Growth and age at maturity of North American tortoises in relation to regional climates

DAVID J. GERMANO[1]

Museum of Southwestern Biology, Department of Biology, University of New Mexico, Albuquerque, NM 87131, U.S.A.

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North American tortoises (*Gopherus* spp.) are long-lived species that occur in a variety of habitats. I described growth of tortoises using Richards' growth model based on measures of scute annuli. *Gopherus flavomarginatus* is the largest species and grows the fastest, and *Gopherus berlandieri* is the smallest species with the slowest growth rates. *Gopherus polyphemus* and *Gopherus agassizii* are intermediate in size, with intermediate growth rates. All species grow relatively fast for 18–22 years, after which time growth rates decrease greatly. Estimates of mean age at maturity are 13.3 years for *G. berlandieri*, 13.9 years for *G. flavomarginatus*, 14.4 years for *G. polyphemus*, 13.8 years for Sinaloan *G. agassizii*, 14.4 years for western Mojave *G. agassizii*, 15.4 years for eastern Mojave *G. agassizii*, and 15.7 years for Sonoran *G. agassizii*. Several measures of growth did not correlate with precipitation among species of *Gopherus*, although mean yearly growth was negatively correlated with mean annual precipitation in populations of *G. agassizii*. Also, a matrix of growth variables did not correlate with a matrix of environmental variables. Although other environmental variables should be measured within the ranges of *Gopherus* spp., preliminary analyses suggest that the environment is not the main determinant of growth rates of North American tortoises.

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Les tortues terrestre de l'Amérique du Nord (*Gopherus* spp.) sont des espèces qui vivent longtemps et qui habitent diverses régions. J'ai descrit la croissance des tortues suivant le modèle de croissance de Richards fondé sur les mesures des écailles de la carapace. *Gopherus flavomarginatus* est l'espèce la plus grosse à la croissance la plus rapide et *Gopherus berlandieri* est la plus petite espèce, au taux de croissance le plus faible. *Gopherus polyphemus* et *Gopherus agassizii* sont intermédiaires en taille et en taux de croissance. Toutes les espèces croissent à un taux relativement rapide pendant 18–22 ans, après quoi le taux de croissance diminue beaucoup. L'évaluation de l'âge moyen à la premiere reproduction est 13,3 ans chez *G. berlandieri*, 13,9 ans chez *G. flavomarginatus*, 14,4 ans chez *G. polyphemus*, 13,8 ans chez les *G. agassizii* de Sinaloa, 14,4 ans chez les *G. agassizii* de l'ouest de Mojave, de 15,4 ans chez les *G. agassizii* de l'est de Mojave et de 15,7 ans chez les *G. agassizii* du désert de Sonora. Beaucoup de taux de croissance sont indépendants des précipitations chez les espèces de *Gopherus*, mais la croissance annuelle moyenne est en corrélation négative avec les précipitations annuelles moyennes chez les populations de *G. agassizii*. Une matrice des variables de la croissance s'est avérée sans corrélation avec une matrice des variables de l'environnement. D'autres variables de l'environnement devraient être mesurées dans les zones de répartition de *Gopherus*, mais les analyses préliminaires indiquent que l'environnement n'est pas le principal facteur déterminant de la croissance des tortues terrestre de l'Amérique du Nord.

[Traduit par la Rédaction]

Introduction

North American tortoises (*Gopherus* spp.) present an opportunity to study the life-history traits of long-lived organisms that exist in differing environments. In addition, all four species of North American tortoises carry a history of past growth on their shells in the form of growth rings. Growth rings can be used to age many individuals in a population and to accurately assess past variability in growth (Landers et al. 1982; Germano 1988, 1992; Zug 1991). Individual growth is intimately associated with changes in life-history traits (Schaffer 1974; Charlesworth 1980). Growth rate can affect how long a juvenile is subject to most causes of mortality, when a juvenile matures, how many eggs can be produced per year by a female if clutch size is dependent on body size, the size that adults achieve, and the ability of adults to survive over long periods of time. Thus, growth should be subject to intense selective pressure because of its direct link to fitness. Individual growth is affected by a variety of biotic and abiotic factors (Andrews 1982), which then can indirectly affect other

life-history traits. An analysis of growth rates and life-history traits of North American tortoises could reveal how a long life affects the expression of these traits.

There are four species of tortoises in North America (Fig. 1). *Gopherus polyphemus* occurs in sandy upland areas of pines (*Pinus* spp.) and oaks (*Quercus* spp.), often with an understory of wiregrass (*Aristida* spp.) (Auffenberg and Franz 1982). *Gopherus flavomarginatus* is restricted to a small area of the southern Chihuahuan Desert composed of sclerophyll plants and *Hilaria* grass (Morafka 1982). *Gopherus berlandieri* inhabits shrublands in southeast Texas and northeast Mexico (Auffenberg and Weaver 1969). *Gopherus agassizii* occupies the largest range, both geographically and ecologically, of the four species of tortoises. It occurs in valleys and bajadas of Mojave Desert scrub in the northern part of its range, on rocky hillsides of Sonoran upland vegetation in the center of its range, and on hills covered by Sinaloan thorn scrub and deciduous woodland in the south (Auffenberg 1969; Germano et al. 1994). These differences in geography and habitats of North American tortoises allow for the testing of how the environment affects growth, and therefore ultimately the life-history traits, of long-lived species.

[1]Present address: Department of Biology, California State University, Bakersfield, CA 93311, U.S.A.
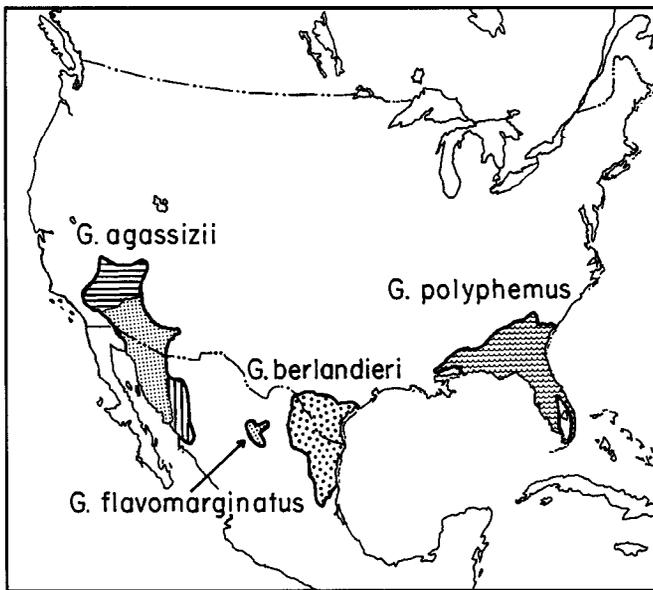
FIG. 1. Distribution of North American tortoises (genus *Gopherus*). *Gopherus agassizii* occurs in 3 distinct biotic regions: Mojave Desert (horizontal lines), Sonoran Desert (dots), and Sinaloan thornscrub and deciduous woodland (vertical lines). Redrawn from Bury (1982).

