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Using Growth Ring Counts to Age Juvenile Desert Tortoises (*Gopherus agassizii*) in the Wild

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ABSTRACT. – Growth rings of costal scutes were counted using 35 mm photographic slides of 192 desert tortoises (*Gopherus agassizii*) from 11 study sites in the Mojave and Colorado deserts of California. From 0 to ≥ 3 rings were formed yearly, but subannular rings could not be distinguished visually from annular rings. Growth ring counts from photographic records of scutes are not a reliable means of determining absolute age in juvenile and immature desert tortoises ≤ 180 mm in carapace length. Ring count data varied by desert region; mean number of rings produced yearly varied from 0.86 in the western Mojave to 1.17 in the northeastern Mojave. Mean numbers of rings formed yearly were significantly different between the western and northeastern Mojave regions and western and eastern Mojave regions, but not between the western Mojave region and Colorado Desert. Grouping data from several study sites and years obscured annual variations, however. At Goffs in the eastern Mojave Desert, numbers of rings formed annually differed significantly between 1983, 1984, and 1985. Numbers of tortoises producing 2 rings per year declined between 1983 and 1985, whereas numbers of tortoises with 0 rings per year increased in the same interval. At Goffs, ring formation was positively correlated with annual precipitation, as well as summer and winter rainfall. Correlations between ring counts and biomass of annual plants used for forage were weaker.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; growth; scute; annuli; age estimation; juvenile; California; USA

Acquisition and analysis of demographic data bases on chelonians, especially species with small or declining populations, are challenges under the best of circumstances. As a group, chelonians exhibit great longevity, and few long-term studies have encompassed even one generation (Graham, 1979; Auffenberg and Iverson, 1979; Swingland and Klemens, 1989). Some additional problems are presented by neonates and juveniles, which are cryptic, inconspicuous, and generally difficult to sample, often for the first several years of life (Berry and Turner, 1986; Morafka, 1994); by the inability to assign absolute age to most individuals; and by the problem of acquiring age-related survivorship statistics. Thus indirect methods, e.g., estimating age from size and counting growth rings on scutes have been utilized (Zug, 1991).

For rare, threatened, and endangered chelonians, comprehensive demographic data bases are a requisite for developing the life tables and population viability analyses that are increasingly part of recovery programs. Accurate assignment of age to individuals is important for determining age at first reproduction, age-specific survivorship and fecundity, generation time, and other life history attributes essential to understanding the potential for a population to respond when its numbers are low. Also critical is an understanding of factors that affect variation in life history attributes, such as local or regional differences in climate, habitat type, and conditions. Inaccurate estimates of ages of individuals, cohorts, and life spans are likely to lead to inappropriate management expectations and responses (e.g., see Tracy and Tracy, 1995; Wilson et al., in press).

The subject of the reliability of aging juvenile and young adult turtles and tortoises by using ring counts or scute annuli is occasionally debated in the literature (Graham, 1979; Zug, 1991; Germano and Bury, 1998; Wilson et al., in press). The basic assumption has been that only one ring or annulus is formed yearly in most species (Germano and Bury, 1998), but this assumption has been challenged in a recent review of the literature (Wilson et al., in press). Accurate counts may be impossible if rings have faded or scutes have shed, or if the turtle produced "pseudo annual growth zones" (Ewing, 1939), "accessory" rings (Sexton, 1959), "minor" rings (Legler, 1960), "subannual" rings (Bourn and Coe, 1978), or "false" rings (Germano, 1988). However, when patterns of growth ring deposition are documented and correlated with age for a population or species, the technique can be a valuable tool for assessing age, especially in young individuals (Bourn and Coe, 1978; Castanet and Cheylan, 1979; Stubbs et al., 1985; Mushinsky et al., 1994; Aresco and Guyer, 1998; see also Wilson et al., in press).

Prior to 1988, ring counts of scutes were not considered a reliable method for aging desert tortoises, *Gopherus agassizii* (Woodbury and Hardy, 1948; Miller 1932, 1955; Patterson, 1972; Jackson et al., 1976, 1978). However, Woodbury and Hardy (1948) primarily used a sample of wild adult tortoises, and the others presented data on captive tortoises. Captive juvenile *G. agassizii* can produce numerous growth rings per year when presented with high quality food and water (Jackson et al., 1976, 1978; Tracy and Tracy, 1995). The use of adults and captives for ring counts have

Table 1. Desert tortoise data used in the analysis of ring counts. *n* = no. tortoises, n_1 = no. tortoises used for ring counts, Years = years with data, CL = range of CL (mm) at initial ring count.

