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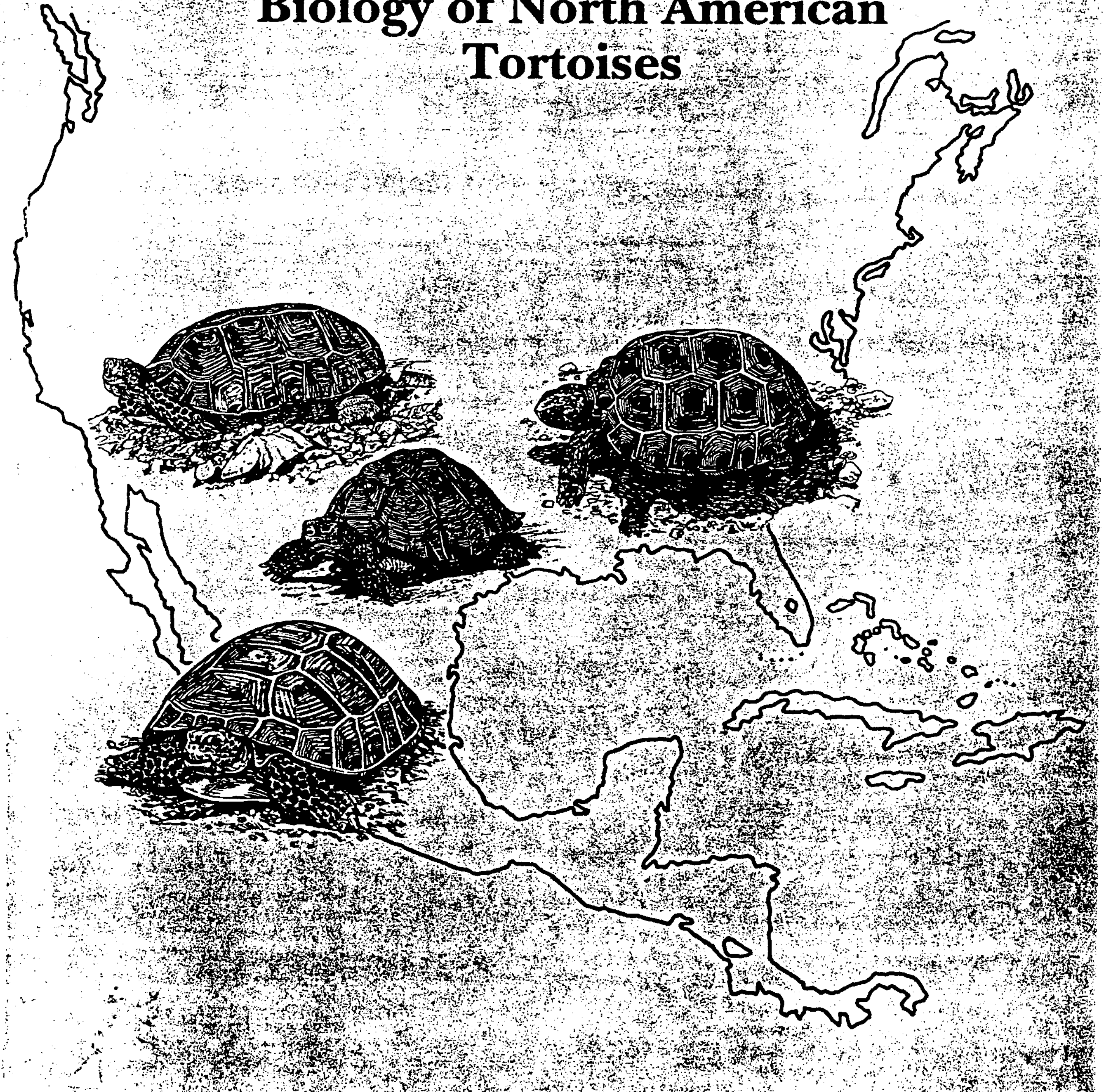
Biology of North American Tortoises



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March 3, 1849

Fish and Wildlife Research 13

Biology of North American Tortoises

Edited by R. B. Bury
D. J. Germano

UNITED STATES DEPARTMENT OF THE INTERIOR
NATIONAL BIOLOGICAL SURVEY
Washington, D.C. • 1994

Dedicated to the Memory of

Clarence J. McCoy

Nuestro mentor y companero

Contents

Frontispiece: Large adult of the desert tortoise (*Gopherus agassizii*) in the Mojave desert. *Photo by Todd C. Esque.*

Biology of North American Tortoises: Introduction

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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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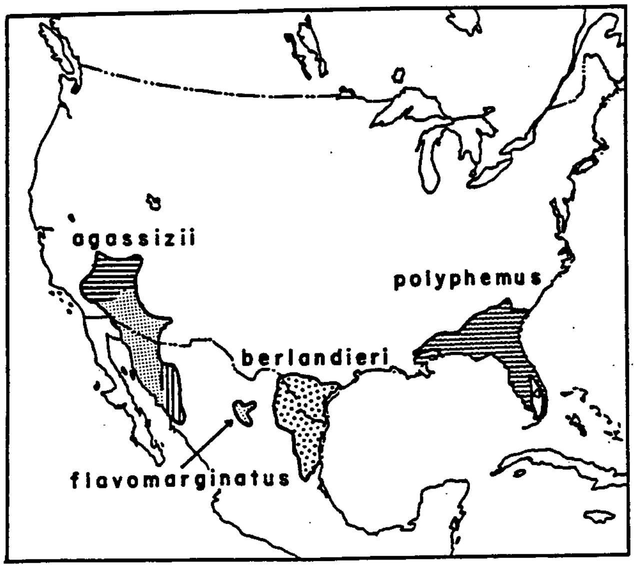

Figure. Distribution of the four extant species of North American tortoises (genus *Gopherus*). *Gopherus agassizii* occurs in three distinct biotic regions: the Mojave Desert (*horizontal lines*), Sonoran Desert (*dots*), and Sinaloan thornscrub and deciduous woodland (*vertical lines*).

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	*G. agassizii* (Cooper)	Large	Large	≈15 (9–21)	Threatened in Mojave Desert
Berlandier's tortoise	*G. berlandieri* (Agassiz)	Small	Moderate	≈13 (11–17)	—
Gopher tortoise	*G. polyphemus* (Daudin)	Large	Large	≈14 (10–21)	Threatened in Alabama (parts), Mississippi and Louisiana
Bolson tortoise	*G. flavomarginatus* (Legler)	Largest	Small	≈14 (12–17)	Endangered species (foreign)
[Baja tortoise]	[*Xerobates*[a] *lepidocephalus* Ottley and Velasques[b]]	Moderate	Small	?	—

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

[b] This 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 accepted 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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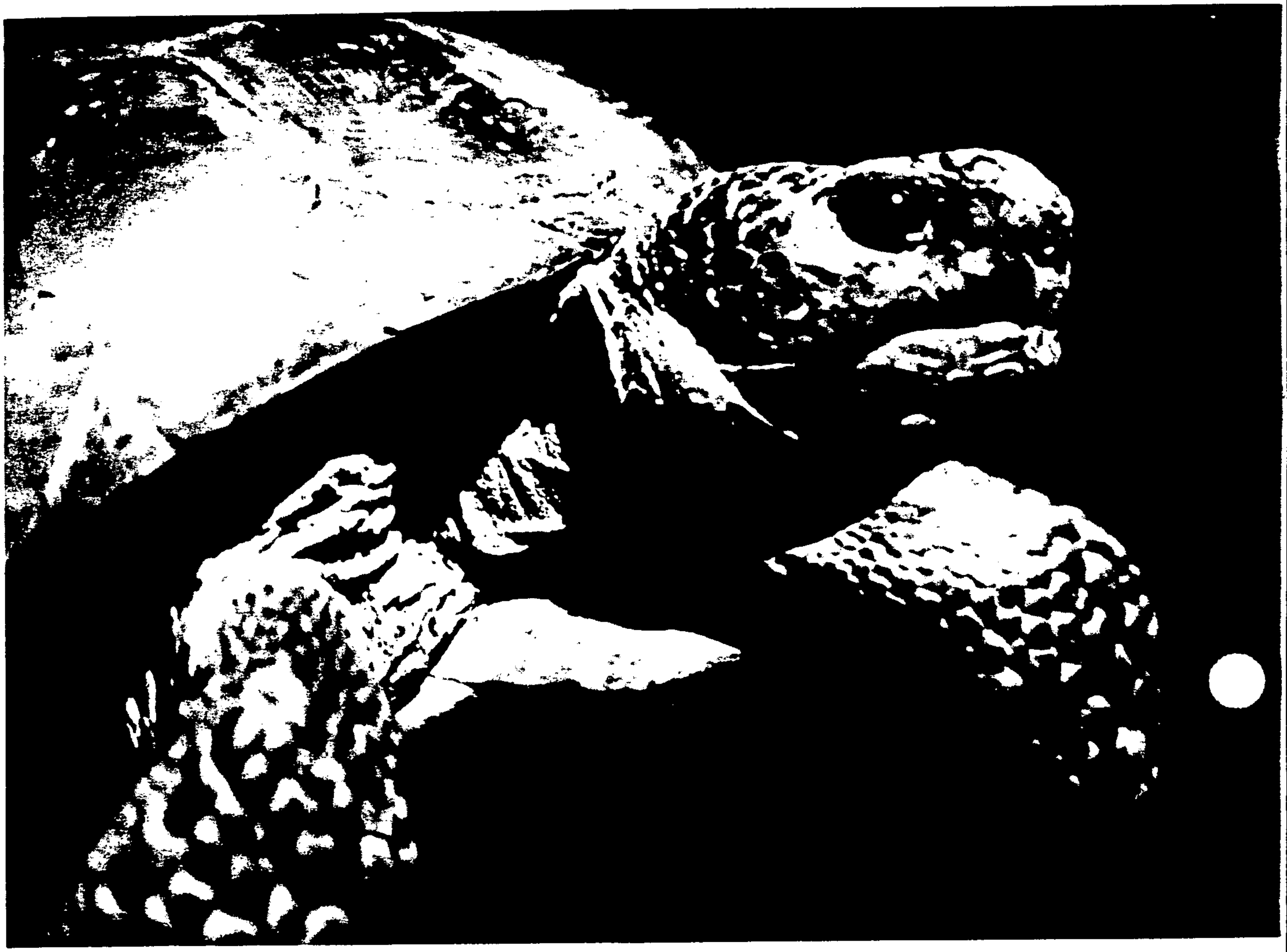

