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Longevity and Age-Size Relationships of Populations of Desert Tortoises

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Based on minimum estimates of longevity of desert tortoises (*Gopherus agassizii*) that died in the field, few individuals live past 50 yr. Approximately 29% of tortoises from the Sonoran Desert, 11% of tortoises from the eastern Mojave Desert, and approx. 5% of tortoises from the western Mojave Desert were estimated to be over 25 yr. The greatest estimate of longevity for any individual was 48–53 yr and came from the eastern Mojave Desert. The oldest individual from the western Mojave Desert was estimated to be 32 yr, and the oldest individual from the Sonoran Desert was estimated to be 35 yr. Comparisons of carapace length to age showed the highest rates of growth (0–25 yr) for tortoises from the western Mojave Desert and Sinaloan habitats. Of the four major regions within the range of the desert tortoise, rates of growth were lowest in the eastern Mojave and Sonoran deserts.

THE study of life-history phenomena has received renewed interest in the past two decades. Theoretical efforts have focused on the interrelationships of various life-history traits (Cole, 1954; Lewontin, 1965; Taylor, 1980) and how they shape populations of organisms (Stearns, 1976; Charlesworth, 1980; Rose, 1983; and others). Specifically, covarying traits that are subject to selection include survivorship, fecundity, age-at-first reproduction, and longevity. For instance, low juvenile survivorship must be accompanied by high fecundity or longevity, or both, for a female's reproductive output to meet replacement levels. Alternately, lowering the age-at-first reproduction contributes as large an increase in fitness as a substantial increase in fecundity in many populations, at least those that are growing in numbers (Lewontin, 1965). Most work on life-history evolution has dealt with variation in survivorship, fecundity, and age-at-first reproduction and their effect on individual fitness and population growth. Additionally, most work has been done on relatively short-lived species (Stearns, 1977). Few studies have investigated the role of longevity and how it interacts with juvenile survivorship and adult fecundity. Theoretically, long life could offset the negative consequences to individuals and populations of low survivorship and/or low numbers of offspring for iteroparous organisms.

Accurate estimates of age are rarely known for individuals of most species, particularly those with long life spans (Gibbons, 1987). Chelonians are reputed to be among the longest lived of all vertebrates, and some captives have lived more than 50 yr (Flower, 1925; Gibbons, 1976; 1987). Among wild populations, life span may not be as great (Gibbons, 1987).

Few estimates of maximum longevity have been made for desert tortoises (*Gopherus agassizii*). This is due, in part, to the inability of researchers to determine ages of individuals in the field. I have previously shown that easily seen scute annuli can be used to determine ages of desert tortoises less than 25 yr (Germano, 1988). Here, I report a technique for estimating the minimum age of desert tortoises older than 25 yr and present the first estimates of desert tortoise longevity for three major regions within the range of this species. I also construct age-size regressions for the first 25 yr of life and compare these regressions among regions.

METHODS

Ages were determined from shells of live and dead desert tortoises from the western Mojave Desert, eastern Mojave Desert, Sonoran Desert, and Sinaloan thornscrub and deciduous forest. Live tortoises include animals measured in the field and individuals that were killed for preservation as museum specimens or as food for people. Only ages of individuals found dead in the field (i.e., shells) were used to estimate longevity. Dead and living tortoises were used to plot age-size regressions.

