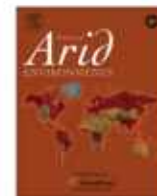




Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Longevity and growth strategies of the desert tortoise (*Gopherus agassizii*) in two American deserts

A.J. Curtin^{a,*}, G.R. Zug^b, J.R. Spotila^a^aDepartment of Bioscience and Biotechnology, Drexel University, 3141 Chestnut Street, Philadelphia, PA 19104, USA^bDepartment of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, PO Box 37012, Washington DC 20013-7012, USA

ARTICLE INFO

Article history:

Received 28 May 2008

Received in revised form

2 September 2008

Accepted 27 November 2008

Available online xxx

Keywords:

Age

Life history

Sexual maturity

Skeletochronology

Southwestern United States

Testudines

ABSTRACT

The desert tortoise occurs in two strikingly different desert regimes in the southwestern United States. In the Mojave Desert, rainfall is more irregular and resources are more limited than in the Sonoran Desert. We examined the age structure of tortoise populations from these two deserts to determine whether the difference in resource availability has driven an evolutionary divergence in life history strategies. Age and growth rates strongly reflect the ecological adaptation of the two populations. The oldest Sonoran males reached 54 years, compared to only 43 years in females. The oldest West Mojave (WM) males reached 56 years, compared to only 27 years in females. WM tortoises grew faster than Sonoran ones, and females reached sexual maturity at earlier ages (~17–19 years) than Sonoran females (~22–26 years). These traits and the higher rate of clutch production in the WM population are likely the evolutionary adaptation for low juvenile survivorship and a significantly shorter life span. Frequent droughts in the WM Desert and the lowest annual rainfall area within the range of the desert tortoise cause chronic physiological stress, likely annually, and are proposed as a major selection force producing contrasting life-history strategies.

© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

Tortoises are portrayed regularly as animals of exceedingly long lives. How long an animal lives fascinates scientists and laymen alike; however, for biologists, an animal's longevity has evolutionary importance in the context of an individual's reproductive potential and its role in population dynamics. Longevity is critical relative to an animal's reproductive life span, that is, the duration of the reproductive interval from first reproduction (attainment of sexual maturity) to the last reproductive act. For tortoises, an individual's reproductive longevity can extend for decades because evidence suggests that turtles lack reproductive senescence (Girondot and Garcia, 1999).

Some individual tortoises do live more than 100 years (Chambers, 2004), but these individuals are captive animals living in protected environments. Is longevity as great in wild and particularly in stressful environments? Desert tortoises, *Gopherus agassizii*,

of the American Southwest are ideal for examining this question. Germano (1992) examined this question by estimating age of four regional populations of desert tortoise with the scute-annulus technique. His sample of 574 tortoises encompassed the entire range of the desert tortoise and allowed him to estimate longevity for the four major biomes (western Mojave Desert, eastern Mojave Desert, Sinaloan thorn-scrub, and Sonoran Desert). With a single exception, he discovered only one individual (eastern Mojave) older than 40 years. In his cautious reporting, he defined longevity as the minimum age of the oldest individuals: 32 years, western Mojave; 35 years, Sonoran; none, Sinaloan scrub. He further noted that the relative portion of adults over 25 years varied greatly: 11% eastern Mojave; 5% western Mojave, 29% Sonoran. These data reflect differences in life span, resulting in differences in age structure of the population. He provided estimates of age of maturity subsequently (Germano, 1994a), although not explicitly but sufficient to allow estimates of reproductive life span (i.e., longevity minus maturity): 25 years, 15 years, and 20 years, respectively. Thus, both longevity and reproductive life span for these populations suggest life-history adaptations, possibly driven by differences in the climatic regime of the three desert areas. Genetic history might also play a role in the reported differences. Using restriction site analysis, Lamb et al. (1989) resolved five different mtDNA genotypes among 22 populations of desert

* Corresponding author. present address: Academic Resource Center, Duke University, Box 90694, Durham, NC 27708, USA. Tel.: +1 919 684 4980; fax: +1 919 684 8934.

E-mail addresses: amanda.curtin@duke.edu (A.J. Curtin), zuggs@si.edu (G.R. Zug), spotiljr@drexel.edu (J.R. Spotila).

tortoises and found three well-defined genetic assemblages: a Mojave assemblage, Sonoran assemblage and Sinaloan assemblage. The genetic distances (5.1–5.6%) observed between Mojave and Sonoran genotypes of desert tortoises are significantly higher than distance values reported for any other turtles species (Lamb and McLuckie, 2002; Walker and Avise, 1998). Consequently, depending on molecular clock timing, the Mojave and Sonoran mtDNA lineages appear to have diverged some 5 or 6 million years ago (Lamb and Lydeard, 1994; Lamb and McLuckie, 2002).

Regardless of the timing of the divergence of the Mojave and Sonoran Desert populations, the genetic distance (evolutionary history) between these two populations is great (McCord, 2002). The Mojave Desert is the youngest biotic province in North America (Van Devender, 2002), and the Mojave population is younger evolutionarily than Sonoran tortoises. Moreover, within the Mojave Desert, West Mojave tortoises are potentially younger than their eastern cousins (Morafka and Berry, 2002). We, therefore, wished to examine age and growth strategies within and between West Mojave and Sonoran Desert tortoise populations because they represent the eastern and western extremes of morphology, behavior, and ecology of desert tortoises (Morafka and Berry, 2002; Van Devender, 2002). Additionally, the accuracy of Germano's scute aging protocol has been questioned (Wilson et al., 2003), so an independent aging technique (skeletochronology) offers an opportunity to test Germano's results and interpretation.

2. Materials and methods

2.1. Materials

Our sample consisted of salvaged carcasses of 72 free-living desert tortoises (24 juveniles, 28 adult females, 17 adult males, 3 sex unknown) from the Sonoran Desert (Maricopa, Mohave, Yavapai, Pinal and Pima Co., Arizona) and 69 carcasses (13 adult females, 30 adult males, 22 juveniles, 4 sex unknown) from the West Mojave Desert (San Bernardino Co., California); hereafter, Mojave equals West Mojave (in Sections 2 and 3). Identification of sex and maturity was made by Arizona Game and Fish Department staff when they collected the carcasses between 1990 and 1997. Similarly, these data were assigned by Californian wildlife staff when salvaging carcasses. The West Mojave Desert tortoise samples were collected between 1991 and 1995 near US highway 58 as part of a long term study on the effectiveness of fences and culverts for protecting desert tortoises along highways (see Boarman, 1992; Sazaki et al., 1995). Mojave tortoises are listed as threatened (US Fish and Wildlife Service, 1994) due to downward trends in population size (especially in the western populations). The use of salvaged carcasses of wild (free-living) individuals allows us to estimate natural age by skeletochronology without disturbing or harming any individuals of this threatened species.

2.2. Skeletochronology

Tortoises, like other ectothermic tetrapods, display a cyclical pattern of growth. Cyclic skeletal growth produces successive bony layers in association with an internal (genetically based) rhythm synchronized and reinforced by seasonal cycles (Castanet et al., 1993; Meunier et al., 1979), hence the number of skeletal growth layers yields an estimate of an individual's age. Unlike tree rings, the bony growth layers do not persist throughout a turtle's life. As the turtle grows, endosteal resorption at the medullary cavity margin removes the earliest growth layers. A simple count of the visible growth layers, thus, yields fewer layers than were actually deposited and an underestimate of the actual number of growth

cycles of an individual. We assume that each bony growth layer (cycle) equals one year and, elsewhere (Curtin et al., 2008) we demonstrated the reliability of this assumption with known-aged desert tortoises.