Region and Site	*n*	n_1	Years	CL
Western Mojave Desert				
Fremont Valley	19	17	1978-9, 81	80-140
Desert Tortoise Natural Area	6	5	1978-9, 82	104-117
Desert Tortoise Natural Area Interpretive Center	10	7	1978-9, 85	62-135
Fremont Peak	2	1	1978, 80	96
Kramer	16	14	1980, 82	54-140
Stoddard Valley	1	1	1979, 81	108
Lucerne Valley	8	8	1980, 86	68-139
Northeastern Mojave Desert				
Ivanpah Valley	13	10	1977, 79, 86	50-114
Eastern Mojave Desert				
Goffs	125	107	1977-80, 83-6	48-129
Colorado Desert				
Chemehuevi Valley	18	17	1977, 79, 82	53-128
Chuckwalla Bench	13	5	1978-80	87-131
Totals	231	192		

limitations (Zug, 1991; Germano, 1998; Germano and Bury, 1998). Two additional studies with contrasting results exist; both involve research on wild juveniles that were confined to enclosures (Germano, 1988, 1998; Wilson et al., in press). Germano (1988, 1998) reported that scute annuli produced during the first 20–25 years of life could be used to age young desert tortoises because they generally produced one ring each year. Wilson et al. (in press) found that juveniles produced variable numbers of rings annually and no rings in drought years. Subsequently, Germano (1994) and Germano et al. (2002) have used ring counts to assign age to desert tortoises at many sites.

I tested three hypotheses about growth rings on scutes for wild, free-ranging juvenile desert tortoises using data from 11 study sites in the Mojave and Colorado deserts of California: (1) juvenile tortoises produce one ring per year on their scutes, (2) counts of rings accurately reflect age, and (3) production of rings on scutes is unrelated to environmental factors. This study was part of a research project to estimate ages of *G. agassizii* for a life table and to understand how life table parameters are influenced by environmental

