Copeia, 1988(4), pp. 914–920

Age and Growth Histories of Desert Tortoises Using Scute Annuli

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Scute annuli, produced during the first 20–25 yr of initial, rapid growth, can be used to age young desert tortoises (*Gopherus agassizii*). Regression analysis did not show a difference between age and the number of scute rings counted on the carapace for 13 desert tortoises from the Nevada Test Site, although ring counts on most individuals were 1–2 rings less than age. The number of scute rings exactly matched the ages of six desert tortoises raised in captivity. No significant differences were found between the estimated length of the plastron based on selected scute rings and the actual length of the plastron as recorded 7–12 yr previous to my handling of individual tortoises from the Nevada Test Site, which supports the accuracy of the ring counts. The number of bone rings did not differ significantly from the number of scute rings for 16 preserved desert tortoises. Growth histories of individual tortoises can be determined from scute annuli.

ANALYSES of population structure and associated life-history traits require an accurate assessment of the age of individuals. Demographic studies that incorporate age determination allow for the detection of temporal variation in age structure. This type of information has practical application in the study of species with declining populations.

The desert tortoise (*Gopherus agassizii*) is a widespread species of the desert southwest that is legally protected where it occurs in the United States and Mexico, and is suspected of experiencing population declines in certain parts of its range. Demographic analyses with accurate age information would be useful in monitoring the effects of habitat alteration on tortoise populations (Medica et al., 1975), and for determining the age at first reproduction of individuals in a population, a life-history trait that can greatly affect a population's growth rate (Lewontin, 1965). Previously, researchers working on desert tortoises only have been able to determine the minimum body size at which reproduction occurs, which is not as useful in life-history analyses as is age.

Several methods are available for determining ages of desert tortoises: mark and recapture of individual tortoises, counting the number of bone annuli visible in histological preparations, and age determination based on shell wear. Mark and recapture of newly hatched tortoises over several decades provides the age of individual tortoises (Turner et al., 1987), but this method requires many years of data collection and provides information only for the population under study. Counting the number of bone annuli is an accurate technique of estimating the ages of mammals (Klevezal and Kleinenberg, 1969), amphibians (Schroeder and Baskett, 1968; Hemelaar and Van Gelder, 1980; Francillon and Castanet, 1985), and reptiles (Castanet et al., 1977; Zug et al., 1986), including the Mediterranean tortoises *Testudo graeca* and *T. hermanni* (Castanet and Cheylan, 1979). However, bone analysis is a destructive technique and therefore is not useful for either long-term studies of populations or studies of populations of protected species. The shell-wear technique involves subjectively categorizing individuals into seven age-wear classes based on the size of the individual and the wear on its shell. Wear is assumed to be highly correlated with age and consistent between individuals and across all habitats. Older and larger individuals tend to be more worn than younger individuals, and very old tortoises often have concave scutes. This method is not useful in life-history analyses because it lumps many possible ages into general age categories and the amount of shell wear may be subject to differences in the substrate on which individuals reside.

When the shells of desert tortoises grow, as in many other chelonians, they form concentric rings on each scute. These rings are hard epidermal layers formed during periods of intensive growth (Carr, 1952; Gibbons, 1976), which continues at a high rate until the individual reaches adult size (Woodbury and Hardy, 1948).

Scute rings may be useful for aging desert tortoises.

Here I present evidence on the accuracy of counts of scute rings as a means of aging desert tortoises. Scute rings have been used to determine the age of young individuals in many species of turtles, including *Pseudemys scripta* (Cagle, 1946), *Chysemys picta* (Sexton, 1959), *Terrapene ornata* (Legler, 1960), *Kinosternon flavescens* (Long, 1986), *Testudo hermanni* and *T. graeca* (Castanet and Cheylan, 1979; Lambert, 1982; Stubbs et al., 1984), *Geochelone gigantea* (Gaymer, 1968; Grubb, 1971), and the desert tortoise congeners *Gopherus berlandieri* (Auffenberg and Weaver, 1969; Judd and Rose, 1983), *G. flavomarginatus* (G. Adest, pers. comm.), and *G. polyphemus* (Landers et al, 1982), but has not been used for desert tortoises. This is due, in part, to the lack of evidence showing scute rings to be annual. If scute rings are produced annually, they would provide an accurate means of determining ages of tortoises with only one handling of an individual. In this study, I compare the number of growth rings formed on scutes to the known age of individual desert tortoises and to the number of bone annuli found in long bones.