Skeletochronology in turtles must incorporate resorption in the estimation of each individual's age. Either the use of known-age individuals or a back-calculation method (Castanet and Smirina, 1990) allows a determination of the rate of periosteal bone resorption. In an initial study, we sectioned all appendicular skeletal elements, together with vertebrae and shell elements (gular, marginal, neural and plastral elements) to determine which elements showed the greatest number of growth marks (GMs). The humerus, femur, ilium, and scapula contain the most "resident" GMs and were the bones we used for our analyses. Additionally, we recorded longitudinal length (LL), proximal width (PW), midshaft width (MW) and distal width (DW) of each bone used for age estimation, and if the carcass was intact, we recorded also carapace length (CL), carapace width (CW) and plastron length (PL).

We fixed, decalcified, and processed bones by standard histological protocol. All bones were embedded in Paraplast Plus®, cut in 20 µm cross sections through the midshaft area of each bone using a rotary microtome, and stained with hematoxylin and eosin. We measured all growth layer diameters, outside diameters, and resorption cores along the longest axis of each element with a stage micrometer and transmitting light microscope, and counted the number of entire and partial growth layers.

Comparisons of skeletochronology age estimates (determined by two protocols) to a sample of known-aged desert tortoises from Rock Valley, Nevada (Curtin et al., 2008) indicated that the correction factor method (CF) provided the most accurate juvenile age estimates and the growth-layer ranking protocol (Rank) the most accurate for estimating the age of adults. Both sets of age estimates are examined below.

Both protocols rest on the basic assumption that each successive growth layer represents one year in the life of a desert tortoise. The ranking protocol (Zug, 1990) uses three data items (resorption core diameter, the set of sequential diameters of the complete growth layers (GLs), external diameter of bone at death) to obtain an age estimate of each individual. The first step is to order individuals by the increasing diameters of their individual resorption cores. The rows created by this ordering consist of sequential growth layer diameters from smallest complete layer to the outside diameter. These sequential GL diameters yield columns of successive increasing diameters, and the innermost diameter for each turtle is assigned to the column to which its diameter most closely matches those diameters of preceding turtles. The assignment of innermost diameter fixes the sequential assignment of column position of all succeeding diameters; no column is skipped in the sequence of diameters. This ranking protocol yields a table with a stepwise appearance due to the increasing size of the innermost diameter of successive individuals. Each column represents one year, and the position of the outer diameter denotes the age at death of an individual.

In the correction factor protocol (Parham and Zug, 1998), an estimate of a tortoise's age derives from the number of growth layers (diameters) observed in the outer region of the bone section plus an estimate of the number of growth layers lost by resorption as the center of bone is remodeled. The latter, unobservable component is estimated as $(D - D_H)/CF$, where D is the diameter of the resorption core, D_H is the diameter of a hatchling's bone (before the beginning of increment formation), and CF is the correction factor. The correction factor is a constant "ageing rate" (years mm^{-1}) assumed to apply to the resorption core and calculated as the mean slope of the successive bone-growth diameters in a sample of the smaller individual turtles.

2.3. Statistical analysis

Because the Arizona sample consisted of multiple populations, we compared all size measurements and age estimations to determine whether differences existed among the populations. We used one-way analysis of variance (ANOVA) tests with a Tukey post hoc test and analysis of covariance (ANCOVA) to examine differences within and between samples of the two desert populations. We conducted least squares regression analyses and ANOVAs to compare shell and bone measurements between the Sonoran and West Mojave population samples. We compared the various shell and bone measurements and age estimates from within and between both groups to discern sexual dimorphism using ANOVA. All statistical analyses were performed using the SYSTAT (Version 9.0) statistical package; we accepted statistical significance as $p < 0.05$.

3. Results

3.1. Body size

A comparison of carapace length (CL), carapace width (CW) and plastron length (PL) between the various Sonoran Desert populations shows no significant differences between localities for any group (adult males, adult females and juveniles). In both the Sonoran and Mojave sample, these three metrics are strongly correlated, for example, Sonoran female CL and CW $r^2 = 0.74$ ($n = 28$), male CL and PL $r^2 = 0.90$ ($n = 17$). Sonoran adult females and males have no dimorphism in the three shell metrics (Fig. 1; CL: $r^2 = 0.06$, $F_{1,33} = 1.95$, $p = 0.17$; CW: $r^2 = 0.76$, $F_{2,28} = 0.23$, $p = 0.64$; PL: $r^2 = 0.90$, $F_{2,23} = 0.63$, $p = 0.44$). In contrast, the Mojave population shows a sexual dimorphism in CL ($r^2 = 0.20$, $F_{1,33} = 8.24$, $p = 0.007$; Fig. 1), but not in CW ($r^2 = 0.90$, $F_{2,23} = 0.56$, $p = 0.46$) or PL ($r^2 = 0.92$, $F_{2,22} = 0.10$, $p = 0.76$) when the effect of size is removed.

Sonoran females are significantly larger than Mojave females in CL (means 232.12 ± 19.50 , 214.50 ± 20.70 mm CL, respectively; $r^2 = 0.16$, $F_{1,33} = 6.46$, $p = 0.02$; Fig. 1). Mojave females, however, are significantly wider than Sonoran females ($r^2 = 0.73$, $F_{2,25} = 6.05$, $p = 0.02$; Fig. 1). There is no difference in PL between Sonoran and

Mojave females ($r^2 = 0.79$, $F_{2,26} = 0.02$, $p = 0.88$). Mojave and Sonoran males have similar body length (means 244.69 ± 35.28 , 243.43 ± 28.29 mm CL, respectively; $r^2 = 0.01$, $F_{1,33} = 0.01$, $p = 0.19$; PL $F_{1,31} = 3.46$, $p = 0.07$). As in females, Mojave males are significantly wider than Sonoran males ($r^2 = 0.89$, $F_{2,26} = 11.26$, $p = 0.002$; Fig. 1). There is no significant difference in male PL between the two areas ($r^2 = 0.88$, $F_{2,26} = 3.64$, $p = 0.07$). Juveniles have similar shell metrics between the two deserts, lacking significance in all tests (CL: $r^2 = 0.01$, $F_{1,42} = 0.44$, $p = 0.51$; CW: $r^2 = 0.97$, $F_{2,32} = 0.09$, $p = 0.77$; PL: $r^2 = 0.99$, $F_{2,30} = 0.56$, $p = 0.46$).

3.2. Resorption core diameters

Resorption core diameters (RCDs) are crucial for the estimation of an individual's age. In Sonoran tortoises, the RCDs for adult males, females or juveniles at all localities are nearly identical. There is no significant difference in RCDs, irrespective of bone, between Sonoran males and females (humerus: $r^2 = 0.06$, $F_{1,21} = 1.43$, $p = 0.24$; ilium: $r^2 = 0.05$, $F_{1,33} = 1.76$, $p = 0.19$; scapula: $r^2 = 0.02$, $F_{1,10} = 0.19$, $p = 0.67$). Similarly, Mojave males and females show no sexual dimorphism in RCDs (humerus: $r^2 = 0.06$, $F_{1,7} = 0.42$, $p = 0.54$; ilium: $r^2 = 0.04$, $F_{1,25} = 0.94$, $p = 0.34$; scapula: $r^2 = 0.22$, $F_{1,13} = 2.74$, $p = 0.13$). Comparison between the two deserts reveals that Sonoran females have significantly larger ilia RCDs (Fig. 2A) than Mojave females ($r^2 = 0.58$, $F_{2,19} = 14.46$, $p = 0.001$). Sonoran males have significantly larger humeri ($r^2 = 0.66$, $F_{2,8} = 8.14$, $p = 0.02$) and ilia RCDs ($r^2 = 0.20$, $F_{2,29} = 6.41$, $p = 0.02$) than Mojave males (Fig. 3B). The juveniles from the two desert populations show no significant difference in RCDs (humerus: $r^2 = 0.12$, $F_{1,26} = 3.37$, $p = 0.08$; ilium: $r^2 = 0.02$, $F_{1,21} = 0.33$, $p = 0.57$; scapula: $r^2 = 0.09$, $F_{1,15} = 1.46$, $p = 0.25$).

We combined adults and juveniles to gain insight into population trends. All three bones in both deserts display a close relationship between body size and RCDs (Table 1).

