Educational Bulletin #08-4
A publication of the Desert Protective Council www.dpcinc.org

Desert Tortoise Ecology, Behavior & Genetics Across the Range

By Michael J. Connor, Ph.D.

Every "desert rat" knows a desert tortoise when he or she sees one. It's that large, flower-loving, desert turtle with the bright eyes and stumpy hind legs. But what many of us desert rats fail to appreciate is that what we call the desert tortoise and what science calls *Gopherus agassizii* is a fascinating complex of populations with very different genetic and behavioral profiles that reflect the very different ecologies of the desert regions that they are found in. In this article we will explore some of this amazing variation.

The range of what we know as the "desert tortoise" is very large indeed. Desert tortoise populations are scattered throughout North America's vast Mojave and Sonoran Deserts. East to west they range from the east side of California's coastal range 300 miles across southern Nevada through to Utah's southwest corner. North to south they extend 900 miles, from Utah through Arizona and across the border through Sonora and into northern Sinaloa, Mexico. Ridgecrest, Victorville, Palmdale, Las Vegas, Phoenix, Tucson and St. George are all cities built within the tortoise's historic range, and have expanded into what was until very recent times prime desert tortoise habitat.

Ecology

Water is a premium and limiting resource in the desert. Even small differences in precipitation rates or season can have remarkable impacts on local and regional desert ecology. Both the quantity and quality of precipitation varies across the desert tortoise's extensive range. In the western Mojave Desert most of the five inches of precipitation falls in the winter. Farther east, the proportion falling in the summer increases. In eastern California, southern Nevada, and California's Colorado Desert, summer monsoonal rain events may occur. Within the Sonoran Desert proper, precipitation tends to be strongly bimodal with rain falling reliably both in winter and in summer. Rainfall patterns determine which particular plant species germinate and grow – with winter annuals following winter/spring rains and summer annuals and warm season grasses following summer rain – and thus affect seasonal and regional variation in available food plants.

Physiology and Behavior

Desert tortoises have a remarkable physiology that allows them to survive extremes, including a high tolerance for dehydration. As they dehydrate, they lose body mass and the concentration of solutes in their body fluids increases and may reach levels unknown in other terrestrial reptiles (Peterson, 1996). Yet even normal desert conditions are physiologically stressful. Desert tortoises are almost entirely herbivorous. Their plant diet contains high levels of electrolytes especially potassium, which is potentially toxic. Desert tortoises lack functional salt glands that help other reptiles such as iguanas eliminate excess potassium and, not having frequent access to rainfall, lack the luxury of being able to eliminate large volumes of urine to deal with it. Instead, they have another trick up their sleeve. Desert tortoises produce uric acid as their major metabolic endpoint of protein breakdown. Uric acid is familiar to all of us as the white substance so prominent in bird droppings. Desert tortoises store uric acid in their bladders which, being only sparingly soluble in water, forms a suspension. Tortoises use this uric acid to accumulate potassium and other electrolytes in their bladder as a colloidal suspension of "urates" (uric acid salts) until opportunities to drink again allow them to eliminate.

Dr. Olav Oftedal, from the Smithsonian Institution, has proposed that desert tortoises select plants in their environment in response to their physiological needs, and has provided impressive support for his hypothesis (Oftedal, 2002). Desert tortoises seek out plants with a high Potassium Excretory Potential ("PEP"): plants with high water and protein contents that help both rehydrate and ultimately produce uric acid that can help bind excess potassium. The availability of high PEP plants in the spring is especially important to tortoises in the Mojave Desert who, unlike their Sonoran Desert cousins, may not get the opportunity to drink during the hot summer months.