Material and methods

Growth measurements

Whole-shell measurements and measurements of annuli from the second coastal scute (either right or left) were taken from live and preserved *G. agassizii*, *G. berlandieri*, and *G. flavomarginatus* and from preserved *G. polyphemus*. The measurements taken on each annulus were length (*L*), width (*W*), and annual width (AW) (Fig. 2). The annual width of an annulus is the distance from its lateral edge to the lateral edge of the preceding annulus. Annulus length (*L*) is highly correlated with total shell length and is useful in predicting past shell size of individuals (Landers et al. 1982; Germano 1988, 1992).

Growth rates were compared among populations in several ways. Richards' (1959) growth curves with jackknife confidence intervals (Bradley et al. 1984) were constructed using growth rings from all individuals in a group (mixed longitudinal data): *G. berlandieri*, *G. flavomarginatus*, *G. polyphemus*, and western and eastern Mojave, Sonoran, and Sinaloan populations of *G. agassizii*. This analysis gave four growth parameters for each population: asymptotic size, weighted mean growth rate, percentage of asymptotic size achieved at curve inflection, and time period in years required to grow from 10 to 90% of asymptotic size (Richards 1959; Ricklefs 1967; Bradley et al. 1984) (Fig. 3). Richards' growth model was deemed superior to other fixed-growth models because it allows the data to determine the shape of the growth curve. Also, if the shape of the growth curve differs from that of fixed-curve models (e.g., the Gompertz and von Bertalanffy models), then Richards' model will produce less biased estimates of the growth function (Leberg et al. 1989). In several instances, the asymptotic size predicted from growth data was unreasonably high, with large confidence intervals. This seemed to occur because either adult growth ended abruptly or very small growth rings (Germano 1992) could not be measured. Because of this, mean upper decile sizes of adults were used as the asymptotic sizes following recommendations of Bradley et al. (1984).

Comparisons of growth rates among tortoises also were made using mean and upper decile carapace lengths (CL) of adults, mean annual widths of growth rings (AW), calculated carapace lengths (CCL) by 4-year intervals, and mean annual increases in CCL over 4-year intervals from ages 1 to 20 years. Mean CCL was calculated for each group using regression equations relating the length of a ring (*L*) to
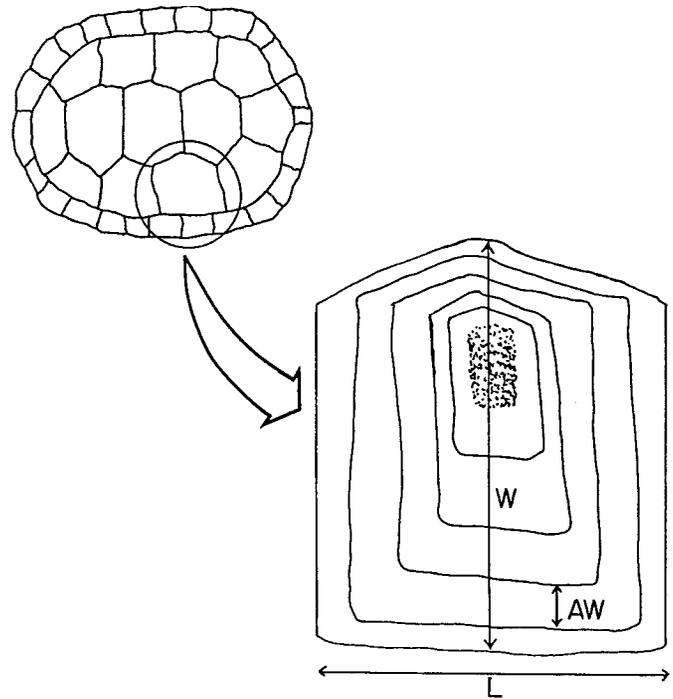

FIG. 2. The second coastal scute of *Gopherus* sp. from which growth measurements and ring counts were taken. The measurements taken on each visible ring were the length of the ring (*L*), the width of the ring (*W*), and the amount of growth from one ring to the next (AW). From Germano (1988).

CL (Table 1). Mean CL and CCL by sample were tested for significant differences among species using ANOVA and Scheffé's test among means. Mean CL by sample was tested for significant differences between sexes within species by means of the Wilcoxon sign test with Bonferroni adjustments to probability values.

I also calculated the degree of sexual size dimorphism using the ratio of the size of the larger sex divided by the size of the smaller sex (Lovich and Gibbons 1992). The sexual size dimorphism index (SDI) is considered positive when females were larger and negative when males are larger. To eliminate discontinuity of SDI values, i.e., simultaneous variation around +1 and −1, I subtracted 1.0 from SDI values if females were larger and added 1.0 if males were larger (Lovich and Gibbons 1992). As a result, SDI values vary around zero (Lovich and Gibbons 1992).

Climate analysis

The climate within the range of each species was described using published climate data (U.S. National Oceanographic and Atmospheric Administration 1953–1981; Hastings 1964; Alvarez Gomez 1972); I used precipitation, average maximum temperatures, and average minimum temperatures by month for 20 years, except for climate stations in the range of *G. flavomarginatus*, where only 13 years of data were available. In addition, only average daily temperatures were available within the Sinaloan range of *G. agassizii*. Means and standard deviations of climate data were calculated and plotted for each species' range. The quality of data available to describe the climate for each species varied according to the number and locations of weather stations whose information was used: 10 weather stations within the range of *G. polyphemus*, 10 Texas stations for *G. berlandieri*, and 5 stations each for *G. flavomarginatus* and the four regions of *G. agassizii*.