3.3. Age and longevity

The ilium and humerus consistently have the most periosteal growth layers and usually yield similar age estimates. In

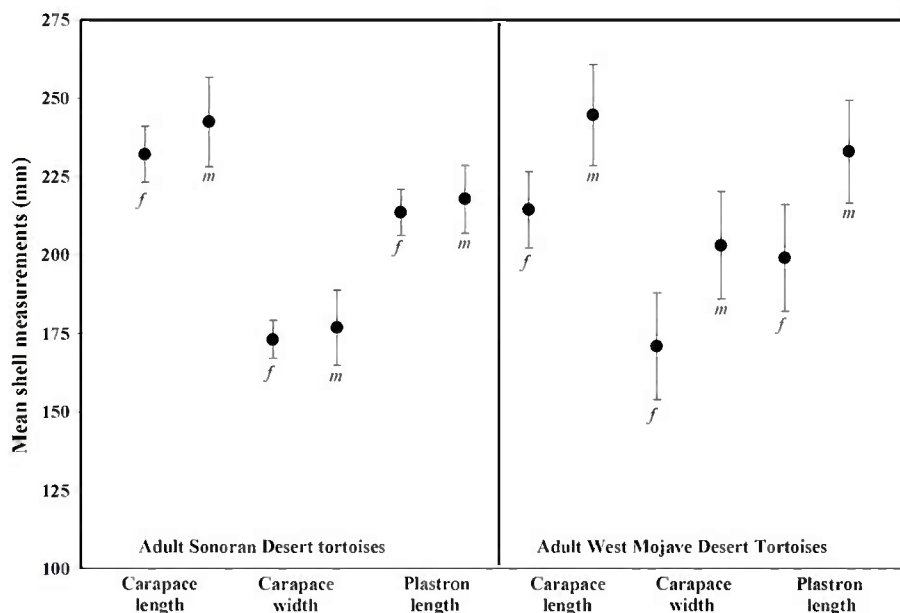


Fig. 1. Mean shell measurements of adult male and female *Gopherus agassizii* from the Sonoran Desert, Arizona and the West Mojave Desert, California. Error bars represent 95% confidence intervals; m, males; f, females.

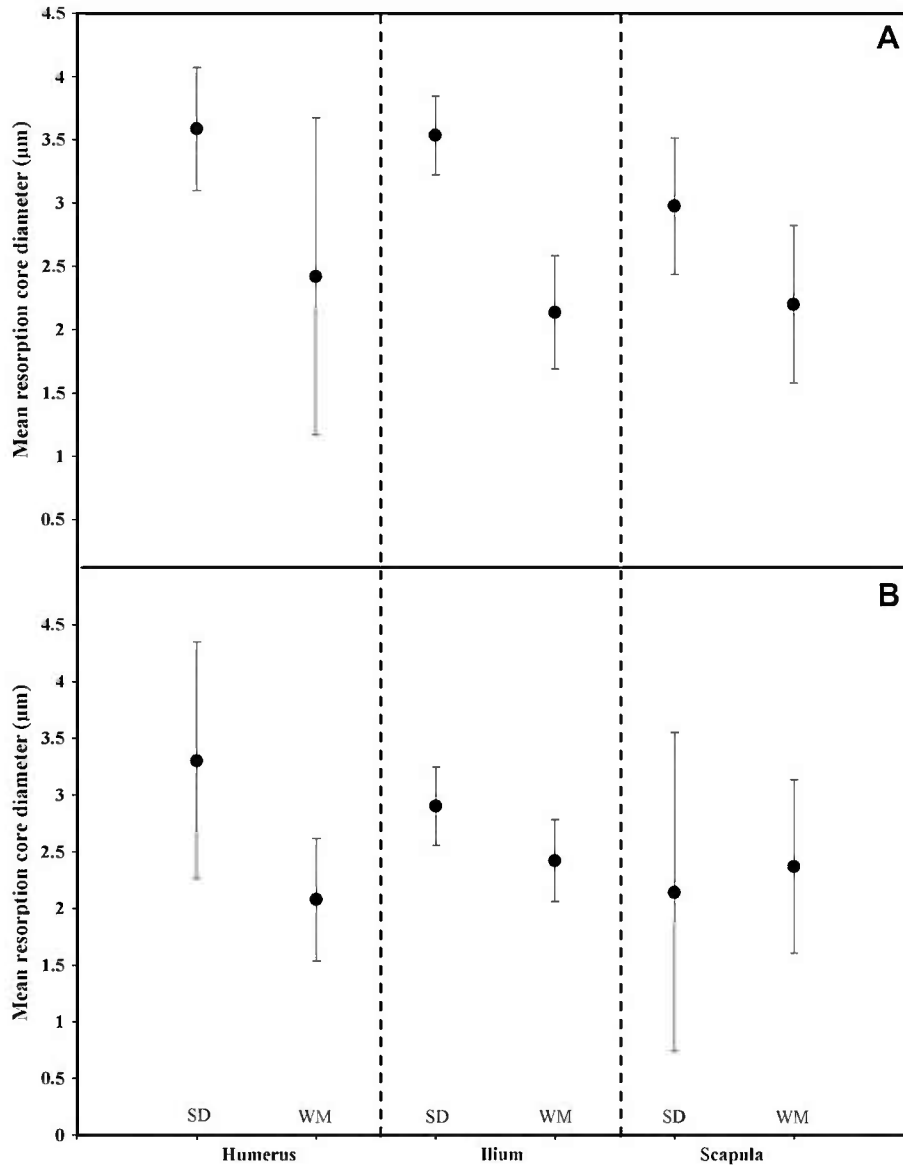


Fig. 2. Mean resorption core diameters for adult (A) female and (B) male *Gopherus agassizii* from the Sonoran Desert (SD), Arizona and the West Mojave (WM) Desert, California. Error bars represent 95% confidence intervals.

juveniles, Rank and CF give similar age estimates (± 1 year) for the Sonoran (30–120 mm CL; $r^2 = 0.01$, $F_{1,34} = 0.56$, $p = 0.46$) and Mojave (40–110 mm CL; $r^2 = 0.003$, $F_{1,21} = 0.07$, $p = 0.70$) samples. Beyond this body size, variation between the two methods increases significantly, especially beyond the reported minimum size at sexual maturity (around 180 mm CL in both Sonoran and Mojave tortoises (Medica et al., 1975; Germano, 1994b)). The Rank age estimates are the most accurate ones for adults, i.e., >180 mm CL, based on the known-age validation study (Curtin et al., 2008).

In adults, regional variation is considerable in the relationship between age and size (Fig. 3). The oldest Sonoran males, estimated at 47–54 years old, range from 241 to 266 mm CL. The oldest Sonoran females, 42–43 years, are 223–239 mm CL. The oldest Mojave male is 56 years old and 262 mm CL. The second oldest male is significantly larger (280 mm CL) but only 36 years. The oldest Mojave female is only 27 years, yet at 235 mm CL, is at the upper end of the size range of the oldest Sonoran females. A much smaller female (198 mm CL) is estimated as 26 years.

In the Sonoran sample, the age estimates of the different localities are similar for adult males, females, and juveniles. The absence of statistical difference in adult males and females from different localities, allow the combination of each sex into a single Sonoran sample and to test for dimorphism in the average age of the two sexes. No dimorphism exists within the Sonoran adults ($r^2 = 0.39$, $F_{2,33} = 1.25$, $p = 0.27$; Fig. 4). Mojave adults derive from the same general area, and they similarly display no dimorphism of female-male age estimates ($r^2 = 0.33$, $F_{2,30} = 0.42$, $p = 0.52$; Fig. 4).

Sonoran tortoises reach significantly older ages than Mojave tortoises ($r^2 = 0.55$, $F_{2,66} = 38.56$, $p < 0.001$; Fig. 4). Sonoran females are significantly older ages than Mojave females, when the effect of size is removed (means 32.82 ± 1.4 , 20.05 ± 1.86 years, respectively; $r^2 = 0.61$, $F_{2,30} = 22.38$, $p < 0.001$; Fig. 4). Similarly, Sonoran males reach significantly older ages than Mojave males with size as the covariate (means 37.03 ± 2.47 , 24.41 ± 1.77 years, respectively; $r^2 = 0.53$, $F_{2,33} = 18.26$, $p < 0.001$; Fig. 4).