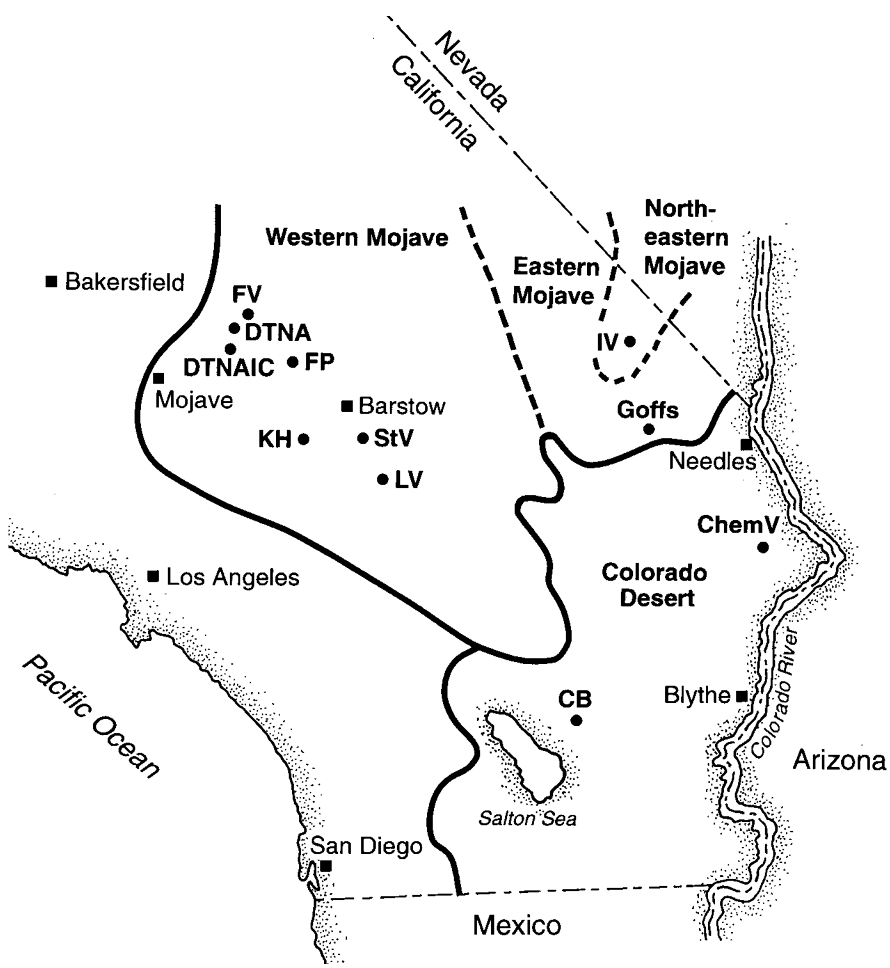

Figure 1. The locations of 11 study sites used in an analysis of growth ring counts for desert tortoises in the Mojave and Colorado deserts of California. The seven sites in the western Mojave Desert are: FV = Fremont Valley; DTNA = Desert Tortoise Research Natural Area interior; DTNAIC = Desert Tortoise Research Natural Area Interpretive Center; FP = Fremont Peak; KH = Kramer Hills; StV = Stoddard Valley; and LV = Lucerne Valley. One site is in the northeastern Mojave, IV = Ivanpah Valley; and one site, Goffs, is in the eastern Mojave Desert. The two sites in the Colorado Desert are ChemV= Chemehuevi Valley and CB = Chuckwalla Bench.

variables (Turner et al., 1986, 1987a). Populations of *G. agassizii* in California, Nevada, Utah, and northwestern Arizona were Federally listed as threatened in 1990 (U.S. Fish and Wildlife Service [USFWS], 1990), and acquisition of more information on demographic attributes is an essential part of the long-term recovery plan for listed populations (USFWS, 1994).

METHODS

Study Sites and Available Data. — Using 35 mm photographic slides, I counted rings on scutes of marked juvenile desert tortoises which were recaptured one or more times. The slides are part of U.S. Bureau of Land Management (BLM) and U.S. Geological Survey data bases for 11 desert tortoise study sites (Table 1) in the Mojave and Colorado deserts of California (Berry, 1984; Turner and Berry, 1984a, 1985, 1986; Berry and Medica, 1995). Tortoise study sites were assigned to four geographic regions according to location (Table 1, Fig. 1): western Mojave Desert; northeastern Mojave Desert; eastern Mojave Desert; and the Colorado Desert (Turner and Berry, 1984b; USFWS, 1994). The Mojave Desert study sites are in regions identical to those described as recovery units for the desert tortoise (USFWS, 1994), whereas the Colorado Desert study sites are grouped as a single sample and not sorted by Colorado Desert recovery units because of small sample sizes.

When tortoises were captured the first time in a sample year, field workers generally took three 35 mm slides: entire carapace, plastron, and a close-up of the posterior costal scutes, focusing on the fourth left costal and including parts or all of the adjacent scutes. For most tortoises, the complete carapace, plastron, or fourth left costal scute filled the frame of the slide. Slides of hatchlings were limited to the carapace and plastron, because of their small size. For most study sites, one set of slides was available for each sample year for each tortoise (Table 1). The exception was the Goffs site, which was sampled in spring, summer, and fall on a yearly basis between 1983 and 1986 (Turner and Berry, 1984a, 1985, 1986). Slides were taken of juveniles and immature tortoises ≤ 140 mm carapace length at the midline (CL) at first capture in spring and at subsequent summer and fall captures. Slides were viewed with a caramate projector or on a large screen.

Analysis of Growth Ring Counts. — For other species of turtles and tortoises, growth ring counts have been made using scutes on the plastron or carapace (Zug, 1991). I made a two-part preliminary evaluation prior to initiating the analysis. For the first part, a sample of 109 tortoises ≤ 180 mm CL, the size at which tortoises are considered to be sexually immature (Turner et al., 1986), was used to determine whether to count rings on scutes of the carapace, plastron, or both. Based on the findings, I limited the sample to tortoises ≤ 140 mm CL when first captured, because rings became increasingly difficult to count on larger tortoises. I also selected the costal and vertebral scutes on the carapace because (1) these rings were easier to observe and count, (2) ring counts from the carapace appeared to vary less than those from the plastron, and (3) rings on the plastron were frequently worn and faded. Counts were most easily made on the third and fourth costal scutes, starting at the ventral edge of the areola and ending at the ventral seam. Rings were considerably wider here than on the dorsal edges of the scutes and the fine rings were more obvious. In some cases, fine rings could only be distinguished along the ventral edges of scute laminae.

Next I examined slides of 231 tortoises (Table 1) to determine when growth rings formed, under what conditions rings could be counted, and whether rings were similar to those described by others for *G. agassizii* (Germano, 1988; Tracy and Tracy, 1995). For each tortoise, data were recorded by study site, tortoise identification number, date of capture, carapace length, number of rings, presence of new growth for the season, and number of rings formed per unit of time (if rings could be counted).