All tortoises from the Mojave Desert were dead; all those from the Sinaloan habitats were alive. Tortoises from the Maricopa, Eagletail, and Arrastra mountains were dead; all other tortoises from the Sonoran Desert were alive. Locations and sample sizes (in parentheses) follow: Western Mojave Desert—Desert Tortoise Natural Area (159), Water Canyon (60), Kramer (75); Eastern Mojave Desert—Piute Valley (153), Sheep Mountains (37), Gold Butte (15), Coyote Spring Valley (23); Sonoran Desert—Maricopa Mountains (37), Eagletail Mountains (7), Arrastra Mountains (8), Tucson area (9), Samaniego Hills (6), Phoenix area (7), Tiburon Island (3), Picacho Mountains (10), near Desert Center (2), southeast of Yucca (3), Alamo Hills area (2), southwest of Aguila (1), Cave Creek (1), Pinto Basin (1), Tortilla Mountains (1), 55 km northeast of La Libertad (4), Ejido San Ignacio (2), Poso de Luis (1), near Noria Agualarena (1), Rancho San Juan (1), Ejido La Cienega (1); Sinaloan thornscrub and deciduous forest—Alamos area (26), Mazatan (3), south of Moctezuma (1), near Matope (1), near La Barranca (1), near Rio Yaqui (1), south of Bacunaro (1), near Tonichi (1), Rancho San Pedro (1).

For many individuals, I determined age by counting scute annuli visible with the unaided eye (Germano, 1988). However, some shells exhibited beveling between scutes, in contrast to those where the last growth ring was flat and smooth, cleanly abutting the last ring of an adjacent scute (Fig. 1). Individuals with scute-edge beveling are likely to be older than estimated by the number of visible scute rings (Grant, 1936). For these apparently older individuals, I used a razor saw to cut out a thin section (approx. 1 mm × 5 mm) of epidermal layer from the edge of a carapace scute, usually from one of the costals (Fig. 2). The section was taken from the edge abutting the marginals. These sections were filed with an emery board until growth lines were visible when viewed at 40× using a light microscope (Fig. 2). For some individuals, small growth annuli could be discerned using a dissecting scope without sectioning the scute. The number of growth lines counted in cross-section was added to the number of larger annuli counted from the whole scute or, in the case of highly worn or weathered shells where an accurate count of rings could not be made, to the number range 20–25. Desert tortoises usually produce 20–25 annuli before growth slows to the point that easily visible annuli can no longer be counted (Germano, 1988).

Distributions of ages among habitats were compared using χ^2 tests (Sokal and Rohlf, 1981). Generalized age-size regressions were constructed for the four major regions within desert tortoise range using the carapace length as the measure of size. In some instances from the western Mojave, either the plastron length (PL) or the length of the second costal scute (LSCS) was used to estimate carapace length when the whole carapace was not present. Both PL and LSCS accurately estimate carapace length ($CL = 1.03 \times PL - 3.30$, $R^2 = 0.997$, $n = 140$; $CL = 4.91 \times LSCS - 9.57$, $R^2 = 0.97$, $n = 257$). Slopes and intercepts were determined using least squares regression on ages 0–25. Regression equations were compared among habitats using F statistics (Sokal and Rohlf, 1981). Pairs of slopes were compared using Newman-Keuls tests. Pairs of intercepts were compared using t-tests. Linear regressions were calculated to facilitate comparison to published regressions, although growth of desert tortoises is nonlinear, especially when data for ages over 25 yr is included (Germano, 1989). These regressions are not intended as a complete description of growth. A complete analysis of growth of the four species of *Gopherus* is being prepared.

RESULTS

Of the 574 tortoises examined that had died in the field, only one individual was estimated to have a minimum age greater than 40 yr. It was estimated to have a minimum age of 48–53 yr. This individual is from the eastern Mojave Desert, for which approx. 11% of individuals are older than 25 yr (Fig. 3). Approximately 5% of individuals from the western Mojave Desert are older than 25 yr, and the oldest individual was estimated to have a minimum age of 32 yr (Fig. 3). Approximately 29% of tortoises from the Sonoran Desert are older than 25 yr, although the oldest individual was estimated to have a minimum age of only 35 yr (Fig. 3). The distribution of ages for the western Mojave Desert is significantly different than the distribution for the eastern Mojave Desert ($\chi^2 = 92.60$, 52 df, $P < 0.001$) and the Sonoran Desert ($\chi^2 = 117.51$, 35 df, $P < 0.001$). The distribution of ages for the eastern Mojave Desert is not significantly different than the distribution for the Sonoran Desert ($\chi^2 = 53.72$, 52 df, $0.50 > P > 0.40$).