The predictability (*P*), constancy, and contingency (Colwell 1974) of precipitation were also estimated for each climatic site, using mean monthly data. Means of these three values were calculated for each species' range. Predictability essentially measures variability: $P = 1$ indicates an absolutely predictable environment and $P = 0$ a
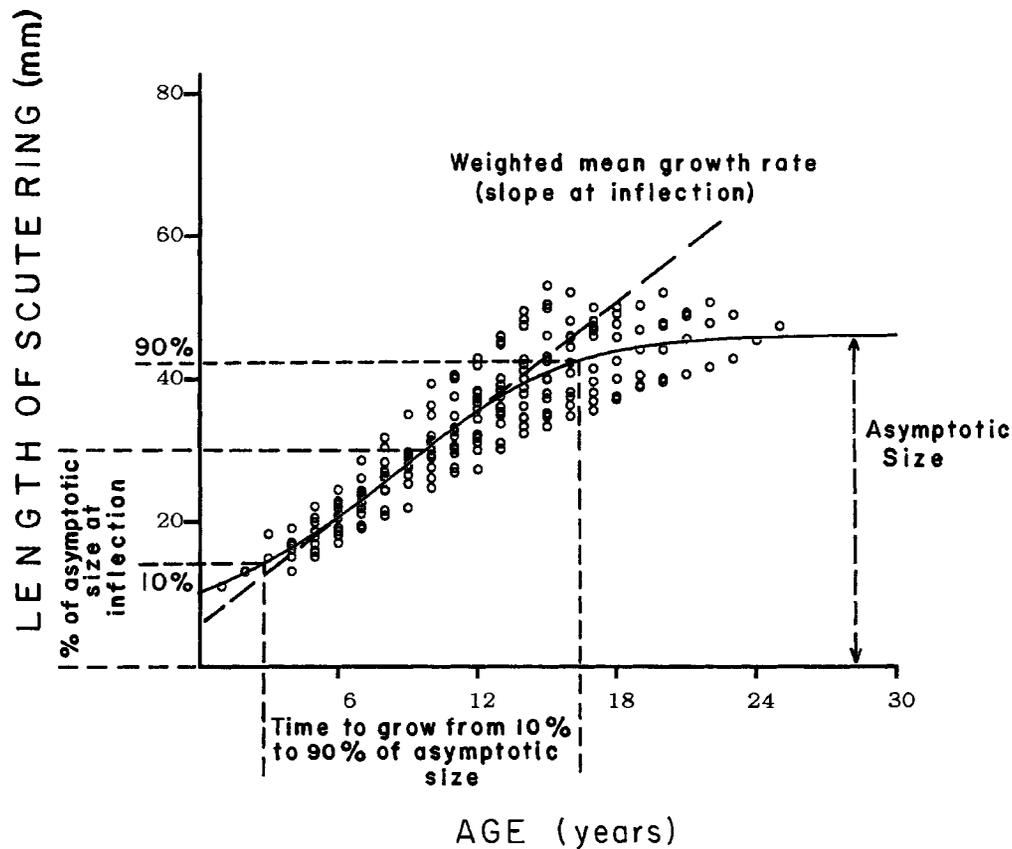
FIG. 3. The four growth parameters determined for North American tortoises. These growth parameters result from fitting lengths of scute rings to Richards' (1959) growth curve.

completely unpredictable environment. Constancy and contingency sum to the value of P. Constancy measures the evenness of rainfall among months and contingency measures the seasonality of rainfall within a year. These measures of climatic data accurately depict the seasonality and variability of long-term data (Stearns 1981).

Age at maturity

I estimated age at maturity (AAM) of females in each region from published minimum sizes of females with eggs for each species: Mojave Desert *G. agassizii*, 190 mm CL (Turner et al. 1986); northern *G. polyphemus*, 250 mm CL (Landers et al. 1982); southern *G. polyphemus*, 232 mm CL (mean value based on Iverson 1980; Linley 1987; Diemer and Moore 1994); *G. berlandieri*, 155 mm CL (Rose and Judd 1982); *G. flavomarginatus*, 280 mm CL (curved carapace length 356 mm; Morafka 1982). Because minimum size at first reproduction is not known for Sonoran and Sinaloan desert tortoises (Germano 1994), I used 190 mm CL as a first approximation. Age at these minimum sizes was ascertained from scute annuli for those females that had reached or exceeded the appropriate size as determined by the scute ring measurement L. In this way, age was determined for each female individually. Mean AAM was tested for significant differences among means of groups using the Kruskal–Wallis test because Bartlett's test of equal variances showed significant differences among within-group variances. I used the Wilcoxon sign test to compare pairs of means. I also determined AAM of females according to group by determining the age from the growth model that corresponds to the length of the scute ring for the smallest females with eggs.

Correlations of growth with climate

Several measures of growth of North American tortoises were correlated with climate. Mean AW was used as an index of total growth, in length, width, and height, of an individual, and it was used to correlate mean growth of individuals in groups with mean precipi-

TABLE 1. Regression parameters and sample sizes (n) used to convert annulus length to carapace length for North American tortoises

| | Regression parameter | | | |
	Slope	Intercept	R^2	n
G. berlandieri	4.80	−14.56	0.93	82
G. agassizii				
Mojave	4.88	−9.17	0.96	158
Sonoran	4.75	−2.08	0.95	80
Sinaloan	4.65	0.70	0.96	42
G. polyphemus	4.87	−11.72	0.96	77
G. flavomarginatus	5.01	−7.18	0.96	92

tation levels for each region. Upper decile CLs were also correlated with mean precipitation levels for each region. In addition, the coefficient of variation of the mean AW for each species was correlated with the predictability of precipitation and the coefficient of variation of mean precipitation level for each range of each species.

I also constructed a matrix of growth measures for North American tortoises using UPGMA clustering with the average linkage algorithm of the BMDP statistical package (Dixon 1981). The growth matrix was made using upper decile CL, mean AW, coefficient of variation of AW, weighted mean growth rate, percent asymptotic size at inflection, time to grow from 10 to 90% of asymptotic size, and estimated mean AAM of each species and for the subregions of *G. agassizii*. I compared this matrix with matrices based on genetic distances (Lamb et al. 1989), climate variables, and shell morphology constructed in the same manner (Germano 1993). The climate variables used were mean precipitation level, winter precipitation

TABLE 2. Mean and upper decile carapace lengths for all adults and mean and upper quartile carapace lengths for male (M) and female (F) North American tortoises.

	Mean (mm)	SD	n	SDI	Upper decile (mm)	Upper quartile (mm)	SD	n	SDI
G. berlandieri									
All	155.3*a*	27.4	74		202.9*a*		8.43	7	
M	166.5*	27.4	44	−0.20		197.7*	9.81	11	−0.24
F	138.8	17.5	30			160.0	8.28	8	
G. agassizii									
Western Mojave									
All	233.4*b*	23.0	49		273.4*bd*		9.40	5	
M	240.2*	26.0	26	−0.07		270.1*	9.49	7	−0.11
F	224.7	14.2	21			243.0	5.87	5	
Eastern Mojave									
All	215.3*c*	20.7	131		255.4*c*		4.59	13	
M	221.8*	23.2	70	−0.07		251.5*	7.26	18	−0.11
F	208.2	14.5	53			227.1	10.9	13	
Sonoran									
All	232.3*bd*	23.4	82		270.5*b*		10.4	8	
M	236.3	24.4	36	0		263.9	9.66	9	0
F	232.2	23.0	38			258.1	12.6	10	
Sinaloan									
All	218.7*bc*	32.1	40		274.0*bd*		10.2	4	
M	209.0*	33.7	24	0.10		251.5	24.0	6	0
F	230.4	21.7	13			255.5	8.50	3	
G. polyphemus									
All	246.1*d*	26.3	65		292.1*d*		11.7	7	
M	248.8	24.2	29	0		281.6	6.65	7	0
F	242.4	27.7	31			279.3	16.9	8	
G. flavomarginatus									
All	311.9*e*	31.7	69		367.6*e*		8.38	7	
M	304.7*	22.7	15	0.10		332.3*	23.89	4	0.10
F	334.3	27.3	19			366.8	10.1	5	