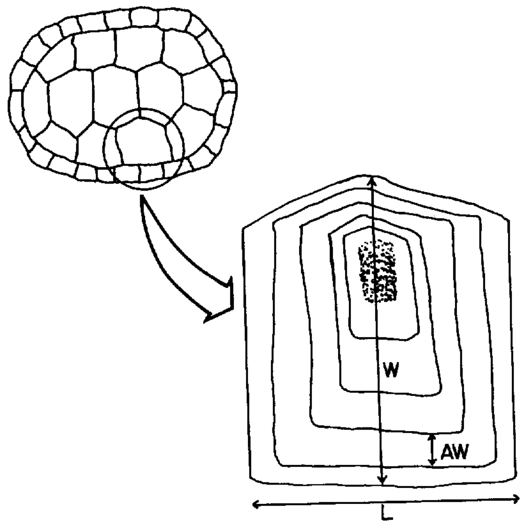

Fig. 1. The second right costal scute of *Gopherus agassizii* on which growth measurements and ring counts were taken. The measurements taken on each ring included the length of the ring (L), the width of the ring (W), and the amount of growth from one ring to the next (AW).

Methods

Growth rings were counted from the second costal scute on the carapace (Fig. 1) because the carapace receives less wear than the plastron. This scute is also the most square on the carapace, which simplifies measuring the length and width of each ring, data used in growth analyses. For the purposes of counting rings any of the costal or vertebral scutes could be used. I distinguished between true annual rings and false rings using criteria that have been developed for box turtles (Legler, 1960) and gopher tortoises (Landers et al., 1982). I judged rings to be annual if they formed a deep groove and the groove was complete or conspicuous on all sides of the scute.

In May 1985, all the desert tortoises in three fenced plots at the Nevada Test Site were recaptured and measured. These tortoises have been studied since the mid 1960s (Medica et al., 1975) and the ages, which have been previously and independently assigned, are believed to be accurate to within 1 yr (Turner et al, 1987). These are the only wild desert tortoises available to me for which ages are known accurately. I took growth information on these tortoises and counted the number of scute rings. I later received the estimated ages of these individuals based on independent assessments (Turner et al., 1987). I compared the number of scute rings I counted to the age of the individual using regression analysis. A significant correlation with a regression slope not significantly different from 1.0 would indicate that scute rings match the age of individuals. Also, I counted scute rings from a group of six desert tortoises that I have raised since hatching in Tucson, Arizona. One hatched in Nov. 1977 and five hatched in Aug. 1978. They have been kept in outdoor pens since hatching, either in Tucson, coastal California, or Albuquerque, New Mexico. These tortoises have been in conditions that roughly approximate what desert tortoises experience within their native range with 5–7 mo activity periods and 5–7 mo winter dormancy each year.

Measurements of ca 150 desert tortoises, both living and museum specimens from throughout their range, produced a linear relationship between the length of the last scute ring of the second right costal scute and overall plastron length (PL) (Fig. 2). I used the length of a ring formed at a prior age to predict the length of the tortoise's plastron in past years. I used this technique as a check on the accuracy of the ring count for tortoises from the Nevada Test Site.