Adult gopher tortoise (*Gopherus polyphemus*). *Photo by J. E. Diemer.*

Phylogenetic Systematics of North American Tortoises (Genus *Gopherus*): Evidence for Their Classification

by

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Abstract. Synapomorphies (shared derived characters) indicate that *Gopherus polyphemus* and *G. flavomarginatus* are closely related and together with *G. canyonensis* form a monophyletic group. These synapomorphies are the end states of morphological transformation series, the intermediate derived conditions of which are represented in *G. agassizii* and *G. berlandieri*. One such feature is a saccular otolith, a unique condition of the membranous labyrinth of the inner ear among tetrapods. Other synapomorphies suggest that *Gopherus*, including all four living North American tortoises, is monophyletic. Although some phylogenies are documented by cladistic analysis, the relationships among the poorly characterized fossil species and the better known living *Gopherus* remain unresolved. Neither analyses of morphological synapomorphies nor mitochondrial DNA support the monophyly of *Xerobates*. Thus, because *Xerobates* is paraphyletic, I concluded that *Xerobates* should be abandoned. Furthermore, the early stratigraphic appearance of relatives of *G. polyphemus* and *G. flavomarginatus* is irrelevant to the issue of *Xerobates* monophyly.

Key words: Biogeography, cladistic comparisons, fossil histories, *Gopherus*, monophyletic lineage, North America, synapomorphic characters, tortoise, *Xerobates*.

The living tortoises of North America, formerly allocated to one genus, are now often referred to two genera: *Gopherus* Rafinesque 1832 and *Xerobates* (Agassiz 1857). The former includes *G. polyphemus* (Daudin 1802) and *G. flavomarginatus* (Legler 1959), and the latter includes *X. agassizii* (Cooper 1863) and *X. berlandieri* (Agassiz 1857). Generally accepted systematic practices require that these genera be monophyletic (i.e., the inclusive taxa should share a common ancestor and include all the known descendants of that ancestor). However, the evidence for the monophyly of *Gopherus* sensu stricto and *Xerobates* has not been critically evaluated.

Auffenberg (1976) showed that *Gopherus*, then including all four of the above-named species, could be divided into two phenetically distinct species groups. Bramble (1971) extensively studied the functional morphology of North American fossil tortoises and proposed that *Scaptochelys* be used to accommodate *G. agassizii* as well as *G. berlandieri* and three extinct taxa. Later,

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Bramble (1982) allocated only two of these fossil species to *Scaptochelys*: *G. laticuneus* and *G. mohavetus* (Table 1). Bour and Dubois (1984) noted that *Scaptochelys* was in fact a synonym of *Xerobates* because Brown (1906) had designated *G. agassizii* as the type species of *Xerobates*.

More recently, I suggested (Crumly 1987) that the evidence for the recognition of *Xerobates* is inadequate because it is mostly symplesiomorphic (shared primitive) characters or shared intermediate stages of transformation series. My earlier suggestions, however, did not represent a phylogenetic analysis of *Gopherus* and closely allied fossil taxa that I present here. This paper is not about the taxonomic status of individual fossil taxa, but the evidence for placing these fossil taxa in a classification with two genera of living North American tortoises is addressed.

Procedures for the Phylogenetic Analysis of *Gopherus*

Determining Monophyly

Synapomorphic (shared derived) characters are the evidence for inferring that a particular taxon is monophyletic (Hennig 1966) because symplesiomorphic (shared primitive) characters are uninfor-

Table 1. Auffenberg (1974) allocated all of the following fossil taxa to *Gopherus*. Below are the suggested allocations of Bramble (1982). Faunal ages are taken from Auffenberg (1974).

Species	Author	Faunal age
Allocated to *Scaptochelys* (*Xerobates*)		
Gopherus laticuneus	Cope (1873:6)	Chadronian, early Oligocene
including *praeextans*	Lambe (1913:61)	Orellan, middle Oligocene
Gopherus mohavetus	Merriam (1919:456)	Barstovian, late Miocene
including *depressus*	Brattstrom (1961:548)	Barstovian, late Miocene
Allocated to *Gopherus*		
Gopherus brevisterna	Loomis (1909:21)	Arikareean, early Miocene
Gopherus canyonensis	Johnston (1937:440)	Late Blancan, early Pleistocene
including *pertenius*	Cope (1892:226)	Early Blancan, late Pliocene
Gopherus edae	Hay (1907:19)	Arikareean, early Miocene
including *hollandi*	Hay (1907:18)	Arikareean, early Miocene
Gopherus hexagonata	Cope (1893:77)	Irvingtonian, middle Pleistocene
including *laticaudatus*	Cope (1893:75)	Irvingtonian, middle Pleistocene
Gopherus pansa	Hay (1908:420)	Barstovian, late Miocene
Gopherus praecedens	Hay (1916:55)	Late Pleistocene and Recent
Gopherus vaga	Hay (1908:414)	Barstovian, late Miocene
Allocated to other genera of land tortoises		
Into *Stylemys*		
Gopherus copei	Koerner (1940:838)	Barstovian, late Miocene
Gopherus emiliae	Hay (1908:419)	Arikareean, early Miocene
Gopherus neglectus	Brattstrom (1961:544)	Whitneyan, late Oligocene
Gopherus undabunus	Loomis (1909:25)	Arikareean, early Miocene
Into *Geochelone* (*Hesperotestudo*)		
Gopherus dehiscus	DesLauriens (1965:1)	Barstovian, late Miocene
Allocated to the synonymy of living species of *Gopherus*		
Into *Gopherus polyphemus*		
Gopherus atascosae	Hay (1902:383)	Middle Pleistocene
Into *Gopherus flavomarginatus*		
Gopherus heucoensis	Strain (1966:24)	Early Pleistocene

mative regarding the monophyletic status of a taxon. Thus, the diagnostic features of *Gopherus* and *Xerobates* have to be evaluated to determine whether they are synapomorphies and therefore support monophyly. Bramble (1982; Table 2) listed several characters to diagnose *Gopherus* and *Xerobates*. However, not all these features are synapomorphies.

Synapomorphies of *Gopherus* sensu lato include the presence of prefrontal pits, an enlarged cavum labyrinthicum containing a saccular otolith (profoundly enlarged in *Gopherus* sensu stricto), class-I mental glands, and the absence of processes on the dorsal surfaces of the postzygopophyses of the posterior cervical vertebrae (Crumly 1984a, 1984b). These synapomorphies and others support the monophyletic status of *Gopherus* sensu lato.

Outgroups

At least two outgroups are necessary (Maddison et al. 1984) to determine character–state polarity at the ancestral node of the ingroup. Here, the ingroup is defined as *Gopherus*—that is, all four of the living species and the fossil taxa allocated to *Gopherus* and *Xerobates* by Bramble (1982) and their most

Table 2. Features used by Bramble (1982) to differentiate *Scaptochelys* (*Xerobates*) from *Gopherus*.

Character	Systematic status
In *Scaptochelys* (*Xerobates* fide Bour and Dubois, 1984)	
Cranium relatively dolicocephalic	Intermediate
Inner ear	
Cavum labyrinthicum not inflated (slightly inflated over usual testudinid condition)	Intermediate
Sacculus contains small otolith	Intermediate
Cervical vertebrae	
Not appreciably shortened	Plesiomorphic
Pre- and postzygopophyses not enlarged	Plesiomorphic
Pre- and postzygopophyses not widely separated	Plesiomorphic
Number eight without elongated postzygopophyses	Intermediate
Dorsal vertebrae	
First dorsal with small zygopophyses	Plesiomorphic
First dorsal neural arch fused to first neural	?
Manus	
Two subradial bones	Plesiomorphic
Ungual phalanges not enlarged or spatulate	Plesiomorphic
Digitigrade	Plesiomorphic
Mesocarpal joint well developed	Plesiomorphic
In *Gopherus* (sensu Bramble 1982; includes *G. polyphemus* and *G. flavomarginatus*)	
Cranium brachycephalic	Synapomorphic
Inner ear	
Cavum labyrinthicum greatly inflated	Synapomorphic
Massive saccular otolith	Synapomorphic
Cervical vertebrae	
Shortened	Synapomorphic
Enlarged pre- and postzygopophyses	Synapomorphic
Widely separated pre- and postzygopophyses	Synapomorphic
Number eight with elongated postzygopophyses	Synapomorphic
Dorsal vertebrae	
First dorsal with enlarged zygopophyses	Synapomorphic
First dorsal neural arch sutured to first neural	?
Manus	
Three or four subradial bones	Synapomorphic
Ungual phalanges both enlarged and spatulate	Synapomorphic
Nearly unguligrade manus	Synapomorphic
Mesocarpal joint movement reduced or eliminated	Synapomorphic

recent common ancestor and all its descendants. This is a node-based form of definition (see de Queiroz and Gauthier 1990 for the distinction between node-, stem-, and apomorphy-based definitions). Characters were polarized with the Testudininae (sensu Crumly 1984a, 1984b; all tortoises other than *Gopherus*, *Stylemys*, *Manouria*, and *Hesperotestudo* are the first outgroup—sister taxon), and *Manouria* (the second outgroup; Table 3). After polarization and during computer analyses, the outgroups *Stylemys* (as redefined by Auffenberg 1964), *Manouria* (including *Hadrianus fide* Auffenberg 1971, 1974 *contra* Bramble 1982), and *Hesperotestudo* and the Testudininae were selected. These taxa were chosen because of their relationships to *Gopherus* as revealed by earlier studies (Crumly 1984a, 1984b).