NOTE: Within groups, lengths followed by a different letter are significantly different. An asterisk denotes a significant difference between the sexes. By definition, when male and female CLs are not significantly different, SDI = 0.
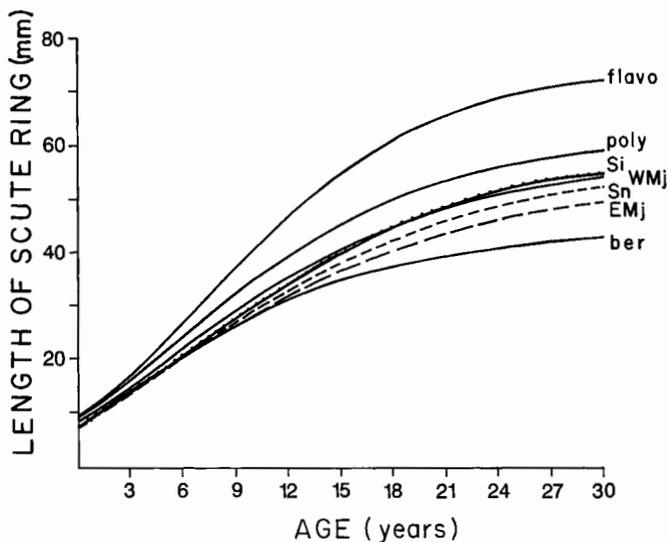

FIG. 4. Composite growth curves, irrespective of sex, of each species of North American tortoise and of populations of *G. agassizii*. flavo, *G. flavomarginatus*; poly, *G. polyphemus*; ber, *G. berlandieri*. For *G. agassizii*: WMj, western Mojave; EMj, eastern Mojave; Sn, Sonoran; Si, Sinaloan. Data points are omitted for clarity.

level (October–March), summer precipitation level (July–September), predictability of precipitation, coefficient of variation of annual precipitation level, mean July temperature, mean January temperature, and the difference between mean January and July temperatures. I compared the growth matrix with the phylogenetic, climate, and shell-morphology matrices using the Mantel test (Mantel 1967; Sokal 1979).

Results

Growth

Adult North American tortoises vary in size from the large *G. flavomarginatus* (370 mm CL) to *G. berlandieri* (200 mm CL) (Table 2). *Gopherus polyphemus* is the next largest species, with a CL about 80% of that of *G. flavomarginatus*. Within the range of *G. agassizii*, eastern Mojave individuals are significantly smaller than individuals from the other three regions (Table 2). *Gopherus agassizii* are smaller than *G. polyphemus* overall, although *G. agassizii* from the western Mojave are not significantly smaller than *G. polyphemus* in either mean CL or upper decile CL (Table 2).

Growth analyses indicate patterns among species similar to those found when CLs of adults are compared. *Gopherus flavomarginatus* maintains a significantly higher rate of growth than other species throughout its first 12 years, which results in the largest CLs among North American tortoises (Fig. 4, Table 3). Individual *G. flavomarginatus* average

TABLE 3. Mean yearly growth rates of North American tortoises, using calculated carapace length (CCL), over 4-year intervals

| | Increase in CCL (mm/year) | | | | | | | | | | | | | | |
| | 0–4 years | | | 4–8 years | | | 8–12 years | | | 12–16 years | | | 16–20 years | | |
	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
G. berlandieri	11.5*ab*	3.27	88	8.8*a*	2.56	83	7.6*a*	2.59	52	6.6*a*	2.28	32	3.5*a*	1.48	12
G. agassizii															
Western Mojave	10.9*ab*	3.21	44	12.3*b*	3.44	50	11.2*bc*	3.58	45	10.0*bc*	3.16	31	7.6*b*	2.42	19
Eastern Mojave	10.5*b*	2.23	101	8.4*a*	2.58	112	9.1*ab*	3.32	105	9.7*b*	2.79	69	7.9*b*	2.77	29
Sonoran	9.9*b*	2.30	35	9.7*ac*	1.93	51	9.2*ab*	2.73	56	9.1*ab*	2.99	53	6.6*ab*	2.70	41
Sinaloan	10.3*b*	1.81	33	11.3*bc*	2.49	38	10.0*ac*	2.32	36	10.4*bc*	4.18	25	6.0*ab*	3.14	12
G. polyphemus	11.5*a*	3.88	74	13.3*b*	3.55	69	12.1*c*	4.32	55	10.5*bc*	3.97	32	5.6*ab*	2.47	14
G. flavomarginatus	15.6*c*	3.05	48	16.0*d*	4.72	56	17.8*d*	5.04	52	13.1*c*	5.25	40	8.0*b*	4.44	14

NOTE: CCL is based on the length of scute rings (see Material and methods). For each age group across species (columns), means followed by different letters are significantly different ($p < 0.05$).

TABLE 4. Mean calculated carapace lengths (CCL, mm) by 4-year intervals for North American tortoises

| | Age | | | | | |
	Hatchlings	4 yr	8 yr	12 yr	16 yr	20 yr
G. berlandieri	31.3*a*	77.6*a*	113.2*a*	143.6*a*	168.8*a*	182.0*a*
	(3.7)	(13.6)	(19.2)	(20.1)	(19.9)	(22.8)
G. agassizii						
Western Mojave	38.2*b*	81.7*a*	131.2*b*	173.4*b*	210.1*bd*	224.0*b*
	(3.5)	(13.7)	(19.7)	(27.8)	(33.1)	(26.8)
Eastern Mojave	38.7*b*	82.3*a*	115.8*ac*	154.4*ac*	186.3*ac*	214.9*b*
	(5.7)	(12.1)	(15.7)	(21.8)	(20.6)	(20.6)
Sonoran	40.2*b*	83.8*ab*	121.5*bc*	160.0*bc*	195.3*bc*	218.1*b*
	(4.9)	(13.1)	(16.4)	(19.5)	(21.8)	(19.5)
Sinaloan	40.6*b*	81.6*a*	126.7*bc*	166.1*bc*	206.0*bc*	239.1*bc*
	(4.6)	(7.9)	(12.7)	(14.3)	(21.4)	(28.8)
G. polyphemus	41.0*b*	92.1*b*	145.0*d*	192.3*d*	231.6*d*	259.2*c*
	(5.1)	(16.1)	(23.1)	(27.5)	(30.2)	(36.0)
G. flavomarginatus	42.6*b*	106.6*c*	170.7*e*	239.2*e*	292.8*e*	318.0*d*
	(4.3)	(13.6)	(25.7)	(33.7)	(32.0)	(37.5)

NOTE: CCL is based on the length of scute rings (see Materials and methods). Values in parentheses show standard deviation. For each age group across species (columns), means followed by different letters are significantly different ($p < 0.05$).

