Copeia, 1987(4), pp. 974–979

Age-size Relationships of Desert Tortoises (*Gopherus agassizi*) in Southern Nevada

FREDERICK B. TURNER, PHILIP A. MEDICA AND R. BRUCE BURY

We assigned ages of 1–4 yr to 15 desert tortoises originally marked in Rock Valley, Nevada, between 1963 and 1965, at which time their plastron lengths ranged from 47–74 mm. Continued measurements of these tortoises enabled us to estimate mean body sizes of tortoises from 1–26 yr of age. Growth of males and females over this period did not differ significantly. Tortoises grew to plastron lengths of 100 mm in 6–7 yr, to 130 mm in 10–11 yr, to around 150 mm in 13–14 yr and were 215 mm long at estimated ages of 24 yr. Four females 23–24 yr old were X-rayed in 1985; three had clutches of 4–5 eggs. If Rock Valley female tortoises are sexually mature at the same body size as those in eastern San Bernardino County, California, sexual maturity is attained at an age of 17–20 yr.

THE development of life-tables for turtles requires estimates of age-specific fertility and mortality, as well as information as to age of females at sexual maturity (Wilbur, 1975; Tinkle et al., 1981). It is also important to understand variations in these parameters, and how such differences are influenced by changing environmental conditions.

Growth of desert tortoises (*Gopherus agassizi*) has been estimated from measurements of captives maintained over a period of 20+ yr (Miller, 1955; Patterson and Brattstrom, 1972). The relevance of such data to natural populations is questionable because captivity can strongly affect health and growth. For example, Jackson et al. (1976, 1978) reported striking examples of accelerated growth of desert tortoises apparently stimulated by special diets. Conversely, L. Miller (unpubl. notes) observed that two young tortoises hardly grew over periods of 12–18 mo. Legler (1960) stated that "Young box turtles reared in the laboratory grew more slowly than turtles of comparable ages under natural conditions . . . . "

Early growth (ca. 1–10 yr) of desert tortoises occupying three 9 ha enclosures in southern Nevada differed between years. These differences were shown to be related to year-to-year variations in rainfall which, in turn, affected growth of ephemeral plants consumed by tortoises (Medica et al., 1975; Auffenberg and Iverson, 1979). Average annual growth between 1963 and 1973 was about 9 mm, ranging from 2 mm (1972) to around 12 mm (1969). None of the tortoises measured was sexually mature. Based on a general estimate by Woodbury and Hardy (1948) and observations of captive tortoises (Miller, 1955), the age of female desert tortoises at sexual maturity has been assumed to be 15–20 yr. However, this idea has never been tested among wild tortoises. Radiography of female tortoises at Goffs, in eastern San Bernardino County, California, showed that some females begin to lay eggs at carapace lengths of

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TABLE 1. PLASTRON LENGTHS (mm) AND ESTIMATED AGES (IN YEARS) OF 15 DESERT TORTOISES IN ROCK VALLEY, NEVADA (1963–87). Sexes are indicated when known.

	Tortoises															
Age	1 m	2	3 f	4 m	5 m	6 f	7 f	8 f	9	10 m	11 m	12	13 m	14 f	15	Mean plastron length (mm) ± SE
1	49	47														48.0 ± 1.00
2			51	53	54	55										53.3 ± 0.85
3		61		56		65	61	66	66	66	68					63.6 ± 1.40
4					83		68	71	71	80	72	71	71	72	74	73.3 ± 1.46
5				77		83		79	83	87			74		88	80.5 ± 1.93
6					109			86	97					101	97	98.0 ± 3.72
7	108		112	108		112	95	104	113	113			96			106.8 ± 2.35
8	119		115	112	122	116	111	106	126	116				115	119	116.1 ± 1.64
9	123		118	120	130	128	119	107	132	122	120		127	126	126	122.9 ± 1.80
10	134	120	125	129	132	133	122	114	138	130	121	108	128	133	131	126.5 ± 2.11
11			132	140		141	124		144	136	126	115	133	139	134	133.1 ± 2.59
12				146		147		131	147	138	130		138	145	139	140.1 ± 2.20
13	149	137	145		154			136	157				149		142	146.1 ± 2.68
14	152	139	148		160	166	145			150	142					151.9 ± 3.20
15		139	158		165	169	147			151			162	160		158.9 ± 2.91
16	169	139	165	194	167	174	154	159		157	157			164		166.0 ± 3.68
17	176	139	174		170	176	160			162						169.7 ± 2.89
18										167			207	183		185.7 ± 11.6
19	188	145	179		185											184.0 ± 2.65
20		145	190		194	193	177									188.5 ± 3.93
21		148	205			200					204					203.0 ± 1.53
22	209	151	213		213									188		205.8 ± 5.99
23		154		234	220	210	203			206						214.6 ± 5.34
24	216		232		222	213		205		214	221			215		217.3 ± 2.60
25				240		215				217		237	216			225.0 ± 5.54
26											227		216			221.5 ± 5.50