I began this study with the assumption that the immediate closest sister group of the genus *Gopherus* sensu lato was *Stylemys*. This relationship was supported by the median premaxillary ridge, a feature found only in these two genera and nowhere else in the Testudinoidea. The presence of this median premaxillary ridge convinced Williams (1952) of the close relationship of *Stylemys* and *Gopherus*, which he united in his Group 3 of tortoises. In 1984, I was unsure of the phyletic position of *Hesperotestudo* relative to *Gopherus* and *Stylemys* or to the Testudininae. However, I remain convinced that *Manouria* is the sister taxon of all remaining tortoises. This a priori hypothesis was suggested earlier by Auffenberg (1971, 1974). The evidence for these relationships (Fig. 1) shows *Hesperotestudo* and the Testudininae in an unresolved tritomy with the *Gopherus* and *Stylemys* clade. Thus, my analysis began with poorly resolved relationships between the ingroup and outgroups.

Fossil and Living Gopher Tortoises (Genus Gopherus*)*

Bramble (1982) recognized nine fossil species, and I included all in the data matrix (Appendix A). This is done despite the largely incomplete data for some of these taxa because Gauthier et al. (1988a, 1988b) demonstrated (contra Patterson 1981) the importance of fossils for inferring phylogeny. Three of these nine taxa, *Gopherus edae*, *G. hexagonatus*, and *G. praecedens*, are represented only by shells, and much of Bramble's (1982) and my data come from forelimbs and skulls. Because these species are so incompletely characterized, they were not included in the computer-aided analyses of phylogenetic relationships.

Auffenberg (1974) recognized more fossil taxa of *Gopherus* than Bramble (1982). Some of these were synonymized by Bramble with other species of *Gopherus*, whereas some taxa were allocated to different tortoise genera (Table 1). Almost all taxa recognized by Bramble (1982) were also recognized by Auffenberg. The only exception is *Gopherus praecedens* (Hay 1916), recognized by Bramble (1982) but placed in the synonymy of *G. polyphemus* by Auffenberg (1974).

Table 3. The taxa selected as outgroups for this study and apomorphic characters that support the monophyly of each. All North American tortoises that cannot be assigned to either *Manouria*, *Gopherus*, or *Stylemys* are here recognized as members of the genus *Hesperotestudo* (Auffenberg 1963). This includes members of the subgenus *Caudochelys*. *Cymatholcus* and *Floridemys* are considered Testudinidae incertae cedis and not included in this analysis.

Taxon	Apomorphic characters
Stylemys	Median premaxillary ridge present Expanded ventral jugal contacts the pterygoid
Hesperotestudo	Accessory triturating ridges present in advanced forms Mandibular rami not fused in some
Testudininae	Interdigitating surangular process present Medial centrale prevents the articulation of the distal radius and the first carpal Mental glands absent Cervical scute longer than broad (this scute is sometimes absent)
Manouria	Enlarged canalis caroticum lateralis

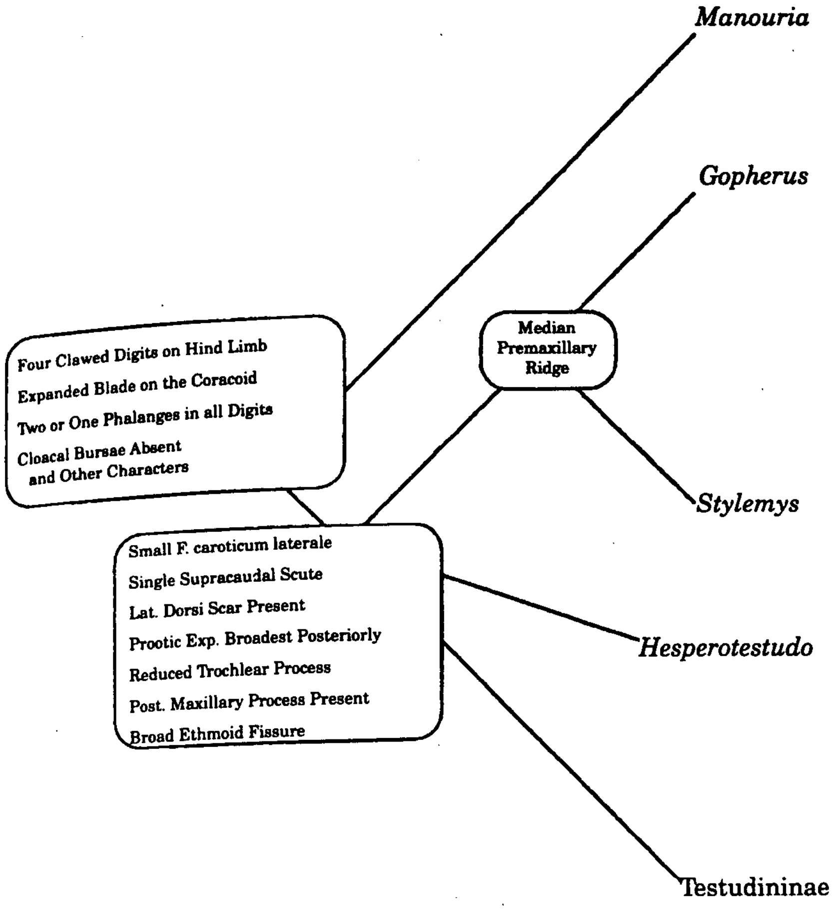

Fig. 1. An a priori estimate of the phylogenetic relationships of North American testudinids.

For living taxa, I used data from earlier studies (Crumly 1984a, 1984b). Data of fossil species are from original descriptions, the subsequent descriptions of Bramble (1971, 1982) and Auffenberg (1962, 1964), and a 35-mm photographic slide catalog of examined fossils (Crumly 1984a). I employed 42 characters to compare relations of tortoises (Appendix B), including illustrations of key osteological features of the skull (Figs. 2 and 3) and manus (Fig. 4).

Phylogenetic Analysis

Two computer programs were used to analyze data (Appendix C). The Macintosh version of Swofford's (1989) Phylogenetic Analysis Using Parsimony (PAUP version 3.0a) was used to obtain the shortest (i.e., most parsimonious) phylogenetic trees. Several algorithmic approaches to the analysis of phylogenetic relationships were used.

First, I used an Exhaustive Search algorithm for only the living taxa, which finds all minimum-length trees and produces a frequency distribution of all possible trees (Swofford 1989). This search can only be performed conveniently if the number of taxa is relatively low; Swofford (1989) recommends that fewer than 10 taxa be included. If more than 10 taxa are included (as here), the execution of the program is prohibitively long because the total number of trees becomes impossibly large—for example, more than 7.9×10^{12} bifurcating trees fide Rohlf (1982) for 14 taxa.

Second, I used the Branch and Bound algorithm on data sets that excluded either fossil *Xerobates* or fossil *Gopherus* sensu stricto. To determine how fossils contribute to the recognition of *Xerobates* paraphyly, two separate analyses were done with the Branch and Bound algorithm of PAUP. This algorithm finds all minimum-length trees.

Third, I used a Heuristic Search algorithm with all taxa except *Gopherus edae*, *G. hexagonatus*,

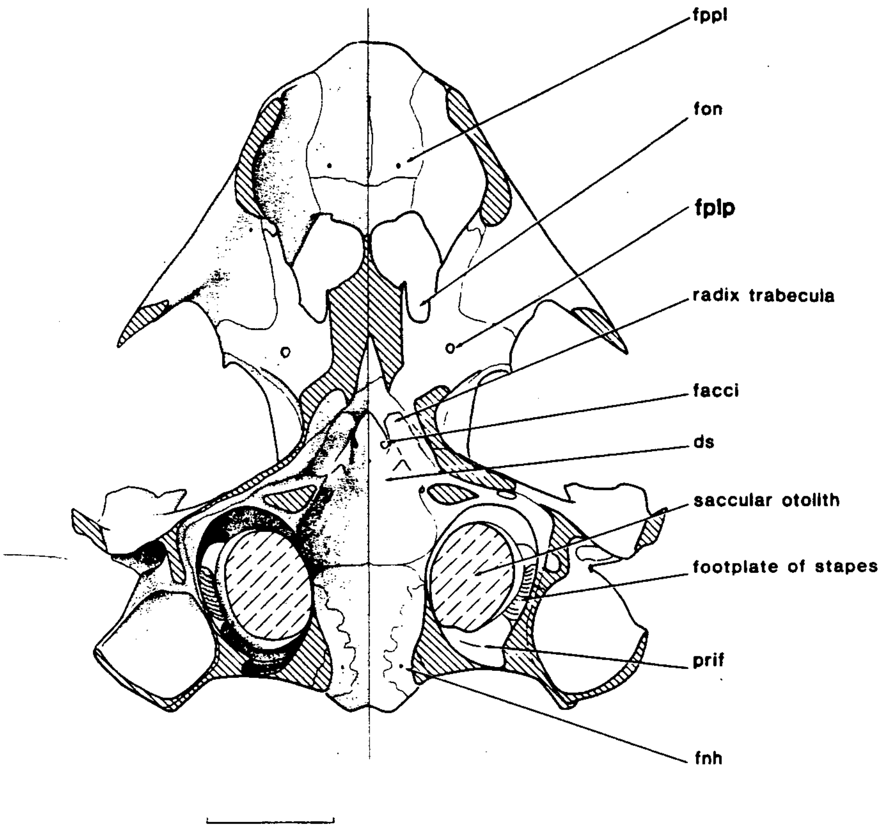

Fig. 2. A horizontally sectioned skull of *Gopherus polyphemus* (USNM 53167, basicranial length = 54.6 mm). The radices trabeculae are short, the dorsum sellae (ds) is reduced, the foramen anterius canalis caroticus interni (facci) are exposed dorsally, the foramen orbitonasale (fon) are large, and the cavum labyrinthicum are large and contain a saccular otolith. From this perspective, the processus interfenestralis (prif) is indicated only by a ridge on the surface of the ventral floor of the cavum labyrinthicum; fnh = foramen nervi hypoglossi; fplp = foramen palatinum posterius; fppl = foramen praepalatinum.

and *G. praecedens*. By excluding these taxa, I discovered a relatively finite number of equally parsimonious trees. Including these poorly characterized taxa resulted in an enormous increase in the number of equally parsimonious trees that differed only in the placement of these three taxa. Unlike the Branch and Bound algorithm, the Heuristics algorithm is not guaranteed to find all minimum-length trees but is more practical when the number of taxa approaches and exceeds 20.