Overall comparison of regression equations

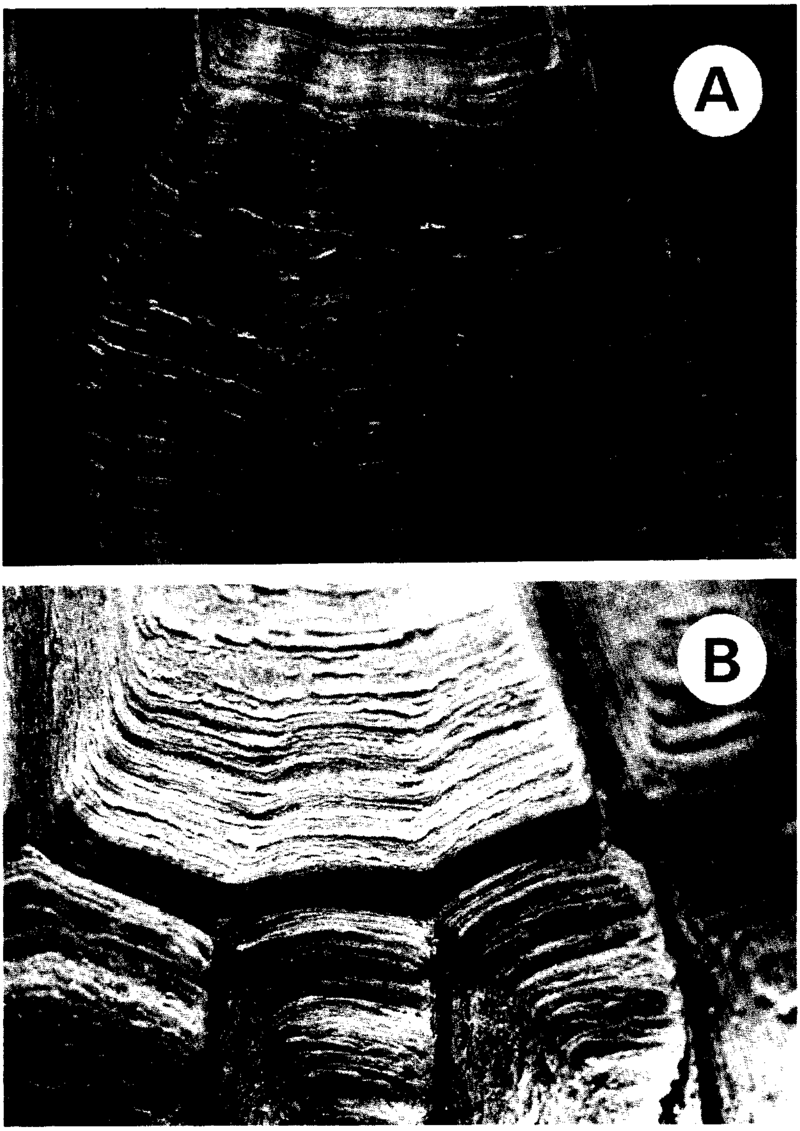

Fig. 1. Desert tortoises are the age of the number of scute annuli when the last ring abutting the adjacent scute is flat and smooth without beveling and the number of rings is less than 20–25 (A). Shells showing beveling on the edge of the scute (B) require sectioning to determine a minimum age because of additional growth plates added during continued slow growth.

of carapace length to age among habitats is significant ($F_{3,452} = 8.797$, $P < 0.001$, Fig. 4). The slope of the regression for tortoises from the western Mojave Desert is significantly steeper than for tortoises from the eastern Mojave Desert ($q_{4,452} = 6.757$, $P < 0.001$) and the Sonoran Desert ($q_{3,452} = 5.016$, $P < 0.01$). Although the slope of the regression for tortoises from Sinaloan habitats is not significantly different than the slope for tortoises from the eastern Mojave Desert ($q_{1,452} = 1.411$, $P > 0.05$), the intercept is significantly larger ($t_{222} = 3.358$, $P < 0.001$).