Slides of first captures of each tortoise were compared with slides from subsequent recaptures to determine the presence of new rings and new growth. If rings were numerous and counts particularly difficult, or if the areola and laminae were worn or had sloughed, numbers of rings added between captures sometimes could be determined by using "markers" or landmarks (Legler, 1960; Galbraith and Brooks, 1987a). Landmarks consisted of an unusual ring or rings, such as a series of four very narrow rings or a very wide ring followed by a very narrow ring. For example, a tortoise captured in 1979 had an areola and eight rings. When recaptured in 1985, it had lost the areola, and rings adjacent to the areola were worn away. However, the 1979 slide showed two very fine and one wide ring (rings 6–8) adjacent to the seam. This cluster of rings was located on the 1985 slide, and the number of new rings counted. I discarded 39 of the 231 tortoises from the analysis, because rings could not be counted for one or more of the sample years.

Comparisons of Ring Counts. — Estimates of ring counts produced annually were made for 192 tortoises captured at intervals ranging from 3 months to 9 years. The data were grouped by region, and measures of central tendency and dispersion were calculated for the number of rings produced per year.

Year-by-Year Production of Rings. — Data were available on number of rings produced in a particular year for 113 of the 192 tortoises: 25 such records existed for western Mojave Desert study sites, 83 for the eastern Mojave (Goffs), and 5 for Colorado Desert study sites. Measures of central tendency and dispersion were calculated for the number of rings produced in a specific year. The t-test (sample difference in means) was used to compare ring counts from different desert regions. For the Goffs data sets, an ANOVA (fixed effects model) was used to determine if rings counts differed significantly between years.

Correlations Between Ring Counts. — Ring count data for the 1983–86 Goffs study site were compared with two environmental variables, precipitation and annual plant pro-

Table 2. Measures of central tendency and dispersion for grouped growth ring data for juvenile and immature desert tortoises from four regions of the California deserts. Tortoises were ≤ 140 mm CL when ring counts were initiated.

Desert region	*n*	Number of growth rings per year: Mean	Mode	Median	SD	Range	s^2	% tortoises with < 1 or > 1 ring/year
Western Mojave	53	0.86	1.0	1.0	0.29	0-1.5	0.08	43.4
Northeastern Mojave	10	1.17	*	1.0	0.43	0-2	0.19	70.0
Eastern Mojave	107	1.11	1.0	1.0	0.56	0-2.5	0.31	72.9
Colorado Desert	22	0.95	1.0	1.0	0.36	0-2	0.13	59.1

*Four modes were present.

duction (biomass) using Pearson correlation coefficients. Biomass data on annual plants (forage used by tortoises) were taken from Turner and Berry (1984a, 1984b, 1985, 1986) and Turner et al. (1987a). Precipitation data were grouped by hydrologic year and season. The hydrologic or water year extends from 1 October to 30 September (Manning, 1992). Winter precipitation was defined as rainfall occurring from October through March, and summer rainfall was defined as occurring from July through September. Results of all statistical tests were considered significant when $p \leq 0.05$.

RESULTS

Formation and Definitions of Rings. — New growth first appears as a faint white or light gray line between scute seams. As growth continues, the newly-formed epidermis widens and is paler and softer than the older parts of the scutes (Legler, 1960). The first ring may form after hatching in late summer or fall. Such fall rings can consist of a single fine, barely visible ring or a substantial ring. Fine rings can fade or wear away in a few years. Subsequent rings vary considerably in width and definition also.

Rings can be formed in spring, late summer, and fall. No rings developed between mid-October and late March. Termination of growth and completion of rings formed in spring appeared to coincide with the onset of summer estivation in late June or early July. Growth and development of late summer and/or fall rings ceased with onset of winter inactivity.

I classified rings into two types: subannular (rings formed within a single year); and annular (a single ring formed in a given year). The type of ring could be determined only by observing the sequence of ring formation

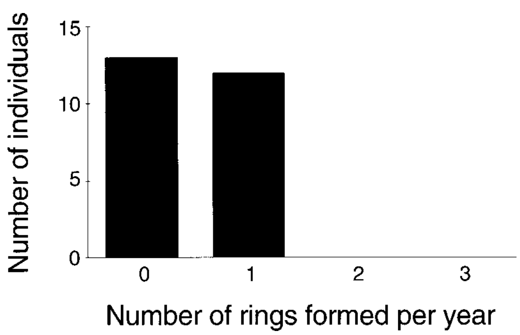

Figure 2. Numbers of growth rings formed by juvenile tortoises each year in the western Mojave Desert (includes Fremont Valley, Desert Tortoise Natural Area, and Kramer Hills sites).

over time with the 35 mm slides, but not by the appearance of the ring. Subannular and annular rings were distinguished by using two or more slide sets per year, preferably one for late winter or early spring, a second for summer (late June through August), and a third for fall (October).