Finally, I used a Bootstrap algorithm on all taxa, excluding *Gopherus edae*, *G. hexagonatus*, and *G. praecedens*. Following the recommendation of Hauser and Presch (1991), all characters were considered unordered.

I examined the distribution of particular characters, double-checked the data matrix, and examined alternative, slightly less parsimonious cladistic hypotheses with MacClade 2.1 (Maddison and Maddison 1987). I also used illustrations of the cladograms obtained by PAUP with a prerelease version of MacClade (with the permission of Maddison and Maddison, personal communication).

Relationships Among North American Land Tortoises–Genus *Gopherus*

An Analysis of Only Living Testudinidae

The Exhaustive Search algorithm of PAUP yielded three equally parsimonious trees (length = 48, consistency index = 0.938; see Table 4; Fig. 5). One of these three trees supported the recognition of a monophyletic *Xerobates* based on a single synapomorphy: the presence of a vomerine foramen. The remaining two trees did not corroborate *Xerobates* monophyly and differed only in which species of *Xerobates* was basal with respect to the remaining living species of *Gopherus*. A strict consensus tree for these trees supported the recognition of the following monophyletic groups: (1) *Gopherus* and the Testudininae, (2) *Gopherus*, and (3) *G. flavomarginatus* and

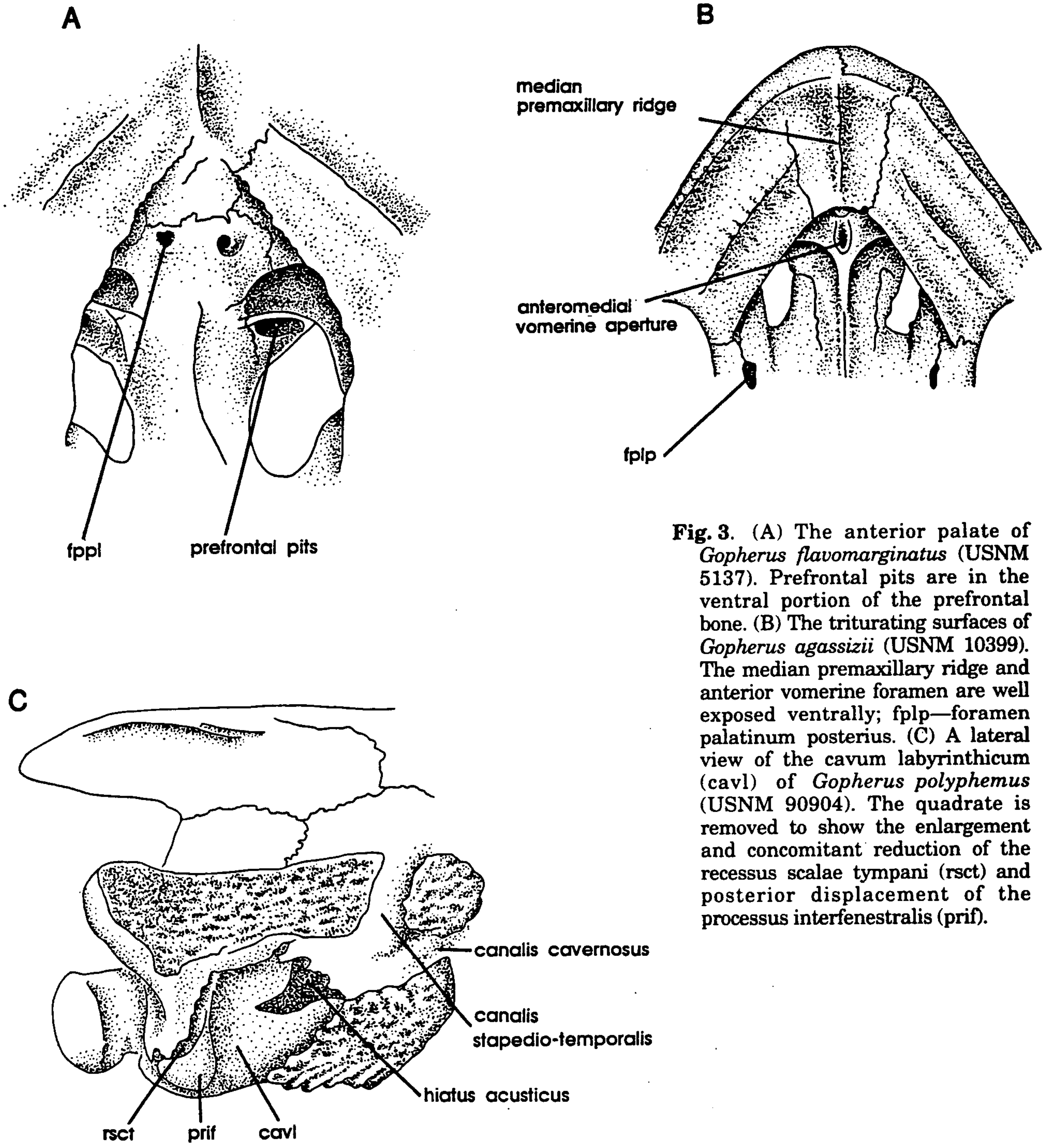

Fig. 3. (A) The anterior palate of *Gopherus flavomarginatus* (USNM 5137). Prefrontal pits are in the ventral portion of the prefrontal bone. (B) The triturating surfaces of *Gopherus agassizii* (USNM 10399). The median premaxillary ridge and anterior vomerine foramen are well exposed ventrally; fplp—foramen palatinum posterius. (C) A lateral view of the cavum labyrinthicum (cavl) of *Gopherus polyphemus* (USNM 90904). The quadrate is removed to show the enlargement and concomitant reduction of the recessus scalae tympani (rsct) and posterior displacement of the processus interfenestralis (prif).

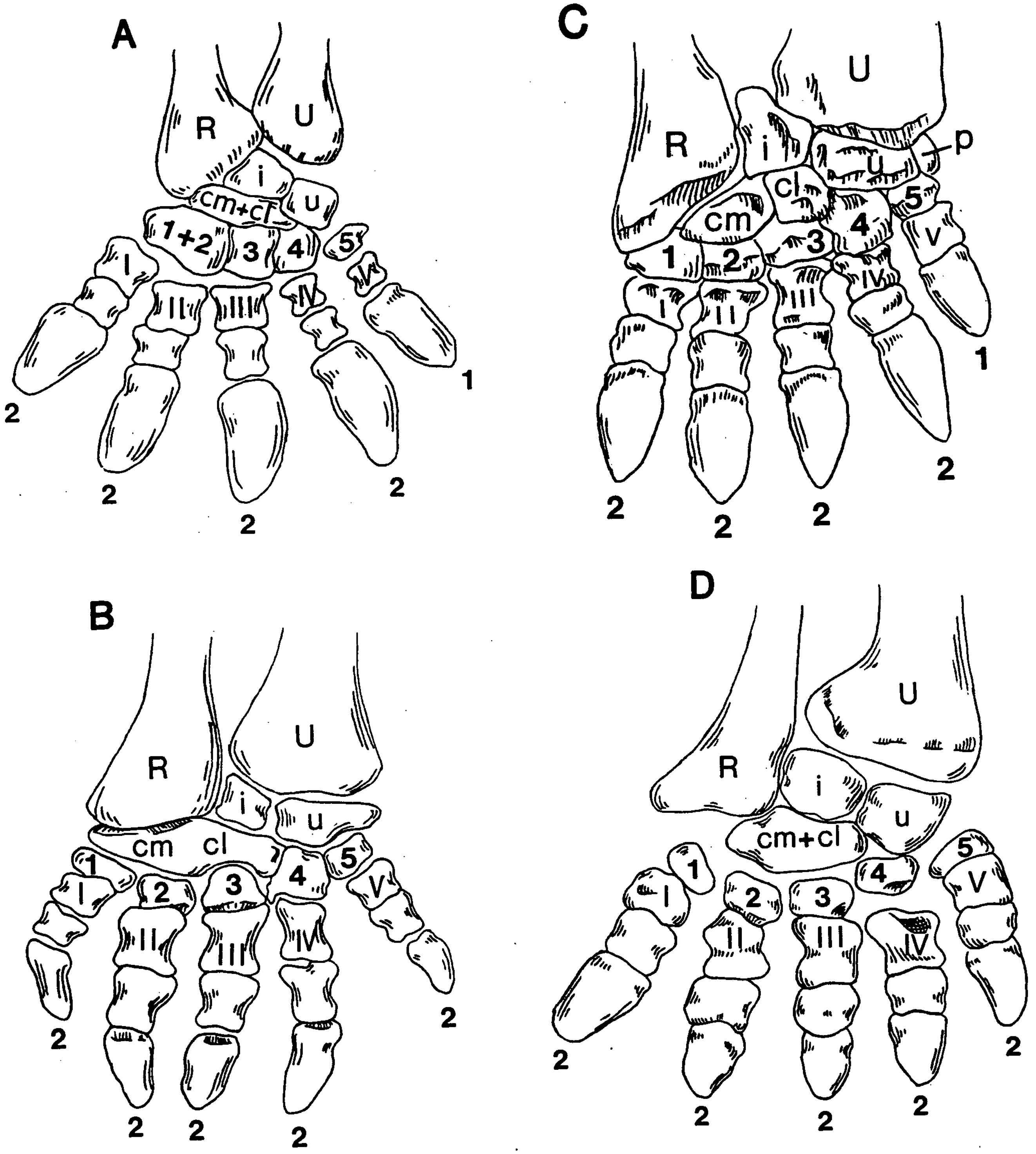

Fig. 4. The manus of tortoises; R = radius, U = ulna, cl = lateral centrale, cm = medial centrale, i = intermedium, p = pisiform, u = ulnare, 1–5 = carpals 1–5, I–V = metacarpals I–V; the numbers at the ends of each digit (1 or 2) refer to the number of phalanges in that digit; (**A**) left manus of *Manouria emys* (SMF 67587); (**B**) left manus of *Geochelone ephippium* (USNM 29309, drawn from a radiograph); (**C**) reversed right manus of *Gopherus laticuneus* (UCMP 15854, redrawn from Bramble 1982); (**D**) left manus of *Stylemys nebrascensis* (UMMP 17600, redrawn from Auffenberg 1961); (**E**) left manus of *G. flavomarginatus* (USNM 51357, drawn from a radiograph); (**F**) left manus of *G. canyonensis* (UCMP 63746, redrawn from Bramble 1982; first metacarpal is my hypothesis); (**G**) reversed right manus of *G. agassizii* (USNM 6718); (**H**) left manus of *G. polyphemus* (USNM 7555, drawn from a radiograph).