DISCUSSION

Maximum ages of desert tortoises rarely exceed 40 yr based on the method of estimating

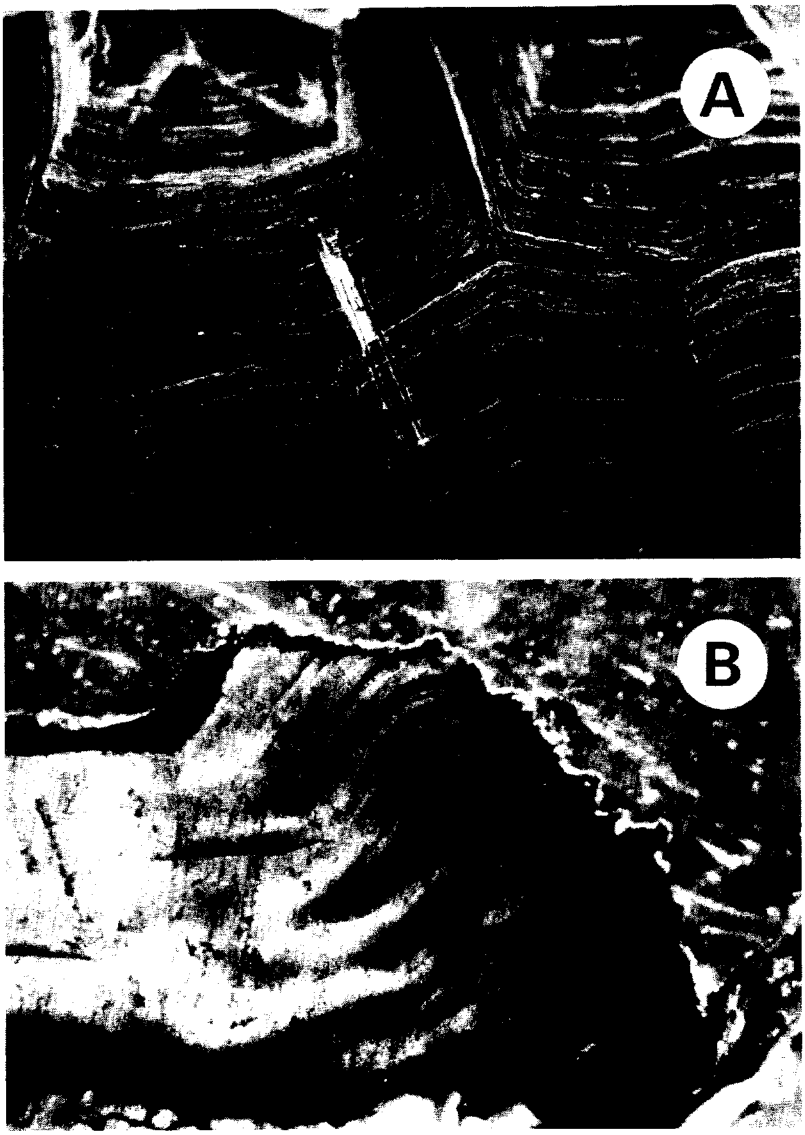

Fig. 2. In older individuals, a small section of scute is cut off the carapace for further analysis (A). After sectioning and thinning, beveled scute sections reveal additional growth plates (B) when viewed by light microscopy (×40).

age presented in this paper. Overall, it appears that most adults probably do not live much beyond 30 yr. However, Hardy (1976) recaptured several previously marked desert tortoises 30 yr after their first capture when they were of adult size. This means these individuals were at least 45–50 yr old because desert tortoises reach adult size (approx. 200 mm carapace length) between 15–20 yr (Turner et al., 1987; Germano 1989). Only one individual in this study was estimated to be older than 40 yr, and it lived to be approx. 50 yr. This individual was from the eastern Mojave, not far from where Hardy (1976) worked.

