

Biology of North American Tortoises: Introduction

by

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Chelonians have fascinated people for centuries and have been the object of biological studies for nearly as long. Perhaps the long life span and harmless demeanor of most species contribute to their wide appeal. They also represent a link to the distant past because their characteristic shell separated this line of ectotherms from all other reptiles and other animals in the age of dinosaurs (Pough et al. 1989). However, the origins of the chelonians remain a mystery.

Many species of freshwater turtles have been intensively studied for decades. The slider (*Trachemys scripta*) is perhaps the best-studied turtle in the world (Cagle 1950; Moll and Legler 1971; Gibbons 1990), and work on painted turtles (*Chrysemys picta*; Sexton 1959; Ernst 1971a, 1971b; Wilbur 1975; Tinkle et al. 1981; Mitchell 1988; Zweifel 1989) has been equally or nearly equally extensive. Marine turtles also have received much attention; advancements in their conservation have been particularly significant (Mrosovsky 1983; National Research Council 1990). However, we lack an understanding of

many aspects of their ecology except nesting behavior.

Information on tortoises also has increased at an exponential rate in the last 20 years. Much attention has been directed at the four species of living tortoises (genus *Gopherus*) of North America, which are mostly restricted to deserts, arid lands, and southeastern coastal regions (Figure). These species are descendants of tortoises that once ranged over a much larger portion of the continent (Williams 1950; Brattstrom 1961; Auffenberg 1964; Morafka and McCoy 1988; Crumly 1994).

North American tortoises have several adaptations for digging and terrestrial life: forelimbs that are flattened and covered anteriorly with thick or bony scales; columnar hind limbs; short, heavy, and rigid toes without webbing; head, tail, and limbs that are fully or partly retractable into the shell (exposed parts are generally armored); and a domed carapace that is firmly attached to the plastron (Carr 1952; Ernst and Barbour 1989). All of these tortoises are long-lived, slow to reach sexual maturity, and moderate to large in body size but have different range sizes and life history traits (Table). The four species have allopatric ranges.

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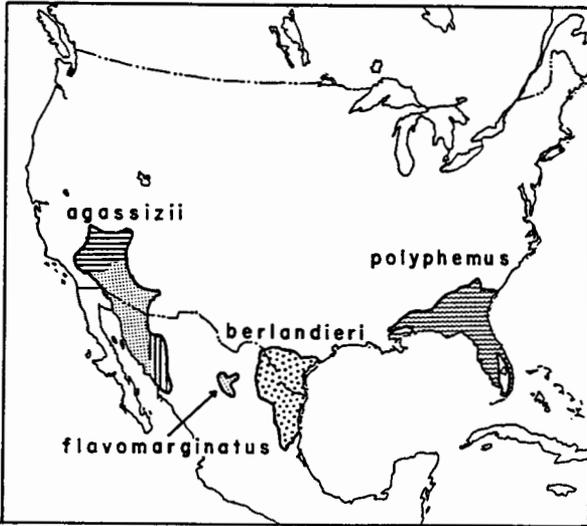


Figure. Distribution of the four extant species of North American tortoises (genus *Gopherus*). *Gopherus agassizii* occurs in three distinct biotic regions: the Mojave Desert (*horizontal lines*), Sonoran Desert (*dots*), and Sinaloan thornscrub and deciduous woodland (*vertical lines*).

Three of the four species were described before the twentieth century. The gopher tortoise (*G. polyphemus*) was first described in 1791, the Berlandier's (Texas) tortoise (*G. berlandieri*) in 1857, and the desert tortoise (*G. agassizii*) in 1863 (Auffenberg and Franz 1978). A surprise was the

discovery of the Bolson tortoise (*G. flavomarginatus*) in north-central Mexico. The Bolson tortoise is the largest species in the genus. Although reports of tortoises in this remote region date to the late 1880's (Bury et al. 1988), individuals were not formally described as a new species until recently (Legler 1959).

North American tortoises attract much attention because of their distinct ecologies as arid- or xeric-adapted species and ecological roles as keystone species: species burrow to some extent, and most construct deep burrows that are used or even required by other vertebrates and by invertebrate animals (Auffenberg 1969; Bury 1982). They are also harmless herbivores that are highly visible when active on the surface because of their relatively large size, slow movements, and diurnal activity. These features also promote public interest in the group, and many efforts to conserve and protect tortoises are under way. However, an increased scope and intensity of scientific studies on all four species are needed.