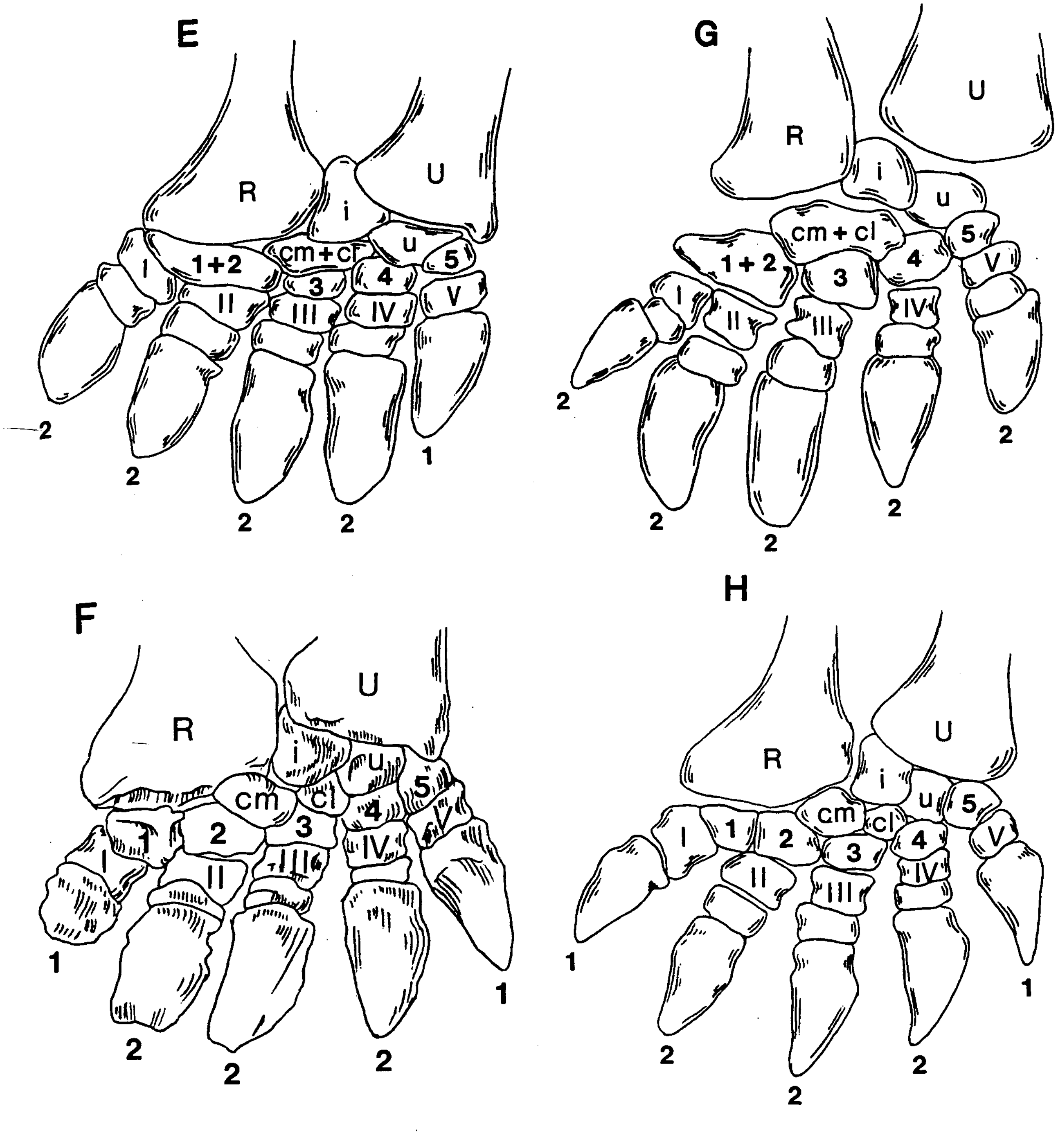

Fig. 4. *Continued.*

Table 4. Statistics from the exhaustive search routine of PAUP (Phylogenetic Analysis Using Parsimony), which provided three trees with the most parsimonious phylogeny of only living taxa of North American tortoises.

Statistics for the three trees that give the most parsimonious phylogeny	
Tree length	48
Consistency index	0.938
Consistency index excluding uninformative characters	0.889
Retention index	0.824
Statistics for the single tree that supports *Xerobates* monophyly	
f value	27
f ratio	0.1646
Statistics for the two trees that support *Xerobates* paraphyly	
f value	24
f ratio	0.1463

Consensus statistics for all three trees	Strict and major rule consensus	Adams consensus
Consensus fork index—component count	3	4
Normalized consensus fork index of Colless (1980)	0.750	1.000
Term information of Nelson and Platnick (1981)	8	9
Total information of Nelson and Platnick (1981)	11	13
Consensus information of Mickevich (1978)	0.667	0.833
Weighted consensus fork index of Colless (1980)	0.786	0.929
Levels sum of Schuh and Farris (1981)	17	18
Consensus index (1) of Rohlf (1982)	0.800	1.000
–ln [consensus index (2)] of Rohlf (1982)	5.753	6.851
Consensus index (2) of Rohlf (1982)	0.003	0.001

G. polyphemus. Monophyly of *Xerobates* was not supported by strict consensus.

On the other hand, an Adams consensus tree supported all three monophyletic groups and monophyly of *Xerobates*. Thus, although there is support for the monophyly of *Gopherus* sensu lato and for the monophyly of *G. flavomarginatus* and *G. polyphemus*, it is not possible when considering only living forms to support unequivocally the monophyletic status of *Xerobates*. At best, *Xerobates* must be considered a metataxon.

An Analysis of Living and Fossil North American Tortoises

With the Branch and Bound and with the Heuristics Search algorithms, 549 equally parsimonious trees (length = 60, consistency index = 0.817; Table 5) were obtained. Both algorithms obtained the same number of minimal length trees. None of the three means of determining consensus (Strict, Adams, and Majority Rule) supported the monophyly of *Xerobates*; in all instances *Xerobates* was recognized as paraphyletic relative to *Gopherus* sensu stricto.

In one analysis of fossils with the Branch and Bound algorithm, *Gopherus* sensu stricto fossils were excluded, whereas in another, *Xerobates* fossils were excluded. In the first PAUP analysis, nine equally parsimonious (length = 56), fully resolved (i.e., no polytomous nodes) trees were obtained. *Xerobates*, as defined by Bramble (1982) and including two living and two extinct taxa, was paraphyletic in all nine trees. Furthermore, *G. agassizii* and *G. berlandieri* were sister taxa in only three of the nine trees. A Bootstrap algorithm with the same abbreviated data set also demonstrated that *Xerobates* is paraphyletic.

The Branch and Bound algorithm was then used on a data set that excluded the *Xerobates* fossils; 183 equally parsimonious (length = 59) trees were

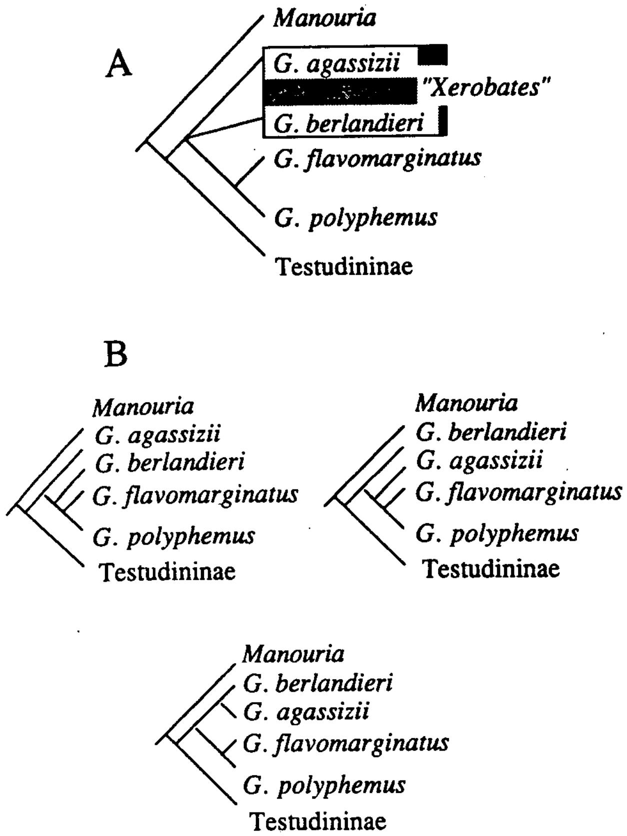

Fig. 5. (A) The Strict Consensus Tree of living taxa in this study. This tree was obtained from three trees (B), each of which had a length of 48 and a consistency index of 0.938.

found. A Strict Consensus tree again recognized *Xerobates* (*G. agassizii* and *G. berlandieri* in this analysis) as paraphyletic, and *Gopherus* sensu stricto as monophyletic within a polytomy. A Majority Rule Consensus tree recognized the same pattern of relationship and also found more resolution (less polytomous nodes) within *Gopherus* sensu stricto. I conclude from these patterns of relationship that *Xerobates* is paraphyletic and should not be recognized.

Because there is no objective character evidence for selecting one tree over the other 548 trees, I chose to provide the character evidence for the Strict Consensus tree (Fig. 6; Appendix C). Alternatively, I could subjectively choose a tree that best reflected the earliest stratigraphic appearance of the fossil and living *Gopherus*. In this tree, *G. laticuneus* of the Chadronian (early Oligocene) is the sister taxon of the remaining *Gopherus*, whereas *G. brevisterna* of the Arikareean (early Miocene) is the sister taxon of *Gopherus* sensu stricto.