Mojave and Sonoran desert tortoises live in desert scrub habitat often dominated by creosote. Sinaloan tortoises live in thorn scrub and tropical deciduous forest habitat. At the north end of the range on the Beaver Dam Slope, long cold winters and lack of suitable, safe burrowing habitat, drive tortoises to overwinter in communal dens. Most desert tortoises, however, tend to hibernate alone or in small groups. Further south, hibernation periods may be short or not occur. Furthermore, seasonal activity shows size dependence. Young Mojave tortoises may be active even in January and February. Their small size and large surface area to volume ratio allows them to take advantage of the weaker winter sun and to exploit any late winter rains or early green up.

The highest desert tortoise densities occur within the Mojave Desert in the intermountain valleys, where easily excavated soils provide for the construction of large, deep burrows. In contrast, highest density tortoise populations in the Sonoran Desert occupy steep, rocky slopes and they are often absent from the hot intermountain valleys (Averill-Murray et al. 2002). Tortoises in the Sonoran Desert often utilize rock crevices or burrow underneath shrubs to find shelter; and, the availability of shelter sites in their boulder-strewn habitat strongly influences tortoise distribution. Local populations are smaller within the more rugged Sonoran landscape than in the Mojave. Sonoran desert tortoises are known to make long distance movements between mountain ranges. This is important for gene flow and for repopulation following local extirpations, although such movement is now heavily constrained due to development.

Reproductive physiology also differs between Sonoran and Mojave populations of the desert tortoise (see Rosmarino and Connor, 2008). Whereas Sonoran females may lay one clutch per year, typically with five eggs, Mojave females can lay as many as three clutches per year with a clutch size of 5-12 eggs. Mojave desert tortoise females typically lay their eggs earlier (April-mid July) than do Sonoran females (early June-August). These significant reproductive differences are likely related to ecological differences between the two regions. Averill-Murray and others hypothesize that Sonoran females employ the strategy of investing all their reproductive effort into a single clutch, prior to the onset of reliable summer rains, attempting to maximize juvenile survivorship by providing them access to abundant post-rain forage. The reproductive strategy employed by females in the Mojave populations is significantly different, with reproduction commencing at smaller body sizes and younger ages, and at higher clutch numbers, in order to maximize juvenile survivorship in the different conditions of the Mojave Desert (Averill-Murray 2002).

Genetics

In the late 1980's, investigations of mitochondrial DNA paved the way to discerning discrete lineages within desert tortoise populations. Mitochondria are small cellular organelles that function as the cell's energy generators. Individuals acquire these mitochondria solely from the ovum; thus, mitochondrial DNA is inherited matriarchally. Mitochondria have their own DNA that codes for essential proteins and this can be tracked to discern matriarchal inheritance patterns. Because mitochondria are so essential to cellular function, mutations in mitochondrial DNA are rare, accumulate very slowly, and tend to be highly conserved. Its analysis offers a useful probe for discerning major lineages among a larger population.

Desert tortoise populations consist of three major distinct assemblages based on their mitochondrial DNA (Lamb et al, 1989). The "western" assemblage is most widespread, occurring north and west of the Colorado River, and includes several discernible subgroups. The second "eastern" assemblage includes most of the Sonoran desert tortoises and extends south into Sonora (Mexico), a linear distance of nearly 500 miles. This assemblage differs markedly from the western assemblage and this difference is so great that it suggests that the western and eastern tortoises have been separated geographically for a long period of time, perhaps as long as two to three million years, and have remained reproductively isolated from each other to the present day. This time period corresponds to a geological time during which great rivers and shallow seas periodically covered much of the lower Colorado Desert and were eventually replaced by the modern Colorado River. The third or "southern" assemblage, almost as different from the western tortoises as the western tortoises differ from the eastern, occurs in southern Sonora and Northern Sinaloa, Mexico. The boundary between the eastern and southern assemblages is unclear but may be the Yaqui River. South of the Yaqui lies deciduous forest, ecologically very different from the desert habitat of the two other major assemblages.

In 2007, Murphy et al. confirmed the distinctive split in maternal lineages between the Mojave and Sonoran populations using defined mitochondrial DNA sequences. They concluded that the substantial sequence differentiation between Mojave and Sonoran (Arizona) populations is consistent with the hypothesis that G. *agassizii* consists of more than one species.