>15.6 mm increases in CL each year for their first 12 years (Table 3). The next fastest growing species is *G. polyphemus*, followed by *G. agassizii* and *G. berlandieri* (Fig. 4, Table 3). During the first 12 years, however, *G. berlandieri* averages the same rate of growth as the eastern Mojave and Sonoran populations of *G. agassizii*, and its growth rate continues to be the same as that of Sonoran tortoises up to 20 years of age (Table 3). Individual *G. agassizii* from the Sonoran Desert eventually attain significantly larger CLs than *G. berlandieri* (Table 2), indicating significantly higher growth rates than *G. berlandieri* past 20 years of age. Individual *G. agassizii* from the western Mojave Desert and Sinaloan habitat grow at a rate similar to that of *G. polyphemus* for the first 20 years (Table 3), and reach approximately the same upper decile CLs (Table 2). All North American tortoises grow at a relatively rapid rate for 18–22 years, after which growth slows (Fig. 4).

CCLs are similar among hatchling tortoises of all species except *G. berlandieri*, which are significantly smaller

(Table 4). By year 4, the mean CCL of *G. flavomarginatus* is significantly larger than that of other species, exceeding 100 mm (Table 4). Also by year 4, the mean CCL of *G. polyphemus* is larger than that of all but Sonoran *G. agassizii* and *G. flavomarginatus*. The mean CCL of *G. flavomarginatus* remains the largest through year 20 (Table 4). The mean CCL of *G. polyphemus* is the second largest from years 8 to 16, but is not significantly larger than the mean CCL of Sinaloan *G. agassizii* at 20 years of age. *Gopherus berlandieri* is significantly smaller than other species by 20 years of age (Table 4).

Summary statistics for growth parameters without the upper decile CLs used in the model gave large confidence intervals for asymptotic size of *Gopherus agassizii* from the eastern Mojave Desert. The calculated asymptotic size is 23% larger than the actual upper decile CL. This indicates that cessation of growth is rapid for eastern Mojave tortoises once adult size is reached, in contrast to *G. agassizii* from the western

TABLE 5. Estimates of growth parameters with 95% confidence intervals (in parentheses) from Richards' growth model of North American tortoises

						Growth parameter			
	n	GC	TRI (years)	SP	AS (CL, mm)	WMGR	%ASI	10–90% AS
G. berlandieri	95	0.104	2.14	0.543	202.9	0.91a (0.131–0.279)	26.3a (18.9–35.0)	25.3a (23.5–27.2)
G. agassizii								
Western Mojave	76	0.112	5.88	0.978	273.4	0.115b (0.098–0.134)	36.4b (30.7–42.4)	27.3ac (25.2–29.6)
Eastern Mojave	151	0.101	5.78	1.004	255.4	0.101bc (0.085–0.119)	36.9b (31.3–42.7)	30.5b (29.0–32.1)
Sonoran	71	0.101	6.07	0.937	270.5	0.107b (0.093–0.124)	35.6b (31.3–40.1)	29.9b (28.4–31.6)
Sinaloan	46	0.118	7.23	1.170	274.0	0.101c (0.091–0.111)	39.7bc (34.9–44.7)	27.8c (25.8–29.8)
G. polyphemus	98	0.130	6.25	1.157	292.1	0.112bc (0.099–0.127)	39.5bc (34.3–44.9)	25.1a (23.3–27.1)
G. flavomarginatus	71	0.147	7.42	1.292	367.6	0.114b (0.105–0.123)	41.6c (38.1–45.1)	23.3d (22.0–24.7)

NOTE: Means in a column followed by different letters are significantly different ($p < 0.05$). GC, growth constant; TRI, time to reach inflection; SP, shape parameter; AS, asymptotic size (upper decile carapace length); WMGR, weighted mean growth rate; %ASI, percent asymptotic size at inflection; 10–90%AS, time to grow from 10 to 90% asymptotic size.

Mojave, in which growth slows over a long time period after initial rapid growth. The calculated asymptotic size of western Mojave G. agassizii is only 10% larger than the actual upper decile CL. The weighted mean growth rate is highest for G. berlandieri and lowest for eastern Mojave and Sinaloan G. agassizii (Table 5); however, when the weighted mean growth rate for G. berlandieri is combined with a significantly lower percent asymptotic size at inflection and the significantly smallest asymptotic size (upper decile CL from Table 2), G. berlandieri has the shallowest growth curve of North American tortoises (Fig. 4). Based on this model, individual G. flavomarginatus have the highest rate of growth, not by having the highest weighted mean growth rate but by maintaining a relatively high rate of growth for the longest period of time, as indicated by the significantly greater percent asymptotic size at inflection and shortest time to grow from 10 to 90% of asymptotic size (Table 5).

The mean CL of males differs significantly from that of females in five of the eight pairwise comparisons and in four of eight pairwise comparisons of upper quartile CLs (Table 2). Males are significantly larger than females in terms of both mean CL and upper quartile CL in G. berlandieri and western and eastern Mojave G. agassizii. The SDI values for G. berlandieri are −0.20 and −0.24 for the mean and upper quartile CL, respectively, but SDI values are less than half these values for western and eastern Mojave G. agassizii (Table 2). Females are significantly larger than males in terms of mean CL in Sinaloan G. agassizii and mean and upper quartile CLs in G. flavomarginatus; the SDI value is 0.10 for both (Table 2). CLs for males and females are not significantly different in Sonoran G. agassizii and G. polyphemus, and therefore by definition the SDI value is zero.

Growth curves show differences between males and females for all groups except Sonoran G. agassizii and G. polyphemus (Fig. 5). Females show distinctly slower growth rates than males in G. berlandieri starting at about 9 years, in western Mojave G. agassizii at about 16 years, and in eastern Mojave G. agassizii starting as early as 3 years,

although differences in growth rates are minimal until about 20 years of age (Fig. 5). Female Sinaloan G. agassizii become larger than males at about 9 years and continue to be larger throughout the model description, but asymptotic sizes are larger in males than in females (Table 6). In G. flavomarginatus, females are smaller than males between about 3 and 12 years but become larger than males beyond 15 years (Fig. 5). In a comparison of growth parameters between the sexes, most or all differ significantly in groups for which sexes differ in size but are nearly identical for the sexes in both Sonoran G. agassizii and G. polyphemus, for which the sexes do not differ in size (Table 6).