Mojave tortoises grow faster than Sonoran tortoises and attain adult size (>180 mm CL) at younger ages (Figs. 3 and 4). Hence,

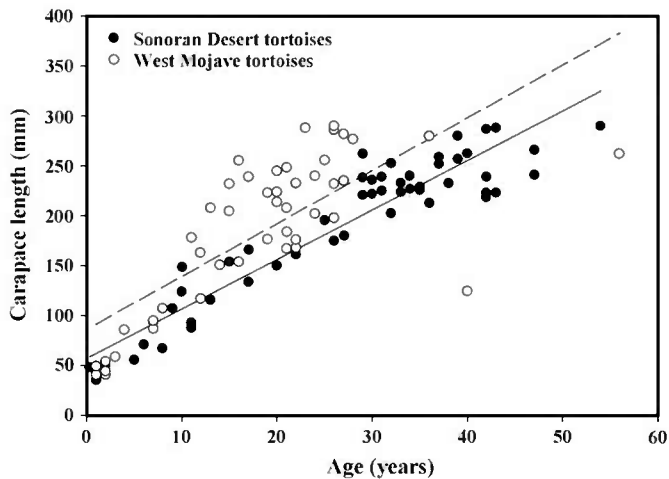


Fig. 3. Relationship of skeletochronology age estimates to carapace length for *Gopherus agassizii* from the Sonoran Desert, Arizona (solid circles) and the West Mojave Desert, California (open circles).

Sonoran tortoises of similar sizes to Mojave ones are older in age and are also older at death (Fig. 3). A comparison of the size/age relationships between Sonoran and Mojave populations, where the effect of age is removed, shows that Mojave tortoises grow significantly faster than Sonoran tortoises ($r^2 = 0.72$, $F_{2,105} = 16.04$, $p < 0.001$). The adjusted least squares mean for Mojave sample is 200.6 mm CL (± 6.0 SE) and for Sonoran tortoises 168.2 mm CL (± 5.8 SE) at the mean age of 21.8 years.

Males not only live longer but are also larger at similar ages than females. There is a significant relationship between age and size for all adults (Sonoran females: $r^2 = 0.23$, $F_{1,20} = 6.00$, $p = 0.02$; Sonoran males: $r^2 = 0.46$, $F_{1,12} = 10.01$, $p = 0.008$; Mojave females: $r^2 = 0.51$, $F_{1,9} = 9.36$, $p = 0.01$; Mojave males: $r^2 = 0.25$, $F_{1,20} = 6.74$, $p = 0.02$). Comparison of CL between adults, absent the effect of age, shows no significant difference between the sexes for either Sonoran ($r^2 = 0.37$, $F_{2,33} = 0.13$, $p = 0.72$) or Mojave tortoises ($r^2 = 0.34$, $F_{2,30} = 0.84$, $p = 0.37$).

The distribution of ages among the Sonoran and Mojave samples is highlighted by size classes. To obtain a better idea of size/age relationships, we compared variance in age between the two groups using ANOVA (Fig. 5). We excluded a 125 mm CL Mojave tortoise from the analysis; although classified as a juvenile based on size, its estimated age is 40 years and represents an extreme outlier in its size class (101–150 mm CL). Sonoran tortoises are significantly older than Mojave tortoises within the 51–100 mm CL ($r^2 = 0.53$,

$F_{1,15} = 16.68$, $p = 0.001$), 201–250 mm CL ($r^2 = 0.72$, $F_{1,35} = 90.63$, $p < 0.001$) and 251–300 ($r^2 = 0.25$, $F_{1,22} = 7.40$, $p = 0.01$) mm CL size classes (Fig. 5).

3.4. Age at sexual maturity

The minimum size at sexual maturity allows us to associate our age estimates to age at sexual maturity. The minimum carapace length of a sexually mature individual is 176 mm CL for Mojave tortoises (Germano, 1994b) and 180 mm CL for Sonoran tortoises (Germano, 1994b; Averill-Murray and Averill-Murray, 2005). In the Sonoran sample, three individuals of 175, 180 and 195.5 mm CL, show ages of 26, 27 and 25 years, respectively (mean age 26 years). In comparison, we extrapolated age at maturity (~ 180 mm CL) from the age versus size regression line, and obtained an estimate of around 25 years (Fig. 3), similar to that obtained from the actual data. The Mojave (WM) sample has four individuals (168, 176, 177 and 178 mm CL) around the minimum sexual maturity size and their estimated ages are 17, 22, 19 and 11 years (mean 17 years). When we extrapolated age at maturity from the age/size regression line, we obtained a similar estimate of around 17 years (Fig. 3). Even with Mojave individuals of similar size to Sonoran tortoises, the estimated ages of the Mojave tortoises average lower (mean 18.7 years for 176–195 mm CL tortoises).

4. Discussion

4.1. Body size

We found no significant difference in adult or juvenile body size or bone metrics between the various Sonoran Desert localities. Our small sample sizes for the different populations might prevent the recognition of populational size differentiation. In previous studies at two of the localities from which we received samples, namely Little Shipp Wash (LSW, Yavapai) and Eagletail Mountains (EM, Maricopa), those studies found sexual dimorphism of body size. Averill-Murray (2002) and Murray and Klug (1996) noted that males reached larger maximum sizes than females (LSW: 299 mm, 267 mm CL; EM: 288, 268 mm CL; males, females, respectively). At the Granite Hill sites (Pinal County), they reported that the two sexes attained a similar maximum size (around 244 mm CL) and were significantly smaller than the preceding two populations (Murray and Klug, 1996). Averill-Murray (2002) found that females reached the same or larger CL than males at three plots south of the Gila River (of which we had carcasses from San Pedro Valley and West Silver Bell Mountains). These conflicting data on sexual dimorphism in the different populations suggest either sampling problems or populations of different age structure. Our age and size data cannot resolve the conflicting results.

Our West Mojave sample shows males larger than females (CL; Fig. 1), matching the results of Germano (1994a). In both sexes, CL and bone lengths are highly correlated. Sonoran females reached significantly larger sizes (CL) than Mojave females, but this difference was not observed in male body size comparisons. Whereas the mean CLs of our samples match those of (Germano, 1994a, Table 2) for West Mojave males and Sonoran females, our Mojave females have a strikingly smaller mean and the Sonoran males a larger mean. We interpret these differences as sampling error from smaller samples.

The striking size dimorphism between Mojave females and males possibly results from females channeling all or most of their non-maintenance energy into reproductive effort, a physiological trait directly influenced by food (quantity and quality) availability (Peterson, 1996). Mean annual rainfall in the Arizona Upland subdivision of the Sonoran Desert (where most of our sample

Table 1

Regression statistics of carapace length (CL) versus resorption core diameter (RCD) for Sonoran Desert and West Mojave Desert tortoises.