Three overviews (Auffenberg 1969; Auffenberg and Iverson 1979; Bury 1982) presented important information on the four species of North American tortoises and indicated necessary areas of research on each species. Since then surveys and studies of all four species have continued, yet the anticipated increase in knowledge of these species has been slow.

Table. Names and life history features of the four extant species of North American tortoises (genus *Gopherus*).

Common name	Scientific name	Body size	Geographic range size	Age to maturity (years)	Federal status
Desert tortoise	<i>G. agassizii</i> (Cooper)	Large	Large	≈15 (9–21)	Threatened in Mojave Desert
Berlandier's tortoise	<i>G. berlandieri</i> (Agassiz)	Small	Moderate	≈13 (11–17)	—
Gopher tortoise	<i>G. polyphemus</i> (Daudin)	Large	Large	≈14 (10–21)	Threatened in Alabama (parts), Mississippi and Louisiana
Bolson tortoise	<i>G. flavomarginatus</i> (Legler)	Largest	Small	≈14 (12–17)	Endangered species (foreign)
[Baja tortoise]	[<i>Xerobates</i> ^a <i>lepidocephalus</i> Ottley and Velasques ^b]	Moderate	Small	?	—

^a*Xerobates* is not recognized as a valid genus (Crumly 1994).

^bThis species is not recognized herein (Crumly and Grismer 1994).

Several bibliographies summarize studies of the past 50 years (Douglass 1975, 1977; Hohman et al. 1980; Diemer 1981; Beaman et al. 1989), but the wealth of entries obscures the lack of critical knowledge of many aspects of the biology of tortoises including life histories, nutrition, physiology, and behavior. The absence of basic data and critical questions on these four species became acutely obvious to us during an examination of growth patterns and life histories of the North American tortoises (Germano 1994; Germano and Bury 1994). Furthermore, available data often were not comparable between species. Because there has been a lack of coordination among researchers, a comprehensive understanding of this group of reptiles has not been achieved.

More than half of the ranges of *G. agassizii* and *G. berlandieri* and the entire range of *G. flavomarginatus* are in Mexico (Figure). Thus, a complete understanding of North American tortoises can only be gained by conducting research in Mexico with its leading scientists. There has been substantial research and interest in the Bolson tortoise by Mexican scientists and their colleagues (Aguirre et al. 1984).

Research on North American tortoises benefits from an understanding of studies of other chelonians because most of the theoretical bases of chelonian biology have been derived from research on freshwater turtle species. Furthermore, we have observed in studies of tortoises a lack of the hypothesis-testing and the scientific rigor that are characteristic of most research on freshwater turtles (Congdon and Gibbons 1985; Gibbons 1990; Congdon and van Loben Sels 1991).

Work on North American tortoises, particularly on the desert tortoise, is increasingly reported in in-house and contract reports. These reports are unobtainable or difficult to locate (for example, through interlibrary loans) and are rarely reviewed by critical peers. References to unpublished reports in this collection of papers, however, could not be avoided because the bulk of the information on desert tortoises is unpublished. We identified the unpublished works in the cited-literature sections by asterisks. Although cited, the data and premises of such material are frequently criticized. We are critical of the use of unpublished reports because we cannot rule out the probability that such material becomes widely albeit indiscriminately ac-

cepted dogma and a weak foundation of our knowledge and management of the tortoises.

This volume is a collection of papers that was initiated by the Guild of North American Tortoise Research Biologists, which was formed in 1989 to stimulate communication and cooperative investigations by researchers of the North American tortoises (genus *Gopherus*). Members include graduate students and professors, government scientists, wildlife biologists, and resource managers. The guild is unique because it does not address governmental regulations or advocate conservation. The guild's credo is rigorous and objective research to provide better knowledge and a solid basis for the effective conservation of tortoises. Many guild members contributed empirical studies or reviews of several research and management issues on North American tortoises.

Acknowledgments

We are grateful for reviews or assistance with one or more manuscripts to G. A. Adest, J. W. Burkhardt, J. F. Congdon, P. S. Corn, C. K. Dodd, Jr., R. Estes, T. H. Fritts, J. W. Gibbons, M. A. Griffith, F. W. Judd, C. J. McCoy, R. W. McDiarmid, E. L. Peters, G. H. Rodda, F. L. Rose, N. J. Scott, F. B. Turner, and J. H. Wolfheim. We thank the many anonymous peers for their critiques and advice that improved the quality of the papers. Errors or indiscretions remain our responsibility.

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