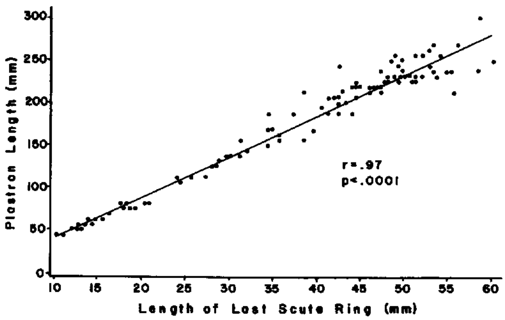

Fig. 2. The relationship between PL and the length of the last scute ring of *Gopherus agassizii* measured on the second costal scute. Each point represents one or more different individuals. This relationship was used to predict the PL of tortoises from the Nevada Test Site in past years from the length of previously produced scute rings.

Plastron lengths have been recorded for tortoises from the Nevada Test Site for approx. 20 yr. I estimated PL for 15 Nevada Test Site tortoises from the length of scute rings that I predicted had been formed 7–12 yr previously. If my ring count reflects the age of the individual, then the estimated PL should not be significantly different from the actual plastron lengths measured in a given year by Medica et al. (1975). The year used for comparison varied by individual based on whether the individual's PL had been measured late enough in a given year to account for all or most of its growth in that year (Medica et al., 1975). The estimated PL were compared to the actual PL by regression analysis.

I also compared the number of scute rings to the number of bone annuli found in the long bones of desert tortoises. A high correlation between scute rings and bone rings with a regression slope of 1.0 would support the hypothesis that scute rings accurately reflect the age of a desert tortoise. I prepared long bones from 16 preserved desert tortoises from the Museum of Southwestern Biology following standard histological techniques and suggestions made by Castanet and Cheylan (1979) and Zug et al. (1986). After decalcification, I sectioned bones with a razor blade, stained sections with lactic orecin for 20 min, and fixed and mounted each section. Using a light microscope (40×), I counted rings on five separate occasions for each specimen and took the average as the bone ring count for that specimen. I compared bone ring counts to scute ring counts by regression analysis.

Growth histories were determined for tortoises at this site by converting the length of each ring visible on the second costal scute to carapace lengths using a regression equation similar to Figure 2. The smallest carapace length was subtracted from the largest carapace length yielding total growth in a praticular time period. Total growth was divided by the number of years involved giving growth per year for each tortoise. These yearly growth rates were averaged across individuals for three time periods: pre-1974, 1973–84, and overall growth rates for as many years back as could be discerned on the scute. Differential scute wear among individuals meant that growth histories were of different lengths of time. Growth by year also was compared to rainfall, specifically winter rainfall, which has been shown to be correlated to tortoise growth at this site (Medica et al., 1975). A correlation analysis was performed using the average percent growth each year for all tortoises, as measured by annual width of growth ring (AW)/carapace length, compared to winter rainfall.

Results

Plastron length and scute annuli are positively correlated up to 20–25 rings, at which time PL continues to increase with no increase in the number of easily seen annuli (Fig. 3). Of the approx. 150 desert tortoises that I have analyzed to date, I have never seen a desert tortoise with more than 25 large, easily perceivable rings. I found a correlation of 0.77 ($P = .002$) and a slope of 0.66 between the actual ages of the Nevada Test Site tortoises and the number of scute rings, which was not significantly different from a slope of 1.0 ($t_{11} = 2.08$, $.10 > P > .05$, Table 1). When differences between ring number and age occurred, ring number was less than age (Sign Test: $Z = 3.317$, $P < .01$). For the Nevada Test Site tortoises, the ring count either exactly matched the age or was one to two rings less than the age, but in no cases were there more rings than the age of an individual. One individual was not used in the analysis because it did not grow for 5 yr (Turner et al., 1987). For captive tortoises, the number of scute rings was identical to the age of each individual (Table 1).