CL vs RCD	F	p	r ²
Humerus			
Sonoran Desert	92.553	<0.001	0.77
West Mojave Desert	50.503	<0.001	0.71
Ilium			
Sonoran Desert	135.045	<0.001	0.77
West Mojave Desert	10.682	0.003	0.27
Femur			
Sonoran Desert	128.824	<0.001	0.90
West Mojave Desert	–	–	–
Scapula			
Sonoran Desert	34.421	<0.001	0.62
West Mojave Desert	27.848	<0.001	0.70

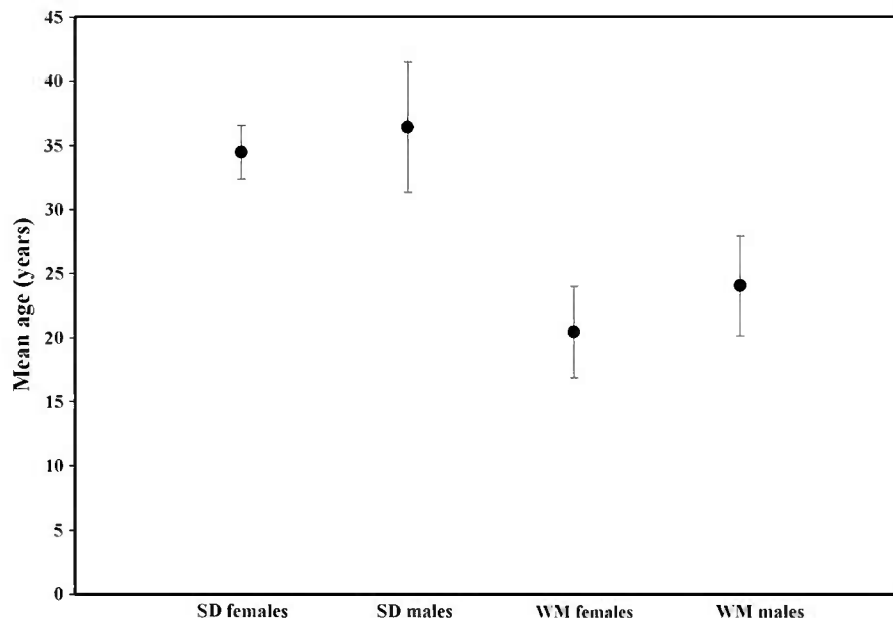


Fig. 4. Mean ranking protocol age estimates for adult *Gopherus agassizii* from the Sonoran Desert (SD), Arizona and the West Mojave (WM) Desert, California. Error bars represent 95% confidence intervals.

derived) is much more reliable than rainfall in the Mojave Desert (Averill-Murray, 2002). The Sonoran Desert receives about 85–300 mm more annual rainfall than the Mojave Desert, and the western portion of the latter receives even less annual rain (~50–75 mm) than the eastern portion (Wallis et al., 1999). Because rainfall affects the availability of food and its digestion (Ofstedal, 2002), rainfall will affect growth and reproductive effort. This association is demonstrated by the correlation of geographic

variation in rainfall with the variation in reproductive traits of *G. agassizii* (Wallis et al., 1999). These researchers observed that East Mojave females lay eggs at smaller body sizes, lay proportionally smaller eggs, and lay more eggs than West Mojave females. Sonoran tortoises often invest their entire annual reproductive output in a single clutch laid prior to more predictable rainfall (Averill-Murray et al., 2002a). Rainfall seems to influence mean clutch size and the proportion of females reproducing each year

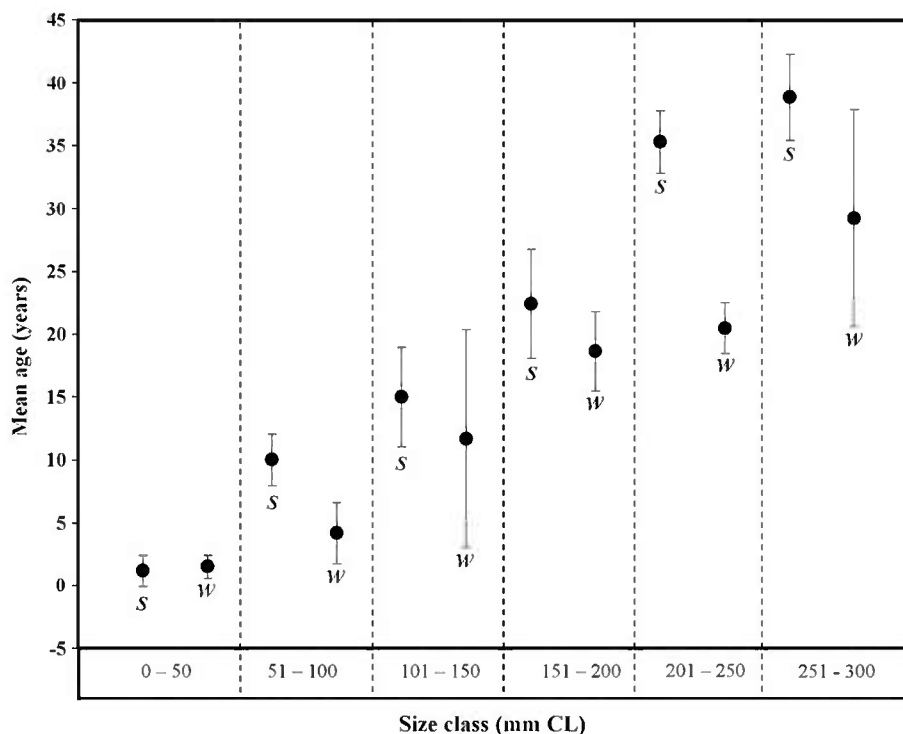


Fig. 5. Mean age within size classes of *Gopherus agassizii* from the Sonoran Desert (SD), Arizona and the West Mojave Desert (WM), California. Error bars represent 95% confidence intervals; s, Sonoran Desert; w, West Mojave Desert.

(Averill-Murray et al., 2002b). In dry years, smaller females are less likely to lay eggs than larger ones. Sonoran females lay on average only one clutch per year (Averill-Murray et al., 2002b), and in drought periods, they often do not reproduce. Wirt and Holm (1997) reported that only two of the six females they studied in the Maricopa Mountains in 1994 laid eggs after almost 10 years of drought, whereas all seven female tortoises under observation laid eggs at a nearby site, which apparently was less influenced by drought. The average annual egg-laying date does not appear to be directly related to recent rainfall in Sonoran tortoises (Averill-Murray et al., 2002a). Rainfall, however, greatly influences Mojave tortoise reproduction, and Mojave females can lay as many as three clutches in a year (although the average is 1–2 clutches; Wallis et al., 1999; Averill-Murray, 2002). The energy investment of a single clutch may allow Sonoran females to invest more energy into body growth than West Mojave females (Wallis et al., 1999). Additionally, annual resource availability appears to be more consistent in the Sonoran Desert (Van Devender et al., 2002). In contrast, West Mojave females generally produce more than one clutch each year, even during periods of drought (Turner et al., 1986; Wallis et al., 1999). The physiological stress of low food resources constrains the amount of energy available for growth. In addition, resources available during egg development would generally affect the health and energy input available to female desert tortoises. Annual field metabolic rate (FMR) of female desert tortoises has been positively correlated with the number of eggs laid (Henen, 1997), which indicates that energy expenditures associated with reproduction (e.g. digging nests, producing eggs and increasing foraging effort to gather extra nutrients for producing eggs) are substantial (Henen et al., 1998). Droughts of 18 months or longer occur regularly in the Mojave Desert (Oftedal, 2002). Absence of rain precludes germination of annuals and re-growth of perennials. At these times, the desert is nearly devoid of food for tortoises, except for some of the smaller, less armored cacti that tortoises can eat and whatever non-woody senescent material that has not disintegrated or blown away, like dried grasses (Oftedal, 2002). In years of low winter rainfall, foraging choices are limited by the small number of plant species that germinate and grow, not to mention that many of them are introduced weedy species (Oftedal, 2002).

4.2. Resorption core diameters

Resorption core diameter (RCD) gives an indication of bone remodeling, which involves the removal of primary (first bone deposited) bone layers and, thus, the early growth layers. Sexual dimorphism in RCD is not evident in either sample. A comparison of adults between the two samples reveals that Sonoran females had larger RCDs than West Mojave females (Fig. 2), and Sonoran males had larger humeral and ilial RCDs than West Mojave males (Fig. 2). There was an association between body size and RCD for all bones in both groups. Sonoran tortoises displayed larger RCDs at similar carapace lengths than West Mojave tortoises. Resorption core diameters include not only the medullary cavity area, but also any secondary (endosteal) bone deposited in the area of resorption. Larger RCDs indicates higher rates of bone removal and, in some instances, higher rates of secondary bone deposition, usually associated with intracortical remodeling (Castanet and Smirina, 1990). Sonoran tortoises generally had a greater rate of endosteal remodeling than West Mojave tortoises, especially since juveniles start off with similar RCDs at similar sizes.