generally we also made regression analyses of data pertaining to the four tortoises of unknown sex in Table 1 (using only the first four measurements for tortoise #2). The mean of the 15 slope coefficients (7.25, SE = 0.24) and the mean of the 15 intercepts (50.1, SE = 2.1) were then the basis of a graphic representation of general growth among these tortoises (Fig. 1). The figure also shows the observed mean sizes of tortoises (±1 SE) at various estimated ages (as in Table 1).

Patterson and Brattstrom (1972) reported percent increases in body sizes of captive tortoises over 5 yr intervals: 71.4% (1–5 yr), 56.7% (5–10 yr), and 33.9% (10–15 yr). Table 1 shows increases of 67.7%, 57.1%, and 25.6% for desert tortoises in Rock Valley over the same age intervals. Patterson and Brattstrom also observed that tortoises showed a rapid growth increase between 15 and 20 yr (41.2%), but this datum was based on growth of a single tortoise. Tortoises in Rock Valley increased an average of only 18.6% between 15 and 20 yr (Table 1). We do not believe that data pertaining to desert tortoises support the idea that growth rate increases after 15 yr of age.

Landers et al. (1982) described an apparent "surge" in growth of gopher tortoises (*G. polyphemus*) in Georgia at carapace lengths of 100–120 mm. Table 1 shows a period of relatively rapid growth of Rock Valley tortoises between the ages of 5 and 8 yr (from around 80–116 mm in PL). Annual growth during this interval averaged around 12 mm. The interpretation of this period of growth is not obvious. In variable environments one must consider the age of the subjects and conditions during the period of increased growth. Thirteen of the 15 tortoises in Table 1 were hatched in 1961 (4), 1962 (5), or 1963 (4), and these individuals were 5–8 yr old between 1966 and 1971. Estimates of net production by Rock Valley annual plants in 1966 and 1968 (Wallace and Romney, 1972:245) were two of the three highest values measured be-

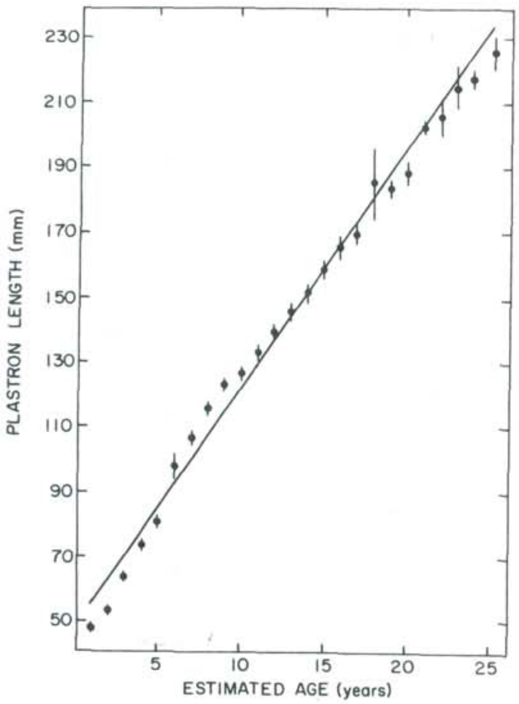

Fig. 1. Relationships between estimated age and body length among 15 desert tortoises in Rock Valley, Nevada. The line is based on means of 15 slopes and 15 intercepts calculated as described in the text. Annual means ±1 SE (Table 1) are also represented.

tween 1964–68 and 1971–76. Production by ephemerals was not measured in 1969 and 1970, but winter rainfall and estimated densities of annual plants were high in these years (Medica et al., 1975: Table 2). Hence, we believe the more rapid growth of tortoises between the ages of 5 and 8 yr reflected unusually good environmental conditions and not some intrinsic process.

Earlier, we estimated a mean growth of about 7.0 mm/yr (SE = 1.8 mm/yr) between 1969 and 1973 (Medica et al., 1975), but the comparisons in Table 1 are not of the same nature as those described previously. The earlier work involved growth of tortoises of different ages during the same annual intervals. Table 1 shows average lengths of tortoises of the same ages during different years. For example, Tortoise #12 hatched in 1959, while Tortoise #5 hatched in 1963. In the first instance, growth between the ages of 3 and 4 yr occurred in 1962 and 1963 while in the latter between 1966 and 1967. Owing to year-to-year variations in growing

Table 2. Results of Radiography of Four Female Desert Tortoises from Rock Valley in mid-May 1985.