Measurements of costal rings were found to be good predictors of size expressed as PL. Pre-

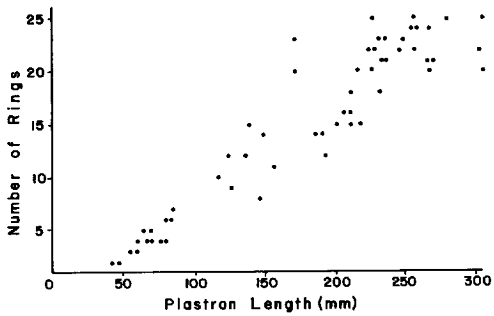

Fig. 3. The number of scute rings of *Gopherus agassizii* counted from the second costal scute compared to the length of the plastron for various sized tortoises. Each point represents one or more different individuals. The number of scute rings increases fairly linearly until 20–25 rings at which point size increases with no increase in the number of easily perceivable scute rings.

dicted PL were significantly correlated with actual PL as independently determined (r = 0.81, $P < .01$, Fig. 4).

Bone rings have been found to be an accurate estimate of age in many species. For desert tortoises, a significant correlation exists between the number of scute rings and the number of bone rings (r = 0.97, $P < .01$, Fig. 5).

The average annual growth of 14 tortoises from this site was 8.5 mm (range = 6.2–10.8 mm, $\bar{X}$ number of years = 14.6). Yearly growth before 1974 was 10.9 mm (n = 11, range = 6.9–13.9 mm, $\bar{X}$ number of years = 5.4) and from 1973–84 yearly growth was 7.6 mm (n = 14, range = 3.5–10.1 mm, $\bar{X}$ number of years = 10.6). Percent growth per year was not significantly correlated to winter rainfall (r = 0.293, n = 14).

Discussion

Miller (1932, 1955) and Woodbury and Hardy (1948) objected to using scute rings to determine ages of desert tortoises because they did not find a correlation between age and the number of scute rings. As Legler (1960) noted, though, the study by Woodbury and Hardy dealt with all sizes and ages of desert tortoises, which meant that some of the individuals studied were past the age of regular, annual growth. It is therefore not surprising that they did not find a correlation between age and the number of scute rings because, for some individuals, easily perceivable scute rings had ceased being pro-

Table 1. Age Versus the Number of Rings on the Carapace for Desert Tortoises from the Nevada Test Site and Those Raised in Captivity.

Number of rings	Age
Nevada Test Site	
21	23
21	22
24	25
21	23
22	22
23	24
23	23
23	23
20	22
21	23
22	24
20	21
21	22
Captives	
7	7
7	7
7	7
7	7
7	7
8	8

duced. Miller studied only captive individuals in unnatural conditions, and he states that several individuals that showed no production of rings for several years died soon thereafter. In addition, Miller does not mention if he found differences in between-year rings and within-year rings. The use of scute rings has been sup-

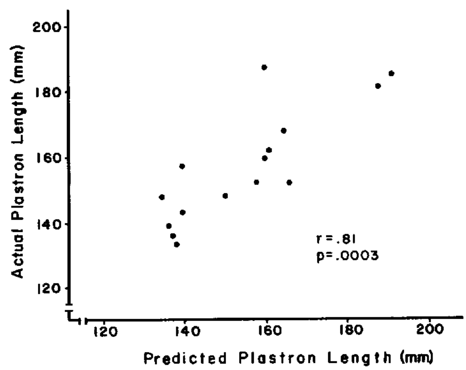

Fig. 4. Regression of predicted plastron length to actual PL for Nevada Test Site tortoises. The predicted PL were based on the relationship shown in Figure 2. The slope of 0.77 is not significantly different from 1.0 (t_{13} df = 1.47 $P > .10$).

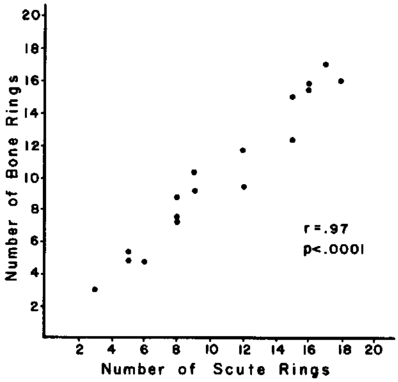

Fig. 5. Regression of scute ring count to bone ring count for 16 desert tortoises. The slope of 0.92 is not significantly different from 1.0 (t_{15} df = 1.45 $P > .10$).

ported by Gibbons (1976) who states that, in many instances, turtle growth rings have proved to be the most accurate and readily available method of determining age ever used in studies of long-lived vertebrates.