Bone was originally seen as a temporary store of calcium and phosphates that remodeling then released back into circulation. However, as Currey (2003) states, bone is being resorbed and deposited at the same time, almost contiguously, so any advantage

to the body as a whole must be small. It is now apparent that other processes, like mechanical competence, changing the grain of bone as an adaptation to muscle insertion, or the replacement of dead cells, are more important (Currey, 2003). Non-mechanical factors also need to be taken into account. For example in Nile monitors (*Varanus niloticus*), bone in juvenile males and females share the same mechanical properties and density, but upon sexual maturity the endosteal cavity of females enlarges with each subsequent egg-laying cycle (de Buffrénil and Francillon-Viellet, 2001). Bone lost while producing eggs is not fully regained before the next egg-laying period. Such differential bone resorption for egg-shell development would explain the sexual dimorphism in RCDs in desert tortoises due to a female's need for extra calcium and phosphates for egg-shell development, but such an explanation is not necessary. A similar explanation for the differences in RCD size between the Mojave and Sonoran samples is contraindicated because with the greater number of clutches produced by the Mojave sample, they should have the larger RCDs. Further, if increased remodeling promoted ion release due to nutrient deficiencies (resulting from a diet of less nutritious exotic species), we would again expect the Mojave sample to have larger RCDs. For the moment without more details on calcium physiology, average annual calcium use in egg-shell production, and related items, this general explanation is unworkable.

Another possible explanation of differential remodeling is as a biomechanical adaptation to different locomotor behaviors. The highest tortoise densities in the Mojave Desert are associated with occurrence in intermountain valleys and flat open land, where friable soils allow for the construction of deep burrows (Germano et al., 1994; McLuckie et al., 1999). In contrast, Sonoran tortoises reach their highest densities on steep, rocky hills and desert mountain slopes and are generally absent from or occur at low densities in intermountain valleys and washes (Averill-Murray and Averill-Murray, 2005; Averill-Murray et al., 2002a; Riedle et al., 2002). The biomechanical constraints of locomotion on mountain slopes and rocky hills may demand greater remodeling in Sonoran tortoise bone, thus producing larger RCDs than in West Mojave tortoises. In addition, the potential dual foraging period and frequent lack of hibernation in Sonoran tortoises (Averill-Murray et al., 2002a; Van Devender, 2002) would cause them to be more active throughout the year than Mojave tortoises, where drought and winter freezes generally promote hibernation. Burrows serve as thermal refugia (Spotila et al., 1994) and during these stressful periods, Mojave tortoises sustain a much reduced metabolic rate, rarely emerging to feed (Nagy and Medica, 1986; Peterson, 1996).

4.3. Longevity and age at maturity

The number of visible growth layers varies among the various limb bones. Our preliminary skeletal screening showed that the tibia, fibula, ulna and radius of an individual had fewer visible growth layers (i.e. thinner cortical bone) than the humerus, scapula, femur and ilium. While these results were expected for the humerus and femur, the "high" number of layers for the two girdle bones was not, and the ability to use these two bones has been especially helpful owing to our reliance on salvaged specimens, which often lack parts of the skeleton. We recommend skeletal screening as a first step in any future skeletochronological study involving a new (unscreened) species. Screening can be performed by x-ray, as in de Buffrénil and Castanet (2000), or preferably by histological sectioning.

Previous studies reported that male and female desert tortoises generally attain similar ages (Germano, 1994a; Germano et al., 2002; Turner et al., 1987). Our results bolster that conclusion; our samples show no sexual dimorphism in age (Fig. 4). Sonoran

tortoises, however, reach significantly older ages than West Mojave tortoises and, in general, are older at similar sizes than West Mojave tortoises (Figs. 3 and 4). Even though Sonoran males are significantly older than West Mojave males, they are similar in body size. The similarity in maximum size, but the difference in the age structure within the equivalent size classes shows that Sonoran tortoise are growing at a slower rate, and under this differential growth regime, the two populations attain sexual maturity at strikingly different ages, West Mojave tortoises ~ 17 years, Sonoran tortoises ~ 26 years.

4.4. Growth strategies, ecological implications and conclusions

The most surprising result of our study is that West Mojave tortoises grow faster and reach sexual maturity earlier than Sonoran tortoises (Figs. 3 and 5, also see Germano, 1992, Fig. 4; Germano, 1994a, Table 4). Because an equitable environment and adequate food promote rapid growth rate and early sexual maturity in captive desert tortoises (Jackson et al., 1976, 1978), Sonoran tortoises would be expected to have the fastest growth rates and earliest maturity of the two desert populations. The Sonoran Desert seems to have an environment more favorable or at least less harsh than the West Mojave Desert. The longer average life span of Sonoran tortoises supports this hypothesis, but their delayed sexual maturity and slower growth rates do not. If the West Mojave Desert is then the more productive of the two deserts, why do West Mojave females average significantly smaller than Sonoran females, and why do West Mojave tortoises have shorter life spans than Sonoran tortoises?

Lagarde et al. (2001) observed that in steppe tortoises (*Testudo horsfieldii*), which live in a similar habitat and climate to the West Mojave tortoises, fast-growing individuals mature early at small body sizes, although females are significantly larger than males (Lagarde et al., 2001). Wikelski et al. (1997) in his study on marine iguanas (*Amblyrhynchus cristatus*), proposed that rapid growth and early maturity at small sizes might be beneficial owing to the lower maintenance requirements of small size. This energy saving can then be invested into reproduction and survival during periods of low resources (Wikelski and Thom, 2000). Lagarde et al. (2001) proposed that early maturity and small size are especially beneficial to male steppe tortoises because annual activity (3.5 months) is strongly constrained by the harsh environment. Alm (1959) proposed that the early maturity in stunted perch (*Perca fluviatilis*) derives from either a genetically fixed maturation age or a change in environmental conditions (i.e., from good growth conditions during early life to poor ones after maturity). Jansen (1996) argued that the wide range of maturation age within and between various populations of perch species, as well as the known response of age at first reproduction to environmental factors (e.g., temperature and nutrient levels) made a strictly genetic basis for the onset of maturity unlikely. Optimal life history strategies allocate resources to maintenance, growth, and reproduction in ways that maximize individual fitness, i.e., age specific fecundity and survivorship (Congdon and Gibbons, 1990). The early reproduction of stunted perch decreases their risk of death before reproducing (Jansen, 1996), and as a consequence of this strategy, stunted perch experienced poor somatic conditions and a reduced life expectancy (Jansen, 1996).

West Mojave females might have adopted this life history strategy of early reproduction, thereby producing more clutches than Sonoran females. This strategy would have a selective advantage for populations with high juvenile mortality and comparatively shorter life spans (i.e., reduced reproductive life) of surviving adults. In iteroparous species with moderate to long potential life span, the benefit of early maturity usually associates

with increased adult survivorship augmented by increasing the number of reproductive episodes each year (reproductive period) (Congdon et al., 1982; Hamilton, 1966; Lagarde et al., 2001). The trade-off, however, is that Mojave females appear tied to annual reproduction, laying at least one, but usually more, clutches per year, and they do this consistently even during the chronic and frequent droughts of the West Mojave Desert. These frequent droughts, coupled with the West Mojave Desert having the lowest annual rainfall of the entire desert tortoise range, even if it may be more productive following winter rains than either the Sonoran or East Mojave Desert (Wallis et al., 1999), likely results in chronic physiological stress, greatest in the females. Peterson (1996) concluded from his studies in the West and East Mojave Desert of California that the desert tortoise is not physiologically adapted to live in the desert, but is a tenuous relic of a less rigorous climate. This conclusion is consistent with the hypothesis proposed by Van Devender (2002) that the Mojave tortoises evolved from Sonoran or Sinaloan tortoises, a population adapted to a summer rainfall cycle.