Mitochondrial DNA Evidence

Harrison (1989) discussed the utility of mitochondrial DNA (mtDNA) for studies of evolutionary and population biology. He described two ap-

Table 5. Statistics obtained from the branch and bound and heuristic search algorithms of Phylogenetic Analysis Using Parsimony (PAUP) applied to living and fossil taxa but excluding *Gopherus edae*, *G. hexagonatus*, and *G. praecedens*.

Statistics common to all 549 trees			
Tree length	60		
Consistency index	0.817		
Consistency index excluding uninformative characters	0.780		
Retention index	1.085		
Consensus statistics for all 549 trees	Strict consensus	Adams consensus	Majority rule (50%)
Consensus fork index—component count	6	8	10
Normalized consensus fork index of Colless (1980)	0.500	0.667	0.833
Term information of Nelson and Platnick (1981)	27	30	34
Total information of Nelson and Platnick (1981)	33	38	44
Consensus information of Mickevich (1978)	0.500	0.571	0.667
Weighted consensus fork index of Colless (1980)	0.367	0.422	0.489
Levels sum of Schuh and Farris (1981)	98	102	111
Consensus index (1) of Rohlf (1982)	0.529	0.588	0.872
–ln [consensus index (2)] of Rohlf (1982)	20.650	24.793	26.991
Consensus index (2) of Rohlf (1982)	1.080^{-9}	1.710^{-11}	1.900^{-12}

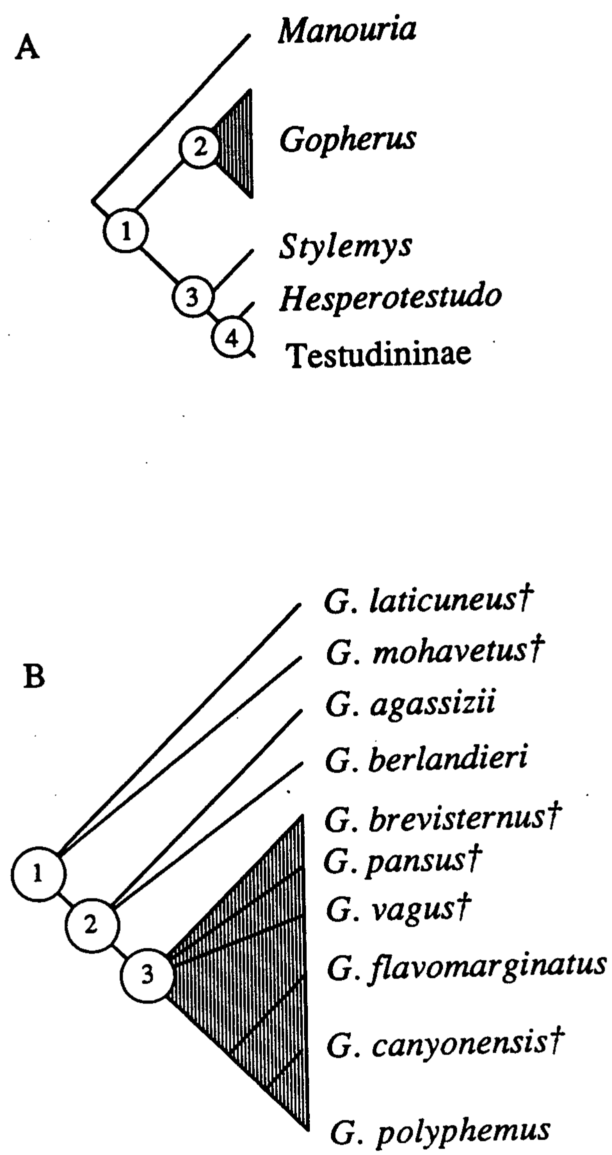

Fig. 6. (A) The Strict Consensus Tree of living and fossil taxa in this study (length = 64, consistency index = 0.766). The relationships among *Gopherus* are illustrated in cladogram B (B). The numbered nodes are supported by synapomorphies (Appendix D).

proaches to the study of phylogenetic history. In one approach, simple measures of genetic distance are used to compare restriction site maps or restriction fragment patterns. Studies of this sort have often focused on the relationships between closely related species. Lamb et al. (1989) used this approach to examine the phylogeny of *Gopherus*, especially *G. agassizii*. They suggested that *G. polyphemus* and *G. flavomarginatus* are sister taxa and that *G. agassizii* is paraphyletic relative to *G. berlandieri*. This kind of analysis of mtDNA variation is not without pitfalls. For example, Harrison (1989) warned that there are unanswered questions especially regarding phylogeny reconstruction. Are distance measures appropriate for studies of historical relationships? With only two character states—presence and absence—will homoplasy be too high? There are many ways to lose a restriction site but only one to gain one; therefore, are some parsimony methods better than others?

In the other approach noted by Harrison (1989), restriction sites are conceived of as characters with two states, either present or absent. He favored this second approach for phylogenetic analysis, which was also used—but less extensively—by Lamb et al. (1989).

Two other admonishments by Harrison (1989) apply to both approaches of historical analysis of mtDNA. First, he notes that it is ill-advised to assume that a molecular clock, which operates for the mtDNA of one group, also operates similarly in a different group of organisms. In fact, the existence of a molecular clock must be determined for each study group by calibration with outgroups. A nucleotide sequence divergence can be estimated from restriction fragments with a method described by Nei and Li (1979). Lamb et al. (1989) did this. Such estimates require that there be outgroups, so that a molecular clock can be calibrated. Lamb et al. (1989) did not do this. Instead, they followed Wilson et al. (1985), who estimated a rate of genetic divergence (i.e., a molecular clock speed) at 2%/million years for selected vertebrates. This supposition remains to be tested for *Gopherus*. Second, Harrison (1989) stated that there seems to be no special correspondence between the amount of sequence divergence and the taxonomic rank assigned to the groups under study. In fact, conspecifics in one group may show more sequence variability than members of different genera in another group. Thus, the range of variation in mtDNA in *G. agassizii* may considerably overlap with mtDNA variation in other species of *Gopherus*. The focus of Lamb et al. (1989) was *G. agassizii*, of which 56 specimens from 22 localities were examined. Seven specimens of the remaining three species of *Gopherus* from three localities were examined. It is possible, indeed probable, that the variation in the mtDNA of other species of *Gopherus* may broadly overlap the variation in *G. agassizii* (Lamb et al. 1989).

Phenetic and cladistic methods of data analysis were employed by Lamb et al. (1989). Phenetic methods, however, do not necessarily reflect phylogenetic affinities. One of the conclusions by Lamb et al. (1989) was that there was cladistic evidence for the monophyly of *Xerobates*, but their unrooted tree was arbitrarily rooted between *Xerobates* and *Gopherus* (Fig. 7). This was done because the phenetic measures indicated that the two groups were the most different from one another and because there was no outgroup. Without an outgroup for *Gopherus* (and *Xerobates*), it is not possible to verify the monophyly of either *Xerobates* or the four living species of *Gopherus*.

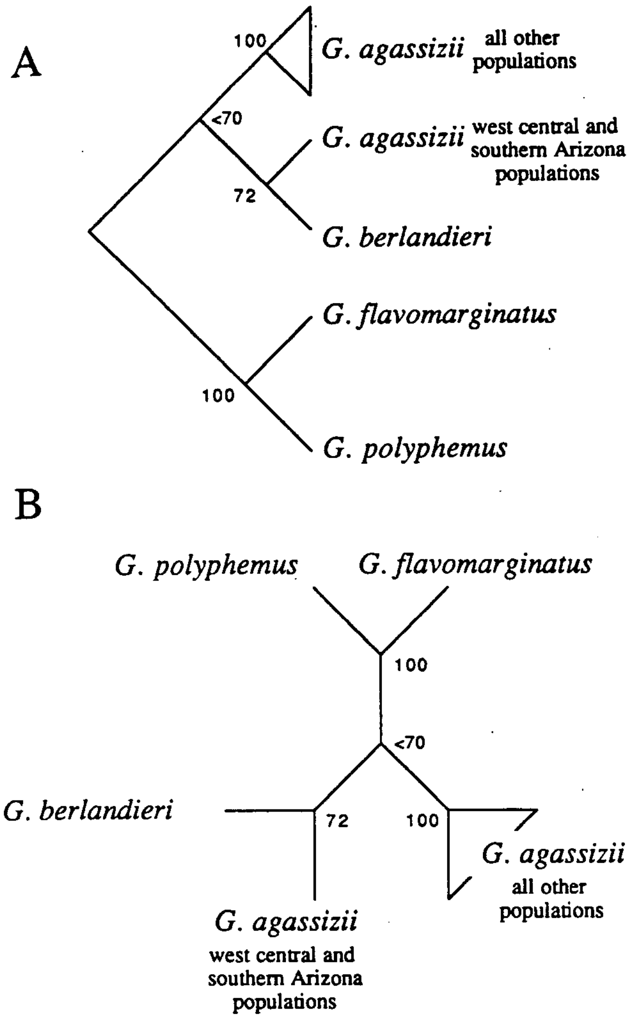

Fig. 7. (A) Figure 4B redrawn from Lamb et al. (1989:82). This illustration was a Wagner parsimony network generated from a presence/absence mtDNA fragment matrix. The root was arbitrarily selected along the branch separating *Gopherus* sensu stricto and *"Xerobates."* The numbers are percentages from a bootstrap analysis and only numbers exceeding 70 were shown. (B) The same figure drawn as a network and illustrating that the selection of a root entirely determines the taxa that may be considered monophyletic.

Phylogenetic Implications of the Geologic and Biogeographic History of the North American Tortoises

Discussions of the geological distribution and historical biogeography of *Gopherus* can be found in Brattstrom (1961), Bramble (1971, 1982), Auffenberg (1974) and Morafka (1988). Most comprehensive of these is Morafka's (1988), which focused primarily on *G. flavomarginatus* but included data that pertained to much of the herpetofauna of western North America. It is beyond the scope or intention of this paper to repeat these analyses. However, some comments are necessary because certain aspects of the biogeographic history of *Gopherus* have been used to support the recognition of the two genera versus one genus classification of living North American tortoises.