Subannular rings were frequently more obvious and well-defined than annular rings. Annular rings were often fine rings with shallow demarcations, and I treated these as true rings. Some fine rings were not distinguishable two to three years later. In some cases, an annular ring was manifested by a barely distinguishable increase in size or by an increase in height of the previous year's ring. Changes in a previous year's ring was not counted as a new ring.

Counting Growth Rings. — During the initial examination of slides for 109 tortoises, I obtained different ring counts for the same tortoise. Once the pattern of ring formation became apparent and the method of defining annular and subannular rings was developed, counting became more consistent. To reduce inconsistencies, I counted only the new rings formed between initial and subsequent captures of each tortoise, noting whether the ring was wide, narrow, or fine.

Ring counts depend on the definitions of rings, as well as what the observer may expect to observe. Data from Chemehuevi Valley offer a clear example. I evaluated slides for 15 tortoises captured both in spring of 1979 and 1982. If 1 ring was produced annually, 3 new rings representing 1979, 1980, and 1981 should be present on the 1982 slides, as well as potential traces of new growth generated in 1982. Seven tortoises showed 2 clearly defined rings only. However, when the ventral edges of costal scutes were examined carefully, a very fine ring was visible on the ventral portion of some (but not all) costal scutes of 6 of the7 tortoises. In all cases, the fine ring, probably generated in 1981, was between the 2 wider rings. The fine line was probably generated in 1981, a year of low rainfall throughout much of the Mojave and Colorado deserts (NOAA, 1980–81). The remaining 8 of the 15 tortoises produced a variety of ring counts, ranging from < 1 or > 1 ring per year and different combinations of wide, thin, very fine, or partial rings. If an annular ring was defined as a ring having a deep demarcation or indentation in the scute produced by a break in the growth period, such as from hibernation, and a subannular ring as a narrow or fine ring with a shallow indentation (e.g., Legler, 1960; Germano and Bury, 1998), then the observer would record different counts. For 6 of the 7 tortoises, 2 annular rings and possibly 1 subannular ring would be reported.

Table 3. Measures of central tendency and dispersion for numbers of growth rings produced annually by juvenile desert tortoises in two regions of the California deserts. Tortoises were ≤ 140 mm CL for initial ring counts.

Desert region and year	*n*	Mean	Mode	Median	SD	Range	s^2	% tortoises with < 1 or > 1 ring/year
		Number of growth rings per year						
Eastern Mojave Desert								
Goffs: 1981-1986	83	0.94	1.0	1.0	0.78	0-3	0.61	54.2
1983	20	1.55	2.0	1.0	0.59	0-2	0.35	65.0
1984	29	1.31	1.0	1.0	0.72	0-3	0.52	34.5
1985	26	0.46	0.0	0.0	0.50	0-1	0.25	53.9
1986	7	0.00	0.0	0.0	0.00	0	0.00	100.0
Western Mojave Desert								
1978-1981	25	0.48	0.0	0.0	0.50	0-1	0.25	48.0

Counting rings became progressively more difficult as tortoises increased in size, because the areola and early rings wore away. Often the areola and first few rings were partially worn by the time the tortoise reached 100 mm CL. Rings were more difficult to count from some sites than others, e.g., Chuckwalla Bench. At the Chuckwalla Bench, rings could not be counted on five of the 13 tortoises in the sample because they were too numerous, narrow, and poorly defined.

Ring Count Data from Eleven Study Sites

Estimates of Ring Counts Produced Annually by Region. — For 192 tortoises, the mean numbers of rings produced per year covered intervals ranging from 1 to 9 years (Table 2). The actual number of rings produced per year by individuals is masked by the lack of yearly data points. Depending on the region, at least 43.4 to 72.9% of the tortoises produced < 1 or > 1 ring/year. The percentages were probably higher. If, for example, a tortoise produced 6 rings in 6 years, there is no way to determine if the tortoise did not produce rings in 1 year, followed by 2 rings in a subsequent year.

Mean numbers of rings produced per year differed significantly for the western Mojave and northeastern Mojave Desert regions (t = 2.8985, df = 61), and for the western Mojave region and eastern Mojave (t = 6.3525, df = 158). There were no significant differences between the western Mojave and Colorado Desert data (t = 1.15, df = 73). Means were lower in the western Mojave and Colorado desert regions than in the eastern and northeastern Mojave desert regions.