Estimates of maximum longevity for wild turtles vary. *Gopherus polyphemus* may live 40–60 yr (Landers, 1980), *Testudo hermanni* to approx. 40 yr (Meek, 1985), and the maximum age of *Geochelone gigantea* may be from 55–70 yr (Bourne and Coe, 1978). An estimate of maximum longevity for individual *Terrapene carolina* was 50–80 yr (Stickel, 1978) but was only 32 yr for *Terrapene ornata* (Blair, 1976). Similarly,

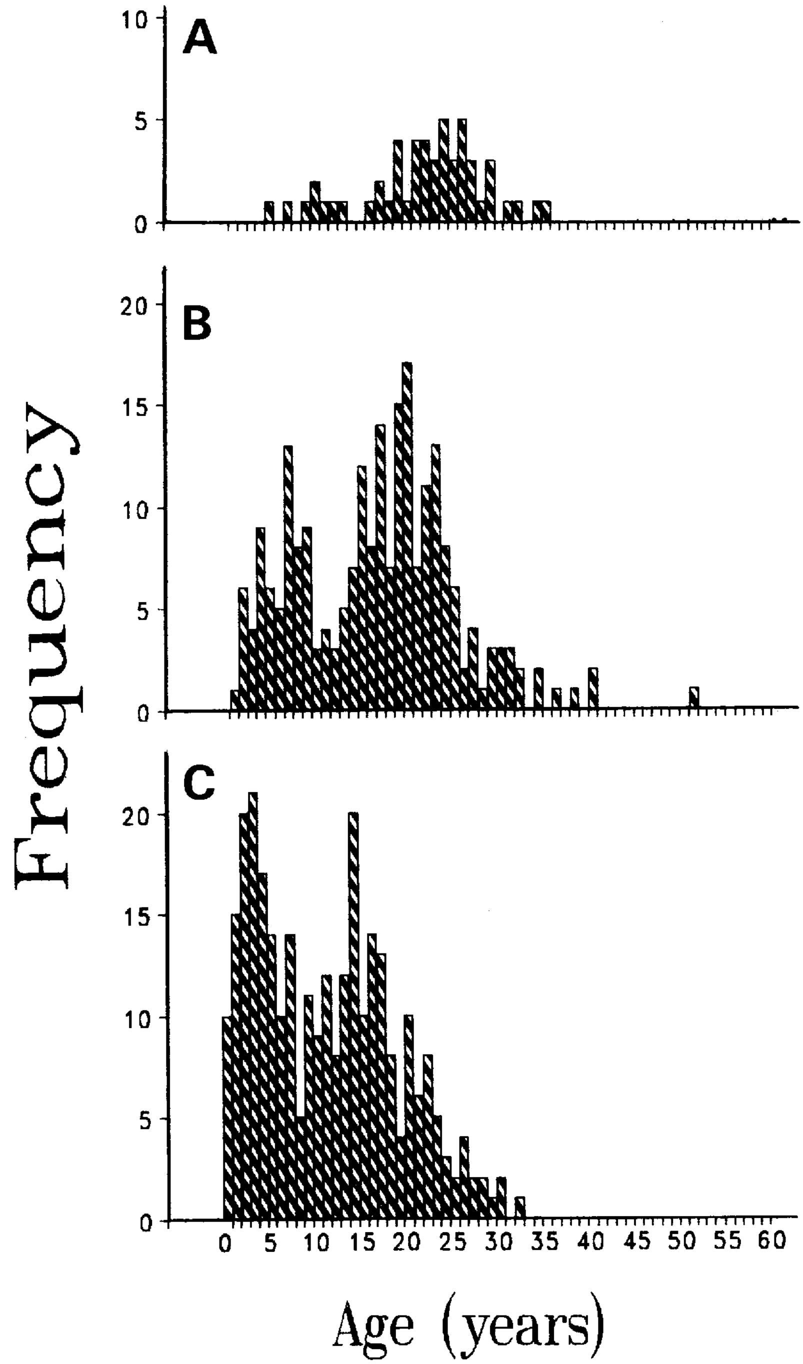

Fig. 3. Ages of desert tortoises found dead in the Sonoran Desert (A), eastern Mojave Desert (B), and western Mojave Desert (C). See methods for the list of sites represented by these data.