Climate

The amounts and patterns of precipitation differ significantly among the ranges of North American tortoises and among regions within the range of G. agassizii (Fig. 6). Annual precipitation levels are highest for G. polyphemus (1162–1593 mm) and G. berlandieri (472–982 mm), with lesser amounts within the range of Sinaloan G. agassizii (278–664 mm) and G. flavomarginatus (310–376 mm) and lowest amounts for Sonoran (140–324 mm), eastern Mojave (101–223 mm), and western Mojave (102–169 mm) G. agassizii. Areas with G. polyphemus receive most precipitation in summer, although the northern part of the range receives relatively even amounts of precipitation throughout the year (Fig. 6). Precipitation patterns within the ranges of G. flavomarginatus and Sonoran and Sinaloan G. agassizii are similar, with the highest amounts falling from July to September (Fig. 6). Precipitation levels within the range of G. berlandieri are highest from May to October, with a noticeable decrease in July (Fig. 6). The lowest amount of precipitation within any region is for G. agassizii from the western Mojave and is limited to November through March. Within the range of G. agassizii, summer precipitation increases towards the south, with little decrease in winter precipitation (Fig. 6).

Average monthly temperatures are similar among the ranges of these species (Fig. 6). Highest summer temperatures
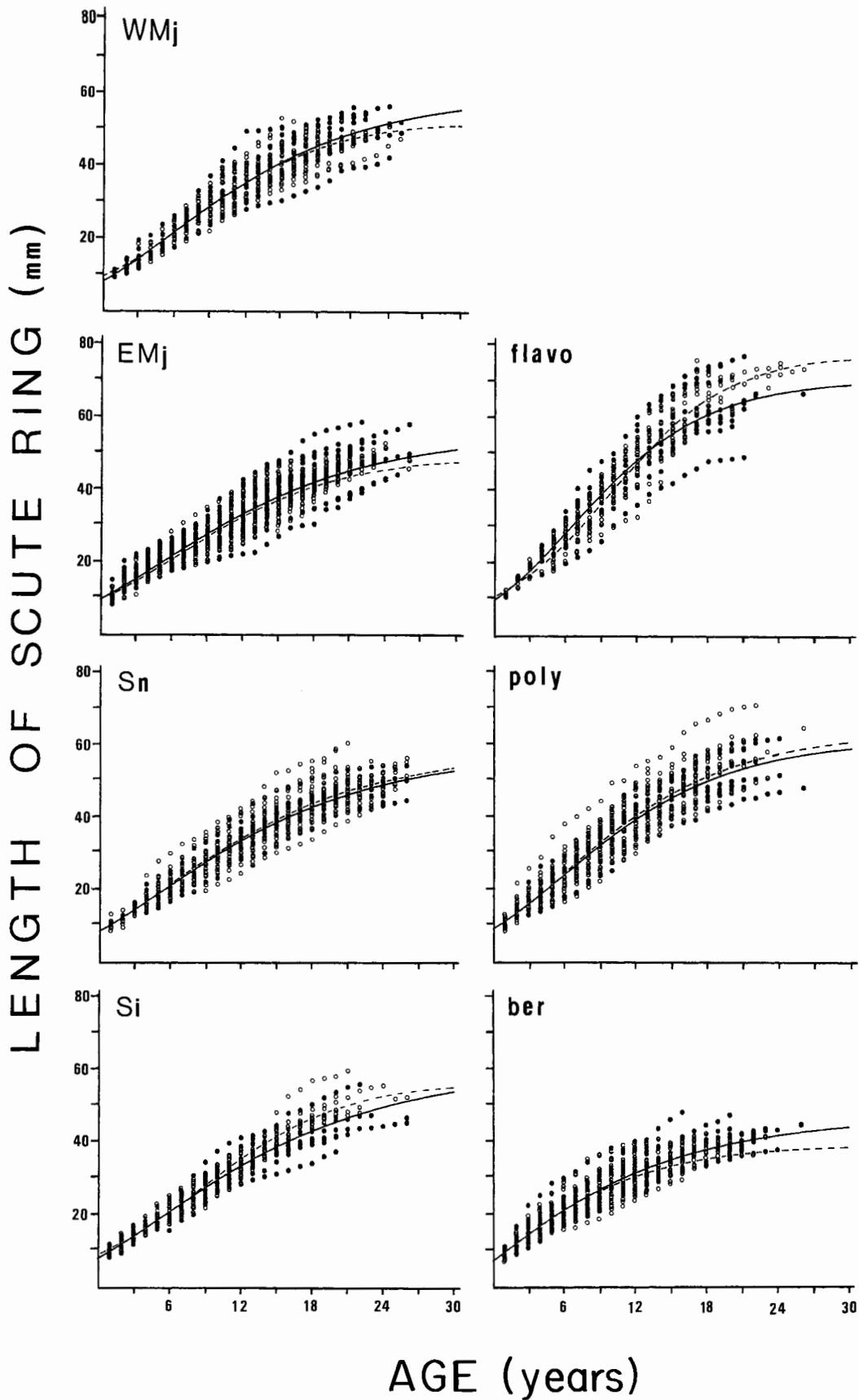
FIG. 5. Growth curves of males (——●——) and females (- -○- -) of each species of North American tortoise and of populations of *G. agassizii*. For explanation of species abbreviations see Fig. 4.

TABLE 6. Estimates of growth parameters with 95% confidence intervals (in parentheses) from Richards' growth model of male and female North American tortoises