Biogeographic history can corroborate a particular classification if that history is concordant with phylogeny. Unraveling distributional history cannot be done without explicit hypotheses of relationship—for example, cladistic hypotheses (Nelson and Platnick 1981; Humphries and Parenti 1986). Based on the stratigraphic record of *Gopherus* (Fig. 8) and on information about the type of sediments wherein *Gopherus* fossils have been recovered, Bramble (1982:864) recognized "separate biogeographic and environmental histories" as support for his division of *Gopherus* into separate genera. However, the cladistic hypotheses derived here do not document separate histories (i.e., recognition of separate genera).

The reviewers of *Gopherus* biography have primarily employed a dispersalist approach to biogeographic analysis. It has not been possible to consider the effect of alternative analytical

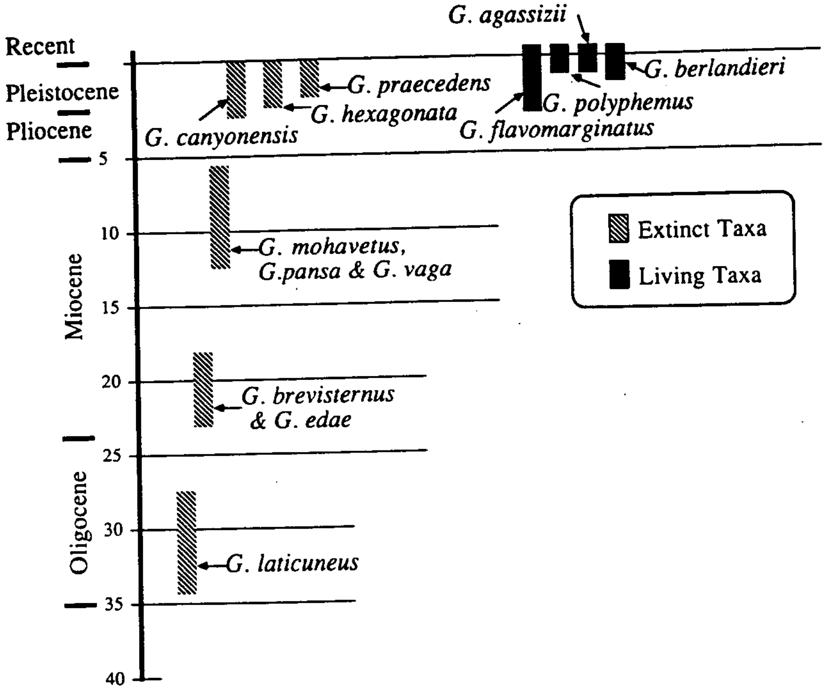

Fig. 8. The geological history of *Gopherus*. The summarized information is from Bramble (1971), Auffenberg (1974), Van Devender et al. (1976), and Van Devender (1986).

paradigms (i.e., vicariance) because there existed no detailed theories of a phylogenetic history for *Gopherus*. A reconsideration of the stratigraphic, sedimentological, and paleoenvironmental evidence and the phylogenetic theories proposed here should provide better insights into the history of North America's largest surviving terrestrial ectotherm.

Acknowledgments

This paper is dedicated to the memory of my friend, teacher, and mentor, Richard Estes; he was accepting and demanding and always had an infectious joy for life. Also, I thank several colleagues for comments on this paper: A. Berta, L. Blinderman, D. Bramble, R. Estes, R. Etheridge, L. Grismer, J. H. Hutchison, G. Pregill, and M. Simpson. Financial support for this study came from the College of Sciences of San Diego State University, the U.S. Fish and Wildlife Service, the Smithsonian Institution (Predoctoral Fellowship), and the National Science Foundation (DEB 81–14467). During the preparation of this manuscript, space and facilities were generously made available by the San Diego Natural History Museum. All of the above interpretations and conclusions are my responsibility.

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Appendix A. The data matrix employed in this study of the phylogenetic history of the tortoise genus *Gopherus*.[a]

Manouria	00010	00000 12	00000	00000	00000	10000	10000	01010 2	00 1
G. agassizii	01121	11220	11111	02101	00000 12	11001 1	01201	01100 1	10
G. berlandieri	01121	11220	11110 1	02101	00000 11	11001	01201	01101	10
G. brevisternus	0?121	1??21	??0?0	0?111	?????	?100?	???01	1??01	2?
G. canyonensis	1?222	1??21	??1?0	0?111	01110	0100?	???01	01?01	10
G. edae	?????	?????	?????	?????	?????	?????	???01	1????	??
G. flavomarginatus	11222	11221	11110	02111	01000 1	11001	01?01	01101	10
G. hexagonatus	?????	?????	?????	?????	?????	?????	???01	01101	02
G. laticuneus	0?021	?1???	100?1	??10?	00000	1?0??	0??01	0??01	1?
G. mohavetus	0????	?????	??0??	?????	0??0?	??0??	0??01 1	0??01	11
G. pansus	?????	?????	?????	??11?	?????	?????	???01	01?01	1?
G. polyphemus	12222	11221	11110	02111	01010 1	01001	01001	01111	10
G. praecedens	?????	?????	?????	?????	?????	?????	?????	?????	??
G. vagus	?????	?????	?????	??111	?????	?????	?????	0??01	??
Hesperotestudo	00000	11000 2	00110 2	0?002	00200	01010	00?11	100?1	21
Stylemys	00020	11020	00010	0?001	00200	01100	0??11	10011	02
Testudininae	00000	11010 2	00010	11002	10000 1	01100 2	01211	10001 1	21

[a] 0 = plesiomorphic; 1 and 2 = apomorphic; ? = unknown.

Appendix B. Characters used to infer the relationships among *Gopherus*.

The following are brief descriptions of characters more fully described and analyzed elsewhere (Crumly 1984a, 1984b). Plesiomorphic character states are indicated by state 0, whereas derived (apomorphic) character states are indicated by state 1 or state 2.

A. **Cranial Characters.** Terminology is from Gaffney (1979) and Crumly (1982, 1984a).

1. Batagurine process and the pterygoid (McDowell 1964; Crumly 1984a).
   State 0. The pterygoid broadly underlaps and contacts the batagurine process in most tortoises and batagurine emydids.
   State 1. The enlarged cavum labyrinthicum of some *Gopherus*, housing a saccular otolith, prevents the pterygoid from underlapping and contacting the batagurine process (Fig. 3C).
2. Basisphenoid rostrum (Crumly 1984a; Fig. 2).
   State 0. In most testudinoids including the outgroups selected for this study, the radix trabeculae are long and converge anteromedially but do not form a mutual contact.
   State 1. The radix trabeculae of *Gopherus* are short and robust and converge slightly but do not contact one another.
   State 2. The radix trabeculae of *Gopherus polyphemus* and perhaps other fossil *Gopherus* are very short and the dorsum sellae is reduced (this region has been prepared in only a few fossil tortoises).
3. Cavum labyrinthicum (Bramble 1971, 1982; Crumly 1984a; Figs. 2 and 3C).
   State 0. In most cryptodires and the outgroups used here, the cavum labyrinthicum is about the same size or slightly larger than the recessus scali tympani.
   State 1. The cavum labyrinthicum is somewhat enlarged. All the extant *Gopherus* are known to possess a small or large saccular otolith within the cavum.
   State 2. In some *Gopherus* like *G. flavomarginatus* and *G. polyphemus*, there is an enlarged cavum labyrinthicum to accommodate a very large saccular otolith.
4. Median premaxillary ridge (Bramble 1971, 1982; Crumly 1984a; Loveridge and Williams 1957; Fig. 3B).
   State 0. The ridge is absent in almost all cryptodires (including outgroups) except *Stylemys* and *Gopherus*.
   State 1. In *Manouria emys*, the anterior vomer and posterior premaxillae possess an incipient ridge.
   State 2. The ridge is present in all *Gopherus* and *Stylemys*.
5. Prefrontal pit (Bramble 1971, 1982; Crumly 1984a; Fig. 3A).
   State 0. In all testudinoids other than *Gopherus*, these pits—which are recesses on the ventral portion of the prefrontal bone in the roof of each nasal canal—are absent.
   State 1. In *Gopherus agassizii* and *G. berlandieri*, prefrontal pits are present only in large adults.
   State 2. Pits are always present, regardless of size, in *Gopherus polyphemus* and *G. flavomarginatus*.
6. Triturating ridges of maxillae.
   State 0. Irregular and dentate ridges occur in *Manouria*.
   State 1. In most tortoises, a ridge forms uniform nonserrated keel on each midventral maxillary surface.
   State 2. Accessory labial ridges are present in many *Hesperotestudo*.
7. Foramen arteriomandibulare (Bramble 1971; Crumly 1982, 1984a, 1984b).
   State 0. In most testudinoids other than land tortoises, a separate F. arteriomandibulare—which is an opening in the trigeminal notch located lateral to the foramen cavernosum—is lacking. Some *Manouria* lack this foramen.
   State 1. Most testudinids possess a F. arteriomandibulare.
8. Apertura maxillare (Bramble 1971; Crumly 1982, 1984a).
   State 0. Most land tortoises and some batagurines possess maxillary apertures. These open-

ings are located in the ventral flange of the parietal and enclose the maxillary branch of the trigeminal nerve.
State 1. In many tortoises, including *Gopherus*, maxillary apertures may be either present or absent with equal frequency.
State 2. Some species of *Geochelone* and some other testudinines usually lack apertures.

9. Shape of exposed prootic (Crumly 1982, 1984a, 1984b).
State 0. In *Manouria* and many testudinoids, the shape of the exposed prootic is widest anteriorly.
State 1. In some testudinines (e.g., *Testudo*), the prootic is concealed from dorsal view.
State 2. In most tortoises other than *Manouria*, the prootic is exposed as a narrow quadrangle or is widest posteriorly.

10. Trochlear processes (Crumly, 1984a, 1984b).
State 0. Manouria, *Hesperotestudo*, *Stylemys* and some *Gopherus* have large trochlear processes. The function of such processes is to translate the largely anteroposterior direction of the jaw adductor musculature into dorsoventral forces applied during jaw closure.
State 1. Some *Gopherus* and most testudinines have reduced trochlear processes.