Year-by-Year Production of Rings in the Western Mojave and Colorado Deserts. — Twenty-one of the 25 western Mojave records were for 2 years, 1980 and 1981, a limited sample (Fig. 2). Precipitation during those hydrologic years varied slightly by NOAA rainfall station in the western Mojave. For 1978–79 and 1979–80, rainfall was above the long-term mean for both annual and winter precipitation; for 1980–81, the rainfall figures were slightly below the long-term mean for annual precipitation and slightly above or below (depending on the rainfall station) for winter precipitation. The number of rings produced per year in the western Mojave differed significantly from the ring counts produced annually at Goffs (t = 2.7735, df = 106).

Year-by-Year Production of Rings at Goffs. — The numbers of individuals producing 0, 1, 2, or 3 rings/year varied between 1983 to 1986 (Table 3, Fig. 3). The proportion of tortoises producing 0 rings per year increased between 1983 and 1986 while the proportion of tortoises producing 2 rings annually decreased. Differences in ring counts between 1983, 1984, and 1985 (the years with larger

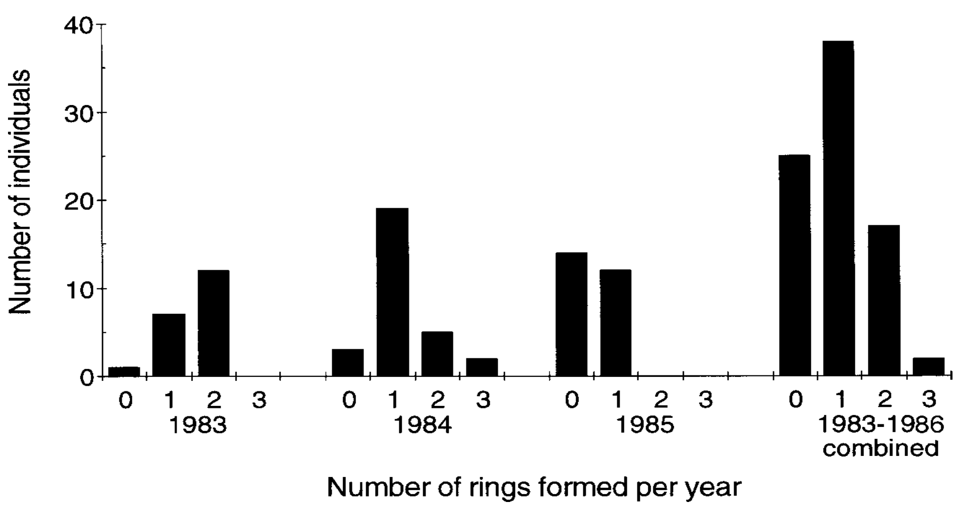

Figure 3. Numbers of growth rings formed by juvenile tortoises each year between 1983 and 1986 at the Goffs study plot in the eastern Mojave Desert, California. None of the seven juveniles recaptured in 1986 produced growth rings for that year and these figures are incorporated in the summary histogram of 1983–86.

Table 4. Summary of precipitation records and annual plant production at the Goffs site, eastern California, 1983–86[1].

Hydrologic year (Oct–Sept)	Annual precipitation (mm)	Winter rain (Oct–March) (mm)	Summer rain (July–Sept) (mm)	Mean dry matter net production (g/m^2) in spring[2]	
				Annual herbs and *Schismus*	Annual herbs only
1982-3	298.0[3]	118.0[3]	161.9	42.0	14.0
1983-4	238.5	135.1	72.7	4.3	0.3
1984-5	110.0	91.0	15.2	3.8	2.6
1985-6	58.3	37.0	21.3	11.1	0.6

[1]From Turner and Berry (1984a, 1985, 1986) and Turner et al. (1987a).
[2]In August 1984, 20.4 g/m^2 of dry matter net production was measured on the plot; *Schismus* was not present on transects. Mean dry matter net production was not measured in August of 1983 or 1985.
[3]Needles Airport, from NOAA 1982–83; no available data for Goffs.

sample sizes) were significant (ANOVA [fixed effects model]; $F_o = 19.31$, df = 74). There was more variation between years than within years. When the data were grouped for 1981–86, yearly differences were obscured.

Individual tortoises responded differently during the four-year period by producing different numbers of rings in different years. For example, one tortoise produced 2 rings in 1983 and 1 each in 1984 and 1985, whereas another did not produce rings in either 1983 or 1984. In contrast, another tortoise produced 2 rings in 1983 and 3 in 1984.