There may be several reasons why the number of scute rings did not exactly match the age of individual tortoises from the Nevada Test Site in all cases. Some of these individuals may have stopped producing large growth rings 1–2 yr prior to my measuring those individuals. It also is possible that I missed a ring when I took measurements or that a ring did not form during a particularly bad growth year due to drought. The growth rate of many reptiles is subject to environmental influences such as changes in temperature and fluctuations in water and food availability (Andrews, 1982). The Nevada Test Site is an area that receives highly variable amounts of rain (Medica et al., 1975, unpubl.) and tortoises at this site grow less in bad rainfall years (Medica et al., 1975). However, given the close match of scute rings to age, there generally is a ring produced each year. Also, the ages assigned to these tortoises is given by Turner et al. (1987) as ± 1 yr, which may account for the discrepancy between the number of rings and age for some individuals.

Growth rates that I found using scute annuli widths compare favorably to those found by Medica et al. (1975) and Turner et al. (1987) for tortoises at this site. I calculated a yearly growth rate of 10.9 mm for pre-1974 growth compared to 9.1 mm found by Medica et al. (1975) for the same time period, and 7.6 mm for 1973–84 yearly growth as compared to 7.6 mm found by Turner et al. (1987) for essentially the same time period. The overall growth rate was 8.6 mm per year, a value between those found for tortoises at this site when measurements were taken over the past 20 yr. The ad-

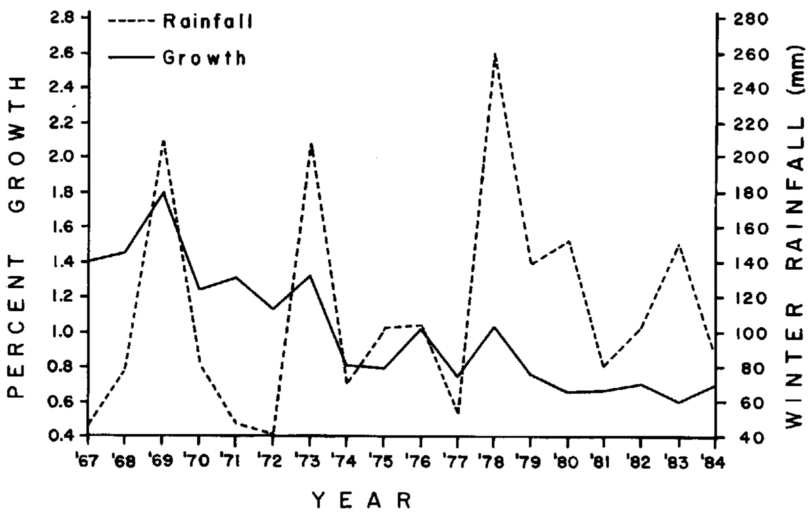

Fig. 6. Comparison of winter rainfall at Rock Valley of the Nevada Test Site to average percent growth of desert tortoises from this site for the years 1967–84. Growth of tortoises responds fairly well to changes in rainfall in early years when the tortoises are small, but growth slows as the tortoises increase in size and no longer reflects the pattern of rainfall in later years.

vantage to determining growth rates in this fashion is that all the information is derived from one handling of an individual.

Mean growth per year for the years 1969–84 are not correlated with winter rainfall in contrast to a correlation of 0.867 found by Medica et al. (1975) for the years 1969–74. It is interesting to note that I found a much higher correlation ($r = 0.723$) for the years 1969–74 than I did for the period 1969–84. Many factors likely influence somatic growth and the data presented by Medica et al. (1975) show large differences in growth with similar amounts of rainfall. Growth of desert tortoises decreases fairly uniformally irrespective of winter rainfall over any long time period (Fig. 6).

