1990) demonstrated that the von Bertalanffy growth-interval equation may not accurately estimate asymptotic size ( $a$ ) and intrinsic growth rate ( $r$ ) when datasets are truncated by lack of larger individuals. However, Frazer and Ladner (1986) obtained a reasonable estimate of asymptotic size in green sea turtles, *Chelonia mydas*, using a dataset lacking both the large and small individuals. Despite the lack of large individuals (> 200 mm CL) in our AW dataset, there were sufficient individuals of adequate size and/or low variability in growth rates among individuals of similar size to model growth consistently.

The growth-interval form of the von Bertalanffy model clearly fit the data better than the known-age form. Significant size variation at each age in the known-age dataset resulted in a considerable decrease in model fit and an overestimation of intrinsic growth rate by the known-age model. Variation in growth rates within each age group is reflected by this size variation and may be due to differences in forage quality among tortoise burrow sites in pine plantations (Aresco, 1998). Investigators should compare model fit between both forms of the von Bertalanffy equation (i.e., known age vs recapture intervals) to determine the more biologically meaningful parameter estimates. The AW method can be used to develop growth rate histories and to compare growth rates of juvenile and subadult tortoises in the same age classes where recapture data are not available. Furthermore, datasets generated by measurements of annulus width can be used to develop nonlinear growth models. The application of this procedure should be useful to biologists con-

ducting demographic studies of gopher tortoises.

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