The skeletochronological estimate of 15–17 years as age at maturity lies within the published data of 9–26 years in Mojave tortoises (Medica et al., 1975; Germano, 1994a,b), but the skeletochronological estimate of 22–26 years is distinctly greater than previously published maturity estimates of 10–20 years for Sonoran tortoises. The delayed maturity in Sonoran tortoises could be related to the more extreme summer temperatures (regularly over 38 °C; Van Devender et al., 2002) experienced in this desert. Berigan and Charnov (1994) suggested that low food quality and/or availability could result in delayed maturity and small body size at maturity but that a reduction or increase of environmental temperatures (causing a reduced period of annual activity) yielded delayed maturity and a larger body size at maturity. For example, in populations of one perch species (*Perca flavescens*) experiencing elevated water temperatures simultaneously with poor feeding conditions, the perch adopted an energy-saving strategy. The perch reduced clutch size or stopped egg production entirely in the year(s) following the year of first reproduction; this strategy reduced the high mortality risk associated with the considerable energy investment into gamete production (Jansen, 1996; Sandström et al., 1995). Delayed sexual maturity could be an energy-saving strategy in Sonoran females, together with the tendency to produce only one clutch or even no clutches as a response to unfavorable environmental conditions (Averill-Murray et al., 2002b).

The estimated longevity in both groups is higher (noticeably so in Sonoran tortoises) than those proposed by (Germano 1992, 1994a,b) for West Mojave (32 years) and Sonoran Desert (35 years) populations. Maximum age estimates are 47–54 years in Sonoran males and 40–43 years in Sonoran females. In West Mojave males, the oldest age estimate is 56 years. The oldest males, however, were typically 27–37 years old. In West Mojave females, maximum age estimates were only 24–27 years. It is significant to note that, irrespective of desert, females had shorter life spans than males, especially West Mojave females. This age differential must be considered in future conservation strategies.

Acknowledgments

We gratefully acknowledge funding provided by a Panaphil Foundation Fellowship to A.J. Curtin. We are also grateful to Dr William Boarman and the US Geological Society for donating the West Mojave Desert tortoise carcasses, and Roy Averill-Murray and the Arizona Game and Fish Department for donating the Sonoran Desert tortoise carcasses used in this study. We also thank Dr Mike O'Connor and especially Dr Hal Avery for comments on earlier drafts of this manuscript and for valuable discussions and insights on desert tortoise ecology.