estimates of maximum longevity for the slider (*Pseudemys scripta*) have varied from up to 75 yr (Cagle, 1950) to not greater than 30–35 yr (Gibbons and Semlitsch, 1982; Gibbons, 1987). *Gopherus berlandieri* lives at least to 60 yr in captivity (Judd and McQueen, 1982; Judd and Rose, 1989).

Estimated ages of desert tortoises past 20 yr

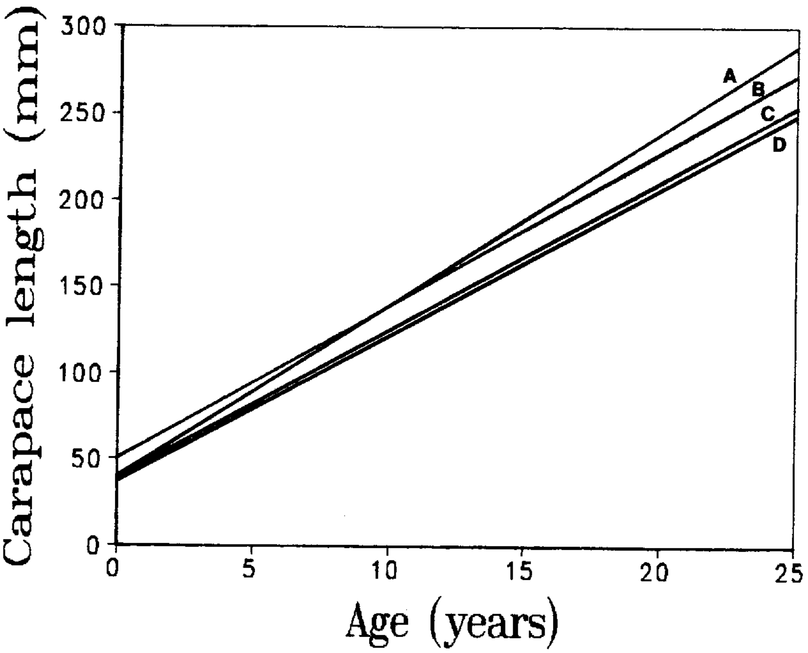

Fig. 4. Carapace length (CL) versus age regressions for living and dead desert tortoises from the western Mojave Desert (A; CL = 9.93age + 40.7, R^2 = 0.93, n = 153), Sinaloan habitats (B; CL = 8.85age + 50.6, R^2 = 0.92, n = 34), Sonoran Desert (C; CL = 8.55age + 39.9, R^2 = 0.88, n = 85), and eastern Mojave Desert (D; CL = 8.46age + 37.8, R^2 = 0.90, n = 188).

are only minimum estimates. Growth of wild desert tortoises slows to a low rate after 20–25 yr (Germano, 1989). Growth in box turtles (*Terrapene* spp.) slows greatly after approx. 15 yr (Legler, 1960; Stickel, 1978). Western box turtles (*T. ornata*) may grow only sporadically or not at all after reaching adult size (Legler, 1960). The wood turtle (*Clemmys insculpta*) continues to grow at an average rate of 0.8 mm per yr as an adult (Lovich et al., 1990). Potential advantages exist for both male (Lovich et al., 1990) and female turtles (Gibbons et al., 1982) by continued growth as adults; therefore, it is not unlikely that turtles are indeterminate growers. Based on layers seen in the edge of scutes of desert tortoises viewed in cross-section, scutes grow in thickness even when not growing appreciably in size. These are the growth plates that I have counted. These small growth plates may, however, be added at irregular intervals. If this is the case, tortoises estimated to be older than 20–25 yr could be even older than the ages given.