Correlations Between Ring Counts at Goffs and Environmental Variables. — Patterns of ring production between 1983 and 1986 were related to rainfall and food production (Table 4). As precipitation and production of spring forage declined between 1983 and 1986, the mean number of rings produced per year also dropped. Ring counts and rainfall were positively correlated: $r = 0.664$ for total annual precipitation, $r = 0.596$ for summer precipitation only, and $r = 0.567$ for winter precipitation only. Correlation coefficients between ring counts and annual forbs and grasses produced by winter precipitation only were weaker: $r = 0.461$ for annual herbs and the alien annual grass (*Schismus* sp.), and $r = 0.449$ for annual herbs only.

DISCUSSION

For juvenile or immature desert tortoises ≤ 140 mm CL, absolute age cannot be determined solely by counting rings in the field or with a single set of 35 mm slides, because annular and subannular rings are difficult to distinguish in this desert species. Young tortoises frequently produce > 1 or < 1 ring per year, and the number of rings produced at a single site in a given year can vary from 0 to at least 3.

Two underlying causes of regional, site, and within-year variation in ring production for *G. agassizii* are precipitation and the resulting forage resources. In the Mojave and Colorado deserts, annual precipitation is generally low (90–210 mm) and unpredictable in occurrence in desert tortoise habitats (USFWS, 1994; Rowlands, 1995). Winter rains are usually regional in scope, and if sufficient and appropriately timed, produce succulent green growth of winter annual forbs and grasses, herbaceous perennial plants, and cacti between late January and late May (Went, 1948, 1949; Went and Westergaard, 1949; Beatley, 1974; Rowlands, 1995). Summer rainfall, which is more sporadic and variable, tends to be more localized (Rowlands, 1995). The resulting flora and forage base are more limited (Mulroy and Rundel, 1977). The tortoises selectively use the plants produced by the rains for forage (Woodbury and Hardy, 1948; Turner et al., 1984; Jennings, 1993). Rains occurring at temperatures when tortoises can be active and above ground are important for more than forage production, because tortoises drink the water, rehydrate, replenish the supply of bladder water, and then can consume dried plants (Nagy and Medica, 1986; Peterson 1996a, 1996b; Henen et al., 1998).

Growth of juvenile desert tortoises, as measured by changes in body length, is closely correlated with rainfall and annual plant production (Medica et al., 1975). In this study, formation of growth rings was also positively correlated with rainfall and, to a lesser extent, food production. Major regional differences exist in seasonal distribution of rainfall in the Mojave and Colorado deserts, such that patterns of growth and the resulting rings on scutes are likely to be different. For example, in the western Mojave Desert, most precipitation occurs in winter and is responsible for production of winter annuals and herbaceous perennial plants (Rowlands et al., 1982), the principal forage of tortoises (Jennings, 1993). Summer rainfall is only 3–10% of the total annual precipitation at most study sites (Fig. 1: DTNA, DTNAIC, FV, FP, KH). Summer precipitation rarely results in production of a second flush of edible annual growth for tortoises, in part because the summer annual flora is limited. Thus, tortoises living in the western Mojave Desert generally forage from March through mid-June. Although they may eat dried annuals after a summer rain, they probably produce one ring annually, except in drought years. The mean number of rings produced per year is likely to remain at < 1.

In contrast, tortoises living in the northeastern and eastern Mojave and northern and eastern Colorado deserts experience substantial precipitation in both winter and summer (Rowlands et al., 1982; USFWS, 1994). Winter precipitation follows a similar pattern as that described for the western Mojave, and summer rainfall composes 34–40% of the total precipitation. The summer flora is well-developed, but not nearly so diverse as the winter flora. Tortoises have opportunities to feed on winter annuals between March and June and summer annuals between August and October (Turner and Berry, 1984a; 1985, 1986; Turner et al., 1987a). Other tortoise foods, perennial grasses, and cacti, are also more abundant in these regions and are an additional source of food in dry years (Turner et al., 1984). These tortoises have more opportunities to produce two rings annually than tortoises in the western Mojave Desert.

The northern and eastern parts of the Colorado Desert have seasonal distribution patterns of rainfall that are similar to that of the northeastern and eastern Mojave Desert (Rowlands, 1995). This desert differs from the Mojave Desert in having a considerably warmer and drier winter with fewer freezing days. Tortoises can hibernate for briefer periods and probably have more opportunities to produce multiple rings annually. The warmer winters, shorter hibernation periods, and potential dual foraging period may contribute to the numerous narrow and poorly defined growth rings that I observed.