Tortoise number	Plastron length (mm) in 1985	Estimated age (yr)	Number of eggs	Estimated age at plastron length of 177 mm
6	210	23	4	17–18
7	203	23	0	20
8	205	24	5	>18
14	215	24	5	17

conditions (as described above), age-specific growth rates may be expected to vary. In spite of this effect, the mean annual increment for years 1–17 in Table 1 (7.6 mm/yr, SE = 0.83) does not differ significantly from that reported for 1969–73 ($t = 0.41$, $P = 0.69$).

Four of the five females in Table 1 were captured and X-rayed in 1985 (Table 2). The absence of eggs in the radiograph of #7 does not necessarily indicate that this individual was sexually immature because it could have already laid eggs earlier in the season. These females are all larger than reproductively active tortoises at Goffs, California. Seven of 26 tortoises X-rayed at Goffs in 1984 were 189–195 mm in carapace length and all produced eggs (Turner et al., 1986). If we assume that Rock Valley females mature at the same size as Goffs females, we can estimate the ages of the former at maturity from Table 1. A PL of 177 mm is roughly equivalent to a carapace length of 190 mm (Medica et al., 1975:640), and Table 2 gives estimated ages of four Rock Valley females when this PL was attained.

In our earlier analysis of tortoise growth between 1969 and 1973, we showed that annual growth increments were positively correlated with winter rainfall (Medica et al., 1975:642). Winter rainfall during this 5 yr interval ranged from 41–209 mm, with a mean of 118 mm. Rainfall records from Rock Valley and Jackass Flats suggest that mean winter rainfall between 1959 and 1963 (the interval during which the tortoises in Table 1 hatched) was less than 118 mm. Early growth may have been correspondingly retarded. For this reason we believe that if some of our initial age estimates are wrong, they are most likely to be too young. In our view, however, the age estimates in Table 1 are not in error by more than 1 yr.

Gibbons et al. (1981) and Congdon and Gibbons (1983) have pointed out that female *Pseudemys scripta* reproduce at body sizes ranging from around 150 to >325 mm in PL. From long-term studies of this species in South Carolina, Gibbons et al. (1981) were able to show that, although size at sexual maturity varied between locales, all females matured at about the same age. These authors suggested that the differences were associated with varying environmental conditions (e.g., water temperature and resource availability).

Because of differences in yearly net primary production and growing seasons in different parts of the range of the tortoise, tortoise growth may be faster in some areas than others. Rock Valley is the least productive of the four major desert sites studied during the U.S. International Biological Program (Norton, 1974; Webb et al., 1983). More importantly, Rock Valley ranks at the low end of the scale of productivity in Mojave Desert communities. The age-size relationships adduced in Table 1 need to be considered in this light. We estimated the age of Rock Valley tortoises at sexual maturity (Table 2) assuming relationships between age, size, and maturity to be the same in Rock Valley, Nevada, as at Goffs, California. The foregoing discussion shows that this may not be true.

We believe that the tortoise growth data from Rock Valley begin to unravel an important aspect of the population dynamics of this species. No other site has been studied over a period of 20 yr. Two avenues for further work are clearly indicated. The program of radiography of female tortoises described by Turner et al. (1986) needs to be extended to other regions. This technique can be used to establish the minimum body size of females at sexual maturity. At the same time, we need to begin analyses of growth rates among individuals of other populations so as to establish age-size relationships similar to those presented here.

Acknowledgments

We are particularly grateful to J. R. Lannom, Jr., who initiated the procedure of marking and measuring tortoises in 1963, as well as to G. A. Hoddenbach and others who worked in Rock Valley for many seasons. P. S. Corn and D. Germano assisted with the field work in 1985. D. C. Randall carried out the statistical analyses. This work was supported by Contract DE-AC03-76-SF00012 between the U.S. Department of Energy and the University of California and the International Biological Program/Desert Biome (National Science Foundation Grant BG32139). We acknowledge the indispensable support of the Civil Effects Test Operations Office at the Nevada Test Site.

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(FBT) LABORATORY OF BIOMEDICAL AND ENVIRONMENTAL SCIENCES, UNIVERSITY OF CALIFORNIA, LOS ANGELES, CALIFORNIA 90024; (PAM) SECTION OF HERPETOLOGY, NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY, LOS ANGELES, CALIFORNIA 90007; (RBB) NATIONAL ECOLOGY CENTER, U.S. FISH AND WILDLIFE SERVICE, 1300 BLUE SPRUCE DRIVE, FORT COLLINS, COLORADO 80524. Accepted 13 Dec. 1986.