	n	GC	TRI (years)	SP	AS (CL, mm)	WMGR	%ASI	10–90% AS
G. berlandieri								
Males	40	0.093	0.96	0.352	207.3	0.263 (0.136–0.509)	20.0* (11.4–31.9)	26.6* (24.6–28.7)
Females	30	0.147	2.01	0.727	167.7	0.202 (0.118–0.347)	31.1* (19.5–45.1)	19.1* (17.0–21.3)
G. agassizii								
Western Mojave								
Males	24	0.104	5.66	0.876	283.0	0.188 (0.094–0.149)	34.4* (26.8–42.7)	28.5* (25.4–31.9)
Females	15	0.173	7.75	1.805	245.7	0.096 (0.079–0.116)	48.0* (36.3–59.7)	23.7* (21.2–26.7)
Eastern Mojave								
Males	54	0.099	5.24	0.942	260.0	0.105 (0.082–0.136)	35.7 (27.8–44.3)	30.4* (28.0–33.0)
Females	34	0.128	5.98	1.297	233.1	0.099 (0.082–0.118)	41.7 (35.8–47.7)	26.8* (25.0–28.7)
Sonoran								
Males	23	0.096	5.36	0.842	270.8	0.114 (0.084–0.154)	33.7 (25.7–42.5)	30.4 (28.0–33.0)
Females	25	0.102	5.64	0.911	269.8	0.112 (0.076–0.165)	35.1 (25.1–46.3)	29.3 (26.8–32.1)
Sinaloan								
Males	22	0.086	5.07	0.706	281.5	0.122* (0.089–0.167)	30.6* (22.1–40.4)	32.4* (28.8–36.5)
Females	10	0.162	8.57	1.745	265.0	0.093* (0.083–0.104)	47.4* (40.2–54.6)	24.8* (22.8–26.9)
G. polyphemus								
Males	25	0.127	5.97	1.100	286.3	0.116 (0.090–0.150)	38.5 (29.7–48.0)	25.1 (22.7–27.8)
Females	32	0.126	5.88	1.066	294.3	0.118 (0.091–0.154)	38.0 (28.1–48.7)	25.1 (21.8–28.7)
G. flavomarginatus								
Males	19	0.164	6.61	1.365	345.0	0.120* (0.101–0.144)	42.6* (34.5–51.1)	21.4 (18.9–24.2)
Females	13	0.207	9.84	2.092	376.5	0.099* (0.086–0.114)	50.9* (44.1–57.5)	21.9 (20.1–23.9)

NOTE: For explanation of abbreviations see Table 5. An asterisk indicates that pairwise means are significantly different ($p < 0.05$).

occur within the Sonoran and eastern Mojave portion of *G. agassizii*'s range and average 6–7°C higher than temperatures within the ranges of *G. polyphemus* and *G. flavomarginatus*. Winter temperatures below freezing are common in all ranges except the southern range of *G. polyphemus*, the coastal range of *G. berlandieri*, and the Sinaloan range of *G. agassizii*.

The most variable environment in terms of precipitation is that of *G. berlandieri* and the least variable environment that of the Sinaloan range of *G. agassizii* (Fig. 6). *Gopherus polyphemus* habitat also has relatively constant precipitation. Within the range of *G. agassizii*, the eastern Mojave is most variable and the western Mojave has the second highest predictability (P) value of all ranges of North American tortoises (Fig. 6). This high P value is due to the predictable lack of rain in the western Mojave from May through September.

Age at maturity

The overall comparison of mean AAM based on attainment of sexual maturity by females gave significant differences among groups (Kruskal–Wallis statistic = 15.51, $p = 0.017$); however, no pairwise comparisons were significantly different. AAM varied from 13.3 years for *G. berlandieri* to 15.7 years for Sonoran *G. agassizii* (Fig. 7). For *G. agassizii*, females from the Sinaloan habitats reproduce earliest, on average (13.8 years), and females from the Sonoran Desert reproduce latest, on average (15.7 years; Fig. 7). Within the range of western Mojave *G. agassizii* are females from the Nevada Test Site, an area of the northern Mojave Desert. Without these six females, which include the three oldest maturing individuals, the mean age for this region decreases from 14.4 to 12.8 years, making it the youngest age group. Similarly, within the range of *G. polyphemus* the oldest maturing females are found in the northern portion of the range, and without them the mean AAM decreases from 14.4 to 13.6 years (Fig. 6) Estimates of AAM based on growth models (Fig. 5) are older than the means determined from individual females. AAMs from growth models are about 15 years for western Mojave and Sinaloan *G. agassizii* and for *G. flavomarginatus*, about 16 years for Sonoran *G. agassizii*,
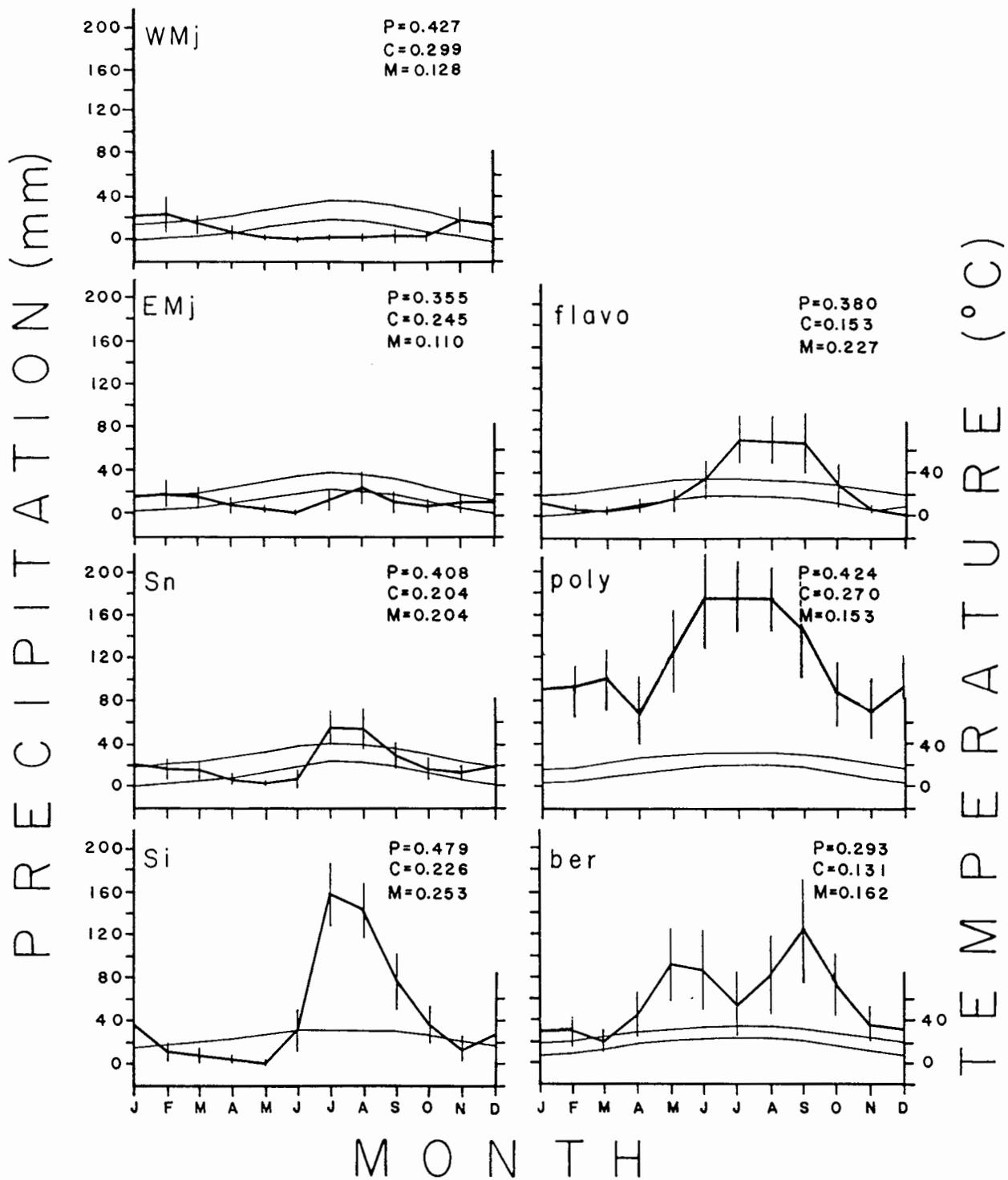
FIG. 6. Patterns of precipitation and temperature in ranges of North American tortoises. Heavy lines with vertical bars (±1 SD) denote precipitation. Thin lines show monthly temperatures; the upper lines show average high temperatures and the lower lines average low temperatures. Only average daily temperatures were available for the range of desert tortoises in Sinaloan habitats. Values are also given for variability of precipitation: P is predictability, C is constancy, and M is contingency (see Materials and methods). For explanation of species abbreviations see Fig. 4.