Use of large, easily seen scute rings for aging desert tortoises does appear to be limited to tortoises under 25 yr of age. The production of easily perceived scute rings ceases somewhere between 20 and 25 rings, but growth continues at a slow rate (Fig. 3). It is well known that reptile growth is relatively rapid until shortly after sexual maturity, at which time growth slows and the growth rate asymptotes to negligible levels (Andrews, 1982). Legler (1960) believed that for box turtles, growth in adults that occurred after large rings were no longer being formed might be sporadic with no new epidermal layers being deposited for many years. In contrast, for desert tortoises, I have seen individuals that have many growth rings crowded close together at the edges of scutes that could not be counted with the unaided eye. These small rings may represent annual growth past the initial rapid growth that produces the large rings that are more easily seen. Until a means of counting these small growth increments is devised however, aging individuals on the basis of scute rings must be confined to those less than 25 yr of age. The use of scute annuli does make it possible, though, to determine accurately the ages of a large segment of a desert tortoise population, including all juveniles and young adults, with only one handling of an individual. Potentially, with an exhaustive search of a site, a profile of recruitment spanning a 25 yr period could be obtained. In addition, yearly growth rates can be determined for as many scute rings as are visible. Although more work is needed to find a technique for determining the ages of all tortoises in a population, it would be wrong to disregard scute annuli for determining age and growth histories of many individuals.

Acknowledgments

I thank T. H. Fritts, R. B. Bury and the National Ecology Research Center of the U.S. Fish and Wildlife Service for their help. I also thank F. B. Turner for his permission to measure tortoises at the Nevada Test Site and to use data that have been collected there over the past 20 yr. Thanks go also to P. A. Medica for his assistance and friendship in the field, and to R. B. Bury and P. S. Corn for helping to capture tortoises. I also thank R. Chiovetti for help with bone ring analyses and to R. B. Bury, T. H. Fritts, R. D. Jennings, M. C. Molles, H. L. Snell, and J. A. Wiens for reviewing earlier drafts of this manuscript and providing helpful criticism that greatly improved its content.

Literature Cited

Andrews, R. M. 1982. Patterns of growth in reptiles, p. 273–320. *In:* Biology of Reptilia. Vol. 13. C. Gans and F. H. Pough (eds.). Academic Press, New York, New York.

Auffenberg, W., and J. B. Iverson. 1979. Demography of terrestrial turtles, p. 541–569. *In:* Turtles: perspectives and research. M. Harless and H. Morlock (eds.). J. Wiley & Sons, New York, New York.

———, and W. G. Weaver. 1969. *Gopherus berlandieri* in southeastern Texas. Bull. Florida State Mus. Biol. Sci. 13:141–203.

Cagle, F. R. 1946. The growth of the slider turtle, *Pseudemys scripta elegans*. Amer. Mid. Nat. 36:685–729.

Carr, A. 1952. Handbook of turtles: the turtles of the United States, Canada, and Baja California. Cornell University Press, Ithaca, New York.

Castanet, J., and M. Cheylan. 1979. Les marques de croissance des os et des ecailles comme indicateur de l'age chez *Testudo hermanni* et *Testudo greaca* (Reptilia, Chelonia, Testudinidae). Can. J. Zool. 57: 1649–1665.

———, F. J. Meunier and A. de Ricqles. 1977. L'enregistrement de la croissance cyclique par le tissu osseux chez les vertebres poikilotherms: donnees comparatives et essai de synthese. Bull. Biol. France Belgique 111:183–202.

Francillon, H., and J. Castanet. 1985. Mise en evidence experimentale du caractere annuel des lignes d'arret de croissance squelettique chez *Rana eculenta* (Amphibia, anura). C. R. Acad. Sci. Paris, t. 300, Serie III, no. 8:327–332.