In their seminal paper, Murphy et al. also reported the most detailed and thorough examination of Mojave desert tortoise population genetics yet to be published. They surveyed 16 microsatellite DNA *loci* in samples taken from 628 tortoises from 31 Mojave Desert locations. Microsatellite DNA are polymorphic *loci* that consist of repeating units of 1-6 base pairs in length. They provide useful molecular markers because mutations are typically neutral, making these markers very useful for kinship and population studies. Murphy et al.'s results are very informative. In 1994, the USFWS had published its science-driven *Desert Tortoise (Mojave Population) Recovery Plan*. This Plan separated the Mojave population into 6 different Desert Tortoise Recovery Units based on ecological, morphological, behavioral, geographic, and genetic data. Murphy and his colleagues' recent microsatellite DNA found strong evidence of "isolation by distance" across the desert tortoise's range, and they were able to differentiate most tortoises from the different recovery units using assignment tests. Murphy et al (2007) supports and offers strong, independent confirmation of the validity of those 1994 Desert Tortoise Recovery Units.

Summation

So, what do we know about what a desert tortoise is? We have established that: (a) the desert tortoise is scientifically extremely interesting, (b) the desert tortoise we know today includes a variety of populations with differing genotypes and behaviors, and (c) desert tortoise behavior and genetics tend to reflect ecological differences across the range. Many scientists believe that these differences are such that G. *agassizii* as currently described includes at least two or three different subspecies or even full species. Understanding these differences is not simply of academic interest. Appreciating the significance of the different desert tortoise populations advances the cause of those of us interested in conserving and protecting these remarkable animals, since it informs our understanding of which populations need more federal protection. Appreciating the differences between desert tortoise populations is also essential in addressing the management of site-specific impacts and underlies the requirement for rigorous scientific input into desert tortoise recovery planning efforts.

Michael Connor is California Director for Western Watersheds Project. He is a longtime desert tortoise advocate and recently coauthored a petition to list the Sonoran desert tortoise population as an endangered species.

References

Averill-Murray RC, Martin BE, Bailey SJ and Wirt EB. 2002. Activity and Behavior of the Sonoran Desert Tortoise in Arizona. *In*: Van Devender TR (Ed.) *The Sonoran Desert Tortoise: Natural History, Biology, and Conservation*. Tucson, AZ: The University of Arizona Press. pp. 135-158.

Berry, KH, Morafka, DJ and Murphy, RW. 2002. Defining the desert tortoise(s): our first priority for a coherent conservation strategy. Chelonian Conservation and Biology 4: 249-262.

Lamb T, Avise JC and Gibbons JW. 1989. Phylogeographic patterns in mitochondrial DNA of the desert tortoise (Xerobates agassizii), and evolutionary relationships among the North American gopher tortoises. Evolution 43(1): 76-87.

Murphy RW, Berry KH, Edwards T and Mcluckie AM. 2007. A Genetic Assessment of the Recovery Units for the Mojave Population of the Desert Tortoise, *Gopherus agassizii*. Chelonian Conservation and Biology 6(2): 229–251.

Oftedal OT. 2002. Nutritional ecology of the desert tortoise in the Mohave and Sonoran deserts. *In*: Van Devender TR (Ed.) *The Sonoran Desert Tortoise: Natural History, Biology, and Conservation*. Tucson, AZ: The University of Arizona Press. pp. 194-241.

Peterson CC. 1996. Ecological Energetics of the Desert Tortoise (*Gopherus agassizi*): Effects of Rainfall and Drought. Ecology. 77(6): 1831-1844.

Rosmarino N and Connor MJ. 2008. Petition to List the Sonoran Desert Tortoise (*Gopherus agassizii*) Under the U.S. Endangered Species Act. 199 pp. Submitted October 9, 2008. Available on line at: <www.westernwatersheds.org>.