17.5 years for southern *G. polyphemus*, 18 years for *G. berlandieri*, 18.5 years for eastern Mojave *G. agassizii*, and about 20.5 years for northern *G. polyphemus*.

Growth and climate comparisons

Neither upper decile CL nor mean AW was significantly correlated with mean annual precipitation (CL: $r_s = 0.214$,
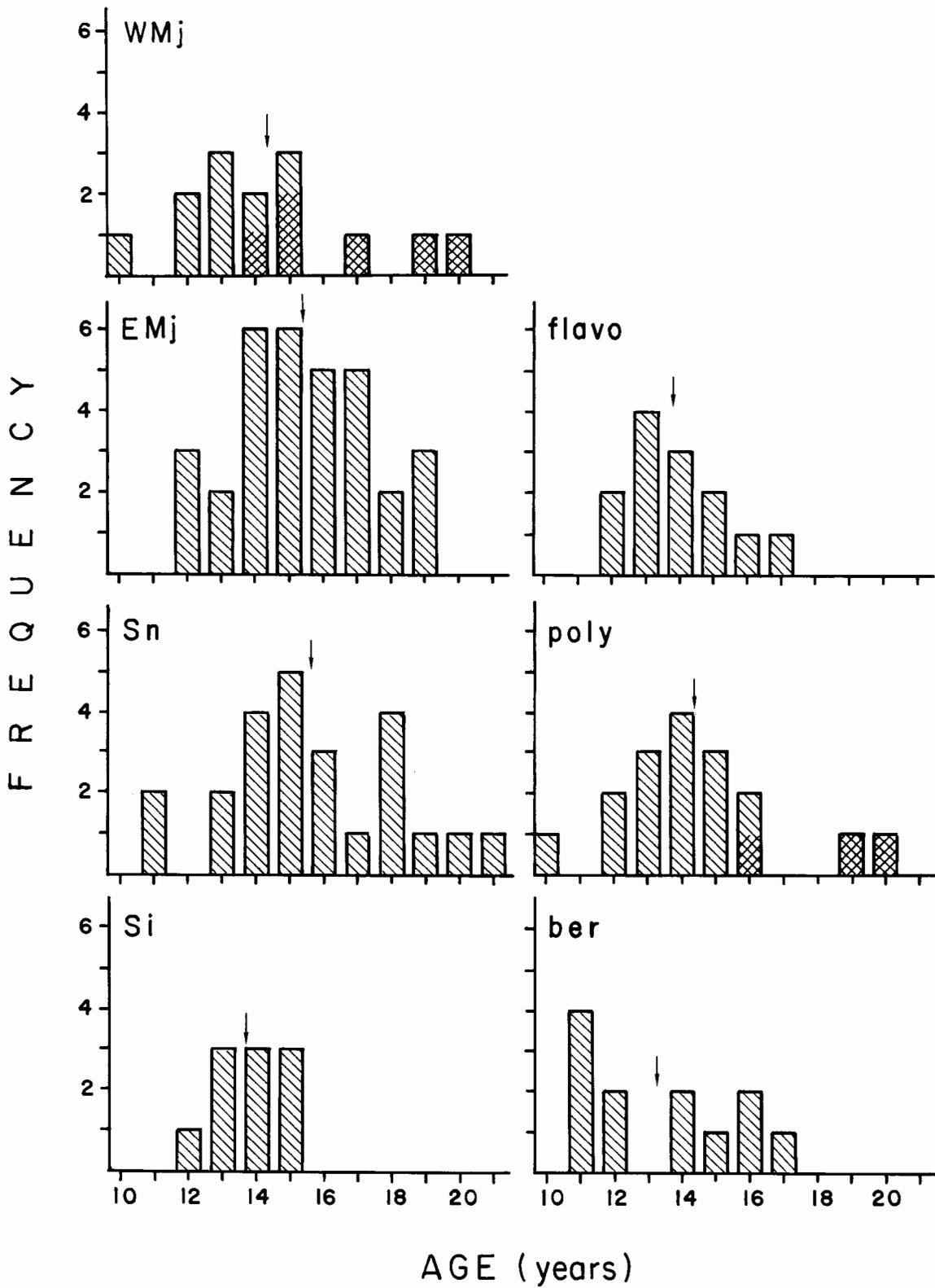
FIG. 7. Histograms of estimated age at maturity of female North American tortoises as determined from the ages at which females equaled or exceeded the minimum CL for tortoises with eggs based on calculated carapace lengths (see Materials and methods). Values above the arrows denote mean age. For "WMj," cross-hatching indicates females from the Nevada Test Site. For "poly," cross-hatching indicates females from the northern portion of the range. For explanation of abbreviations see Fig. 4.

Germano 1992), although, based on minimum ages, most adult *G. agassizii* live only 25–35 years (Germano 1992). Longevities of *G. flavomarginatus* and *G. berlandieri* are not known. Based on this study, ages at reproductive maturity are similar among species, and intraspecific variation is as great as interspecific variation. Fecundity data vary among wild populations. More data are needed on basic life-history traits of these species, particularly in other regions of the range of *G. agassizii* and for *G. berlandieri* and *G. flavomarginatus*, before we fully understand how these species are responding to climatic variability.

The factors controlling growth of North American tortoises are not known. The measures of growth that I have taken are not significantly correlated with either phylogeny or the measures of climate that I have used. Phylogeny does constrain how tortoises grow, but the environmental factors to which North American tortoises respond, through either genetic adaptation or direct physiological response, have not been determined. Precipitation and temperature do not seem to affect growth directly, but more work is needed on other environmental correlates that potentially have an influence.

Acknowledgments

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