Regional groupings of desert tortoises each represent several populations that may have different population attributes, but it has been assumed that this does not significantly affect estimates of longevity. Determination of ages of desert tortoises was based on shells, and it has been assumed that shells represent individuals that died naturally in the wild. It has also been assumed that when older tortoises die, their shells are as conspicuous and persist as long as or longer than, individuals that die at a younger age. This is not known to be true but appears to be true for all four species of *Gopherus* based on museum collections that I have seen. Few shells of young desert tortoises are generally found in the field (K. H. Berry, unpubl.), and shells of older tortoises persist longer than shells of younger individuals (Berry, 1986). In view of this general trend, the significantly higher proportion of young tortoises recovered from three sites in the western Mojave Desert is intriguing. Although search bias is a possible explanation for the high number of young, it is also possible that these individuals represent a real increase in the representation of young tortoises in this region. If these numbers are biologically real, the higher proportion of young could be reflective of a significantly higher birth rate (Sattenspiel and Harpending, 1983).

TABLE 1. PREDICTED CARAPACE LENGTHS (CL) AND PERCENT INCREASE IN CL FOR DESERT TORTOISES BASED ON REGRESSION EQUATIONS FROM FIGURE 4.

	Carapace length (mm)							
Age (yr)	Western Mojave	% Inc.	Eastern Mojave	% Inc.	Sonoran	% Inc.	Sinaloan	% Inc.
1	51	—	46	—	49	—	59	—
5	90	76.5	80	73.9	83	69.4	95	61.0
10	140	55.6	122	52.5	125	50.6	139	46.3
15	190	35.7	165	30.3	168	34.4	183	31.7
20	239	25.8	207	25.5	211	25.6	228	24.6

Older tortoises were not abundant in the western Mojave Desert, but individuals from this region had high growth rates based on size-age regressions. These observations are consistent with growth data from scute ring analyses (Germano, 1989). Based on these regression equations, desert tortoises grow at the highest rate (61–76.5%) from ages one to five and at the lowest rate (24.6–25.8%) from 15–20 yr (Table 1). Desert tortoises from both the western and eastern Mojave Desert grow at a faster rate than tortoises from the Sinaloan habitats. Desert tortoises from the Nevada Test Site (Mojave Desert) increased 67.7%, 57.1%, 25.6%, and 18.6% for the same age groups reported in Table 1 (Turner et al., 1987). However, mean plastron lengths for these tortoises were 48 mm at age one (46 mm CL), 80.5 mm at age five (80 mm CL), 126.5 mm at age 10 (127 mm CL), 159 mm at age 15 (160 mm CL), and 188.5 mm at age 20 (191 mm CL) (Turner et al., 1987), which is similar to the sizes I have found for desert tortoises from the eastern Mojave and Sonoran deserts. Growth of tortoises from the Nevada Test Site is correlated to precipitation, especially winter rainfall (Medica et al., 1975), although this correlation diminishes as tortoises become older (Germano, 1988). Rainfall may play a part in the growth differences across the range of the desert tortoise, but it alone does not account for all the differences in growth seen here (Germano, 1989). The western Mojave Desert is the driest part of the range of the desert tortoise, but it does receive relatively predictable rainfall, both in amounts and timing (Germano, 1989).

Knowledge of maximum and average longevities of populations of desert tortoises is crucial to understanding the life history of this species and is necessary to estimate the long-term viability of populations. Populations of desert tortoises west and north of the Colorado River were listed recently as threatened by the United States Fish and Wildlife Service (Federal Register 1990, Vol. 55, No. 63, p. 12178–12191). Even though much work has occurred on this species in the past 15 yr, few data exist for most life-history traits. The estimates of longevity presented here indicate the potential maximum age that desert tortoise reach. In the future, work should focus on determining complete age structures of living populations in various parts of their range. This information will require an intensive effort combining scute-age techniques used here for establishing minimum age along with mark-recapture over a long period of time (see Gibbons and Semlitsch, 1982, and Lovich et al., 1990).

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