Based on a comparison of data from the four desert regions, mean numbers of rings produced annually differed significantly for some regions. Although in most cases the modes and medians show 1.0 ring formed per year, I believe that regional differences would have been more pronounced and biologically meaningful if sample sizes were substantially larger and were drawn from at least seven to 10 years of data spanning years with different levels of precipitation. If assumptions about ring production are based on 1 or 2 years of data for a region, we are likely to be in error because of the wide variation in environmental parameters.

Desert tortoises in California probably exhibit substantial within-year variation in numbers of rings formed because precipitation and forage are patchily distributed (e.g., see Wiens, 1985), even within small areas of 1–3 km^2. Other factors, such as social dominance, may affect how rapidly some individuals grow (and produce rings) compared with others (Zug, 1991).

The results and interpretations presented here are similar to those of Wilson et al. (in press) but differ from those of Germano (1988, 1998), who conducted a retrospective evaluation of 15 wild, confined tortoises living in three 9-ha enclosures in Rock Valley, Nevada, and concluded that one ring was generally produced per year. The differences in the results are likely the product of methods, location, and small sample size. The Rock Valley tortoises are part of a long-term study (Medica et al., 1975; Turner et al., 1987b). In the first several years of the study, no records were kept of growth rings and no photographs were taken when tortoises were captured and recaptured (Turner et al., 1987b; F. Turner and P. Medica, *pers. comm.*). When first captured between 1963 and 1965, the 15 tortoises were from 47 to 74 mm in plastron length; later their ages at first capture were estimated (Turner et al., 1987b). When Germano (1988) counted rings on these tortoises several years later (in 1985), he found rings to be annual if they formed a deep groove and the groove was complete or conspicuous. Unless individuals are marked as neonates or hatchlings and then subsequently recaptured, their ages will be estimated ages and the reliability will depend on the accuracy of the assignment to a specific cohort (Zug, 1991).

The Rock Valley tortoises are in the northern periphery of the geographic range of the species, and the site is in an area at the low end of the scale of productivity for the Mojave Desert (Turner et al., 1987b). Since the tortoises had been confined for over 20 years to the enclosures at the time Germano (1988) conducted his assessment, they are more likely to have experienced similar microhabitats than free-ranging tortoises at the much larger study sites (≥ 2.6 km^2) in California. If habitat in the pens was relatively constant, some of the lack of variation in ring counts might be explained.

Some chelonians living in more temperate environments produce one ring per year, whereas others respond to availability of precipitation and food. *Testudo hermanni*, which lives in a more mesic and probably more constant environment in southern Europe, produces one ring annually both in the field (Stubbs and Swingland, 1985; Stubbs et al., 1985) and under laboratory conditions (Castanet, 1985). *Testudo hermanni* regularly produced one growth ring per year on scutes and bone to the age of sexual maturity at 12 or 13 years (Castanet, 1985). In contrast, in *Gopherus polyphemus*, the appearance and production of rings are affected by precipitation levels in southern Alabama (Aresco and Guyer, 1998). When rainfall was below average in 1995, 20% of juvenile and subadult tortoises produced “false annuli.” Precipitation levels and grasshopper abundance also affected ring width or “zones of growth” in different years for *Terrapene ornata ornata* (Legler, 1960).

Accurate assessment of age of individual tortoises is an integral part of recovery planning for the desert tortoise (USFWS, 1994; Tracy and Tracy, 1995). If ring counts used to estimate age are inaccurate, then estimates for age at first reproduction, survivorship of young cohorts, and many other important life history traits could be in error. Other important age-size relationships within and between recovery unit populations could be obscured. For example, if the assumption is made that 1 ring is formed per year, but the mean number of rings formed per year is actually 0.6 in the western Mojave and 1.2 in the northern and eastern Colorado deserts, then tortoises in the western Mojave Desert with 6 rings and tortoises with 12 rings in the Colorado Desert would be the same age (10 years). Over a 10- to 15-year period, substantial errors could occur for estimates of age at sexual maturity, age of neonate and juvenile cohorts (thus survivorship values), longevity, and years necessary for population recovery.

Ring counts can be used to rapidly assess gross ages of juvenile desert tortoises. With future research and additional information, the technique might be refined and become more reliable and useful. Some possible directions of research for desert tortoises and other chelonians include determining (1) the sequence of ring development for juveniles and adults, and (2) the relationships between rings and age on tortoises of known (not estimated) age (e.g., see

Wilson et al., in press). Such research should be comparative, carried out under a variety of environmental conditions and in different regions, and validated, where appropriate, on a population-by-population or regional basis. The similarities and differences in ring counts obtained by visual observations, dental casts, and photographs also should be evaluated for the different size-age classes of tortoises in double-blind studies (e.g., Galbraith et al., 1987b).

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