Gaymer, R. 1968. The Indian Ocean giant tortoise *Testudo gigantea* on Aldalbra. J. Zool. 154:341–363.

Gibbons, J. W. 1976. Aging phenomena in reptiles, p. 454–475. *In:* Special review of experimental aging research. M. F. Elias, B. E. Eleftheriou and P. K. Elias (eds.). EAR, Inc., Bar Harbor, Maine.

Grubb, P. 1971. The growth, ecology and population structure of giant tortoises on Aldabra. Philos. Trans. R. Soc. Lond. 260:327–372.

Hemelaar, A. S. M., and J. J. Van Gelder. 1980. Annual growth rings in the phalanges of *Bufo bufo* (Anura, Amphibia) from the Netherlands and their use for age determination. Netherlands J. Zool. 30: 129–135.

Judd, F. W., and F. L. Rose. 1983. Population structure, density and movements of the Texas tortoise (*Gopherus berlandieri*). Southwest. Nat. 28:387–398.

Klevezal, G. A., and S. E. Kleinenberg. 1969. Age determination of mammals by layered structures in teeth and bones. Israel Program for Scientific Translations, Jerusalem, Israel. Translation from Russian by J. Salkind, Opredelenie vozrasta mlekopitaiushchikn po sloistym strukturam zubov i kosti. 1967. Academy of Sciences of the USSR, Severtsov Institute of Animal Morphology.

Lambert, M. R. K. 1982. Studies on the growth, structure and abundance of the Mediterranean spur-thighed tortoise, *Tesudo* (sic) *graeca* in field populations. J. Zool., Lond. 1982:165–189.

Landers, J. L., W. A. McRae and J. A. Garner. 1982. Growth and maturity of the gopher tortoise in southwestern Georgia. Bull. Florida State Mus., Biol. Sci. 27:81–110.

Legler, J. M. 1960. Natural history of the ornate box turtle, *Terrapene ornata ornata* Agassiz. Univ. Kansas Publ., Mus. Nat. Hist. 11:527–669.

Lewontin, R. C. 1965. Selection for colonizing ability, p. 77–94. *In:* The genetics of colonizing species. H. G. Baker and G. L. Stebbins (eds.). Academic Press, New York, New York.

Long, D. R. 1986. Clutch formation in the turtle, *Kinosternon flavescens* (Testudines: Kinosternidae). Southwest. Nat. 13:1–8.

Medica, P. A., R. B. Bury and F. B. Turner. 1975. Growth of the desert tortoise (*Gopherus agassizi*) in Nevada. Copeia 1975:639–643.

Miller, L. 1932. Notes on the desert tortoise (*Testudo agassizii*). Trans. San Diego Soc. Nat. Hist. 7: 187–208.

———. 1955. Further observations on the desert tortoise *Gopherus agassizi*, of California. Copeia 1955: 113–118.

Schroeder, E. E., and T. S. Baskett. 1968. Age estimation, growth rates, and population structure in Missouri bullfrogs. *Ibid.* 1968:583–592.

Sexton, O. J. 1959. A method of estimating the age of painted turtles for use in demographic studies. Ecol. 40:716–718.

Stubbs, D., A. Hailey, E. Pulford, and W. Tyler. 1984. Population ecology of European tortoises: review of field techniques. Amphibia-Reptilia 5:57–68.

Turner, F. B., P. A. Medica and R. B. Bury. 1987. Age-size relationships of desert tortoises (*Gopherus agassizi*) in southern Nevada. Copeia 1987:974–979.

Woodbury, A. M., and R. Hardy. 1948. Studies of the desert tortoise, *Gopherus agassizii*. Ecol. Monogr. 18:145–200.

Zug, G. R., A. H. Wynn and C. Ruckdeschel. 1986. Age determination of loggerhead sea turtles, *Caretta caretta*, by incremental growth marks in the skeleton. Smithsonian Contr. Zool. no. 427.

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Accepted 6 March 1988.