References

- Alm, G., 1959. Connection between maturity, size and age in fishes. Report of the Institute of Freshwater Research, Drottningholm 25, 1–146.
- Averill-Murray, R.C., 2002. Reproduction of *Gopherus agassizii* in the Sonoran Desert, Arizona. *Chelonian Conservation and Biology* 4, 295–301.
- Averill-Murray, R.C., Martin, B.T., Bailey, S.J., Wirt, E.B., 2002a. Activity and behavior of the Sonoran Desert tortoise in Arizona. In: Van Devender, T.R. (Ed.), *The Sonoran Desert Tortoise: Natural History, Biology, and Conservation*. The University of Arizona Press and the Arizona-Sonora Desert Museum, Tucson, AZ, pp. 135–158.
- Averill-Murray, R.C., Woodman, A.P., Howland, J.M., 2002b. Population ecology of the Sonoran Desert tortoise in Arizona. In: Van Devender, T.R. (Ed.), *The Sonoran Desert Tortoise: Natural History, Biology, and Conservation*. The University of Arizona Press and the Arizona-Sonora Desert Museum, Tucson, AZ, pp. 109–134.
- Averill-Murray, R.C., Averill-Murray, A., 2005. Regional-scale estimation of density and habitat use of the desert tortoise (*Gopherus agassizii*) in Arizona. *Journal of Herpetology* 39, 65–72.
- Berrigan, D., Charnov, E.L., 1994. Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos* 70, 474–478.
- Boarman, W.I., 1992. Effectiveness of fences and culverts for protecting desert tortoises along California state highway 58: summary of initial field season. Report to California Energy Commission. Bureau of Land Management, Riverside, CA, 31 pp.
- de Buffrènil, V., Castanet, J., 2000. Age estimation by skeletochronology in the Nile monitor (*Varanus niloticus*), a highly exploited species. *Journal of Herpetology* 34, 414–424.
- de Buffrènil, V., Francillon-Viellot, H., 2001. Ontogenetic changes in bone compactness in male and female Nile monitors (*Varanus niloticus*). *Journal of Zoology*, London 254, 539–546.
- Castanet, J., Smirina, E., 1990. Introduction to the skeletochronological method in amphibians and reptiles. *Annales Science Naturelle. Zoologie* 13 (11), 191–196.
- Castanet, J., Francillon-Viellot, H.J., Meunier, F.J., De Ricqlès, A., 1993. Bone and individual ageing. In: Hall, B.K. (Ed.), *Bone*, Vol. 7. CRC Press, London, pp. 245–283.
- Chambers, P., 2004. *A Sheltered Life: The Unexpected History of the Giant Tortoise*. John Murray, London, 306 pp.
- Congdon, J.D., Dunham, A.E., Tinkle, D.W., 1982. Energy budgets and life histories of reptiles. In: Gans, C., Pough, F.H. (Eds.), *Biology of the Reptilia*, Vol. 13. Academic Press, London, pp. 233–271.
- Congdon, J.D., Gibbons, J.W., 1990. Evolution of turtle life histories. In: Gibbons, J.W. (Ed.), *Life History and Ecology of the Slider Turtle*. Smithsonian Institution Press, Washington DC, pp. 45–56.
- Currey, J.D., 2003. The many adaptations of bone. *Journal of Biomechanics* 36, 1487–1495.
- Curtin, A.J., Zug, G.R., Medica, P.A., Spotila, J.R., 2008. Aging desert tortoises (*Gopherus agassizii*): testing skeletochronology with known-age individuals. *Endangered Species Research* 5, 21–27.
- Germano, D.J., 1992. Longevity and age-size relationships of populations of desert tortoises. *Copeia* 1992, 367–374.
- Germano, D.J., 1994a. Growth and age at maturity of North American tortoises in relation to regional climates. *Canadian Journal of Zoology* 72, 918–931.
- Germano, D.J., 1994b. Comparative life histories of North American Tortoises. In: Bury, R.B., Germano, D.J. (Eds.), *Biology of North American Tortoises*. National Biological Survey, Fish and Wildlife Research 13, pp. 174–185.
- Germano, D.J., Bury, R.B., Esque, T.C., Fritts, T.H., Medica, P.A., 1994. Range and habitats of the desert tortoise. In: Bury, R.B., Germano, D.J. (Eds.), *Biology of North American Tortoises*. National Biological Survey, Fish and Wildlife Research 13, pp. 73–84.
- Germano, D.J., Pough, F.H., Morafka, D.J., Smith, E.M., Demlong, M.J., 2002. Growth of desert tortoises: implications for conservation and management. In: Van Devender, T.R. (Ed.), *The Sonoran Desert Tortoise Natural History, Biology and Conservation*. The University of Arizona Press and the Arizona-Sonora Desert Museum, Tucson, AZ, pp. 265–288.
- Girondot, M., Garcia, J., 1999. Senescence and longevity in turtles: what elomers tell us. In: Maud, Cl., Guyétant, R. (Eds.), *Current Studies in Herpetology*. Societas Europaea Herpetologica, Le Bourget du Lac, pp. 133–137.
- Hamilton, W.D., 1966. The moulding of senescence by natural selection. *Journal of Theoretical Biology* 28, 12–45.
- Henen, B.T., 1997. Seasonal and annual energy budgets of female desert tortoises (*Gopherus agassizii*). *Ecology* 78, 283–296.
- Henen, B.T., Peterson, C.C., Wallis, I.R., Berry, K.H., Nagy, K.A., 1998. Effects of climate variation on field metabolism and water relations of desert tortoises. *Oecologia* 117, 365–373.
- Jackson Jr., C.G., Trotter, J.A., Trotter, T.H., Trotter, M.W., 1976. Accelerated growth rate and early maturity in *Gopherus agassizii* (Reptilia: Testudines). *Herpetologica* 32, 139–145.
- Jackson Jr., C.G., Trotter, J.A., Trotter, T.H., Trotter, M.W., 1978. Further observations of growth and sexual maturity in captive desert tortoises (Reptilia: Testudines). *Herpetologica* 34, 225–227.
- Jansen, W.A., 1996. Plasticity in maturity and fecundity of yellow perch, *Perca flavescens* (Mitchill): comparisons of stunted and normal-growing populations. *Annales Zoologici Fennici* 33, 403–415.
- Lagarde, F., Bonnet, X., Henen, B.T., Corbin, J., Nagy, K.A., Naulleau, G., 2001. Sexual size dimorphism in steppe tortoises (*Testudo horsfieldi*): growth, maturity, and individual variation. *Canadian Journal of Zoology* 79, 1433–1441.
- Lamb, T., Lydeard, C., 1994. A molecular phylogeny of the gopher tortoise, with comments on familial relationships within the Testudinoidea. *Molecular Phylogenetics and Evolution* 3, 283–291.
- Lamb, T., McLuckie, A.M., 2002. Genetic differences among geographic races of the desert tortoise. In: Van Devender, T.R. (Ed.), *The Sonoran Desert Tortoise: Natural History, Biology, and Conservation*. The University of Arizona Press and the Arizona-Sonora Desert Museum, Tucson, pp. 67–85.
- Lamb, T., Avise, J.C., Gibbons, J.W., 1989. Phylogeographic patterns in mitochondrial DNA of the desert tortoise (*Xerobates agassizii*), and evolutionary relationships among North American gopher tortoises. *Evolution* 43, 76–87.
- McCord, R.D., 2002. Fossil history and evolution of the gopher tortoises (genus *Gopherus*). In: Van Devender, T.R. (Ed.), *The Sonoran Desert Tortoise: Natural History, Biology and Conservation*. The University of Arizona Press and the Arizona Sonora Desert Museum, Tucson, Arizona, pp. 52–66.
- McLuckie, A.M., Lamb, T., Schwalbe, C.R., McCord, R.D., 1999. Genetic and morphometric assessment of an unusual tortoise (*Gopherus agassizii*) population in the Black Mountains of Arizona. *Journal of Herpetology* 33, 36–44.
- Medica, P.A., Bury, R.B., Turner, F.B., 1975. Growth of the desert tortoise (*Gopherus agassizii*) in Nevada. *Copeia* 1975, 639–643.
- Meunier, F.J., Pascal, M., Loubens, G., 1979. Comparaison de méthodes squellecto-chronologiques et considérations fonctionnelles sur le tissu osseux acellulaire d'un Oustéichthyen du Lagon NéoCalédonien. *Aquaculture* 17, 137–157.
- Morafka, D.J., Berry, K.H., 2002. Is *Gopherus agassizii* a desert-adapted tortoise, or an exaptive opportunist? Implications for tortoise conservation. *Chelonian Conservation and Biology* 4, 263–287.
- Murray, R.C., Klug, C.M., 1996. Preliminary data analysis from three desert tortoise long-term monitoring plots in Arizona: shelter site use and growth. *Proceedings of the Desert Tortoise Council Symposium* 1996, 10–17.
- Nagy, K.A., Medica, P.A., 1986. Physiological ecology of desert tortoises in southern Nevada. *Herpetologica* 42, 73–92.
- Oftedal, O.T., 2002. Nutritional ecology of the desert tortoise in the Mojave and Sonoran Deserts. In: Van Devender, T.R. (Ed.), *The Sonoran Desert Tortoise Natural History, Biology and Conservation*. The University of Arizona Press and the Arizona-Sonora Desert Museum, Tucson, AZ, pp. 194–241.
- Parham, J.F., Zug, G.R., 1998. Age and growth of loggerhead sea turtles (*Caretta caretta*) of coastal Georgia: an assessment of skeletochronological age-estimates. *Bulletin of Marine Science* 61, 287–304.
- Peterson, C.C., 1996. Ecological energetics of the desert tortoise (*Gopherus agassizii*): effects of rainfall and drought. *Ecology* 77, 1831–1844.
- Riedle, J.D., Averill-Murray, R.C., Bolen, D.K., 2002. Desert tortoise habitat use and home range size on the Florence Military Reservation: progress report. *Nongame Endangered Wildlife Program, Technical Report* 194, pp. 21.
- Sandström, O., Neuman, E., Thoresson, G., 1995. Effects of temperature on life history variables in perch, *Perca fluviatilis*. *Journal of Fish Biology* 47, 652–670.
- Sasaki, M., Boarman, W.I., Goodlett, G., Okamoto, T., 1995. Risk associated with long-distance movements by desert tortoises. *Proceedings of the Desert Tortoise Council Symposium* 1994, 33–48.
- Spotila, J.R., O'Connor, M.P., Zimmerman, L.C., Ruby, D.E., 1994. Introduction: conservation biology of the desert tortoise, *Gopherus agassizii*. *Herpetological Monographs* 8, 1–4.
- Turner, F.B., Hayden, P., Burge, B.L., Roberson, J.B., 1986. Egg production by the desert tortoise (*Gopherus agassizii*) in California. *Herpetologica* 42, 93–104.
- Turner, F.B., Medica, P.A., Bury, R.B., 1987. Age-size relationships of desert tortoises (*Gopherus agassizii*) in southern Nevada. *Copeia* 1987, 974–977.
- US Fish and Wildlife Service, 1994. *Desert Tortoise (Mojave Population) Recovery Plan*. US Fish and Wildlife Service, Portland, pp. 1–73.
- Van Devender, T.R., 2002. Cenozoic environments and the evolution of the gopher tortoises (genus *Gopherus*). In: Van Devender, T.R. (Ed.), *The Sonoran Desert Tortoise Natural History, Biology and Conservation*. The University of Arizona Press and the Arizona-Sonora Desert Museum, Tucson, AZ, pp. 29–50.
- Van Devender, T.R., Averill-Murray, R.C., Esque, T.C., Holm, P.A., Dickson, V.M., Schwalbe, C.R., Wirt, E.B., Barrett, S.L., 2002. Grasses, mallows, desert vine, and more: Diet of the desert tortoise in Arizona and Sonora. In: Van Devender, T.R. (Ed.), *The Sonoran Desert Tortoise Natural History, Biology and Conservation*. The University of Arizona Press and the Arizona-Sonora Desert Museum, Tucson, AZ, pp. 159–193.
- Walker, D., Avise, J.C., 1998. Principles of phylogeography as illustrated by freshwater and terrestrial turtles in the southeastern United States. *Annual Review of Ecology and Systematics* 29, 23–58.
- Wallis, I.R., Henen, B.T., Nagy, K.A., 1999. Egg size and annual egg reproduction by female desert tortoises (*Gopherus agassizii*): the importance of food abundance, body size, and date of egg shelling. *Journal of Herpetology* 33, 394–408.
- Wikelski, M., Carrillo, V., Trillmich, F., 1997. Energy limits to body size in a grazing reptile, the Galapagos marine iguana. *Ecology* 78, 2204–2217.
- Wikelski, M., Thom, C., 2000. Marine iguanas shrink to survive El Niño. *Nature* 403, 37.
- Wilson, D.D., Tracy, C.R., Tracy, C.R., 2003. Estimating age of turtles from growth rings: a critical evaluation of the technique. *Herpetologica* 59, 178–194.
- Wirt, E.B., Holm, P.A., 1997. Climatic effects on survival and reproduction of the desert tortoise (*Gopherus agassizii*) in the Maricopa Mountains, Arizona. Unpublished Report to Arizona Game and Fish Department, Phoenix.
- Zug, G.R., 1990. Age determination of long-lived reptiles: some techniques for sea-turtles. *Annales des Sciences Naturelles, Zoologie, Paris*, 13^e Série 11, 219–222.