11. Os transiliens (Bramble 1974).
State 0. An ossified os transiliens—a small element in the tendon of the adductor mandibula muscle—is absent in most testudinids and other testudinoids.
State 1. Only *Gopherus* are known to possess an os transiliens.

12. Foramen orbitonasale (Albrecht 1967; Gaffney 1979; Crumly 1982, 1984a, 1984b).
State 0. Moderate to small F. orbitonasale are common to many testudinoids. These openings lie between the fossa nasalis to the fossa orbitalis and contain the posterior nasal artery.
State 1. Large F. orbitonasale occur in some *Gopherus*.

13. Posterior maxillary processes.
State 0. In testudinines, *Manouria*, some *Gopherus*, and *Stylemys*, these processes are lacking.
State 1. Hesperotestudo and many *Gopherus* possess posterior maxillary processes, which are extensions of the maxillae that increase the length of the vertical laminae that form the labial edges of the upper jaw.

14. Fissura ethmoidalis.
State 0. In *Manouria* and batagurine turtles, the fissura ethmoidalis is narrow. This fissure is a space at the back of the fossa nasalis that contains the olfactory nerves.
State 1. For most testudinids the F. ethmoidalis is wide.

15. Vomerine foramen (Bramble 1971; Fig. 3B).
State 0. Most land tortoises and other testudinoids lack a vomerine foramen.
State 1. Some *Gopherus* possess this foramen. This small unpaired aperture is usually at or near the vomero–premaxillary suture and may transmit an anterior branch of the palatine artery (Albrecht 1967).

16. Surangular process (Crumly 1982, 1984a, 1984b).
State 0. All North American tortoises (living and fossil) and *Manouria*, like batagurines, lack a suragular process.
State 1. The surangular process is shared by the Testudininae. It is a tongue-in-groove interdigitation of the surangular with the dentary.

B. Neck, Tail, and Soft Anatomy Head Characters

17. Mental glands (Winokur and Legler 1975).
State 0. Class II glands—simple invaginations lined with glandular epithelium—are present in batagurine turtles and *Manouria*.
State 1. Most testudinids lack mental glands.
State 2. Class I glands—which are complex and multilobed and bear a duct to the skin surface—are present only in *Gopherus*.

18. Dorsal vertebral postzygopophyseal crests (Crumly 1984a, 1984b; Williams 1950).
State 0. In almost all testudinoids, these crests are present and represented as raised ridges on the dorsal surfaces of the postzygopophyses that converge at the apex of the neural arch.
State 1. Gopherus lack crests. The only other testudinid lacking these crests is *Malacochersus*, noted as an inhabitant of rocky outcrops and in the habit of retreating into crevices to avoid predators.

19. Postzygopophyses of last cervical vertebrae (Crumly 1984a, 1984b; Williams 1950).

State 0. Most testudinoids have postzygopophyses that are not elongated.

State 1. Elongated postzygopophyses occur only in *Gopherus*.

C. Appendicular characters (for characters 21–26, see Auffenberg 1961, 1966, 1976, Bramble 1971, 1982, and Crumly 1984a, 1984b).

20. Intertrochanteric fossa of the humerus.
    State 0. This ventroposteriorly directed fossa may be narrow and long.
    State 1. The narrow fossae is relatively shorter.
    State 2. A short, deep fossa that may be either broad or narrow.

21. Medial centrale (Fig. 4).
    State 0. The medial centrale does not extend to the medial edge of the manus, thus the radius articulates with the first and sometimes the second distal carpalia (Crumly 1984a). *Manouria*, *Stylemys*, *Hesperotestudo*, and *Gopherus* share this condition.
    State 1. The medial centrale can extend medially to the medial edge of the manus, separating the radius from the distal carpals.

22. Pisiform (Fig. 4).
    State 0. The pisiform—which articulates with the ulna and is located on the lateral edge of the manus—is present in *Manouria* and other tortoises.
    State 1. The pisiform is often lacking in *Gopherus* and other tortoises.

23. Number of phalanges in the first and fifth digits (Crumly 1984a; Fig. 4).
    State 0. Manouria and many other tortoises have two phalanges in the first four digits and only one phalanx in the fifth.
    State 1. In some species of *Gopherus*, the first and fifth digits possess only a single phalanx, whereas the middle three digits bear two phalanges each.
    State 2. Two phalanges in all five digits is common (but not plesiomorphic) for tortoises, especially the larger species.

24. The medial centrale and a lateral centrale (Bramble 1982; Crumly 1984a; Fig. 4).
    State 0. In most testudinoids, including tortoises, the two centralae are fused.
    State 1. In *Gopherus polyphemus* and *G. canyonensis*, the centralae are separate or a suture is present.

25. Distal carpals four and five (Fig. 4).
    State 0. In most tortoises, including *Gopherus*, the fourth and fifth carpals are separate elements.
    State 1. Occasionally, these bones fuse.

26. Distal carpals one and two (Fig. 4).
    State 0. Separate first and second carpals occurs in *Gopherus polyphemus* and *G. canyonensis*.
    State 1. In *Manouria* and many species of *Gopherus*, the first and second carpals are often fused.

27. Scar of the M. latissimus dorsi.
    State 0. For *Manouria*, the M. latissimus dorsi scar is barely visible or absent.
    State 1. For most tortoises, including *Gopherus*, this muscle scar is present as a pit or obvious roughened area located on the proximal shaft of the humerus, opposite from the fossa intertrochanterus.

28. Humerus curvature (Crumly 1984a).
    State 0. The humerus may be relatively straight, as in *Manouria* and many species of *Gopherus*.
    State 1. Conversely, the humerus may be curved, as in *Stylemys* and the Testudininae.

29. Ectepicondylar foramen.
    State 0. In *Manouria*, *Stylemys*, and testudinines, this foramen is present as a canal in the distal end of the humerus.
    State 1. Hesperotestudo lack the ectepicondylar foramen.

30. Fifth digit phalanx of the pes.
    State 0. The phalanx is present in *Manouria*.
    State 1. In *Gopherus*, this fifth digit phalanx is sometimes present.
    State 2. In the Testudininae, this phalanx is absent in some taxa and usually present in other species.

31. The calcaneum and astragalus are ankle bones that are sometimes either fused or fail to differentiate.
    State 0. These bones are represented by a single element in most testudinids.
    State 1. In *Manouria*, the calcaneum and astragalus are separate elements.

32. Forearm scales.
    State 0. Large imbricate scales are plesiomorphic for tortoises and present in *Manouria*.

State 1. Small to moderate scales, usually juxtaposed, is the derived condition for most testudinids.

33. Hip spines.
State 0. Plesiomorphically (e.g., *Manouria emys*), hip spines are present as a group of protuberant, often pointed scales.
State 1. A single large and distinct spine, as in *Manouria impressa*.
State 2. Hip spines are usually reduced or entirely absent, as in *Gopherus*.

D. Shell Characters

34. Cervical scute (nuchal scute).
State 0. In *Manouria* and many *Gopherus*, this scute is broad and nearly square.
State 1. In testudinines, the cervical scute is usually a narrow rectangular scute.

35. Supracaudal scute.
State 0. In *Manouria*, there is a right and left half of this scute divided by a sulcus.
State 1. In most tortoises, the supracaudal scute is a single entire scute.

36. Pectoral scute shape (Crumly 1984a).
State 0. In *Manouria impressa* and most species of *Gopherus*, the pectoral scute is rectangular.
State 1. The pectoral scute is reduced medially to a narrow scute that crosses the plastron to contact the opposite pectoral scute. This is observed in some species of *Hesperotestudo* and some *Gopherus*, like *G. brevisternus.*
State 2. The medial portion of the pectoral scute is absent in *Manouria emys* but is present in *Manouria emys phayeri* (Hoogmoed and Crumly 1984).

37. Shell ossification (Crumly 1984a).
State 0. Plesiomorphically, the shell of testudinids is well ossified and the bones are relatively thick.
State 1. In *Manouria* and many species of *Gopherus*, the shell is relatively thin. It is not as thin as the shell of *Malacochersus* but thinner than the shells of *Geochelone* tortoises.

38. Anal lip of the plastron.
State 0. The anal lip is thickened to some degree in both *Manouria* and most *Gopherus*. In testudinids in general, the posterior lip of the plastron is sexually dimorphic, being thicker in adult males where there is some plastral concavity accompanied by a downturning of the anal lip of the plastron.
State 1. Although the anal lip in *Gopherus* is thickened by comparison to *Kinixys*, *Chersina*, and *Pyxis*, it is relatively less thickened in some of the smaller species of *Gopherus* (e.g., *G. berlandieri*).

39. Gular scute proportions.
State 0. Plesiomorphically, the gular scute is longer than it is wide.
State 1. In *Manouria*, *Stylemys* and some Testudininae, the width of the gular scute is equal to or greater than its length.

40. Gular scute and the anterior entoplastron.
State 0. In *Manouria*, the gular scute does not overlap or just reaches the edge of entoplastron. This also sometimes occurs in *Gopherus agassizii* and *G. berlandieri*.
State 1. In all other *Gopherus* and most other tortoises, the gular scutes broadly overlap the entoplastron.

41. Marginal scutes and the second pleural scute (Crumly 1984a, 1984b).
State 0. In *Manouria*, marginals 5, 6, and 7 contact the second pleural scute and they are about the same size and shape (undifferentiated).
State 1. In *Gopherus*, unlike all other tortoises, the fourth and sixth marginals are enlarged, and marginals 4, 5, and 6 contact the second pleural scute.
State 2. In the Testudininae, marginals 5 and 6 are enlarged and contact the second pleural scute. The fourth marginal does not contact the second pleural.

42. Inguinal scutes.
State 0. Plesiomorphically and in *Manouria*, the inguinal scutes are large, often multiple, and contact the femoral scute.
State 1. In *Hesperotestudo* and plesiomorphically for the Testudininae, the inguinal scutes are large but represented by only a single scute that contacts the femoral scute.
State 2. In *Stylemys* and some *Gopherus*, the inguinal fails to contact the femoral scute, because it is separated by an extension of the abdominal scute that forms a small portion of the plastral rim.

Appendix C. The purpose, means of computation, and interpretation of the consensus statistics of Phylogenetic Analysis Using Parsimony (PAUP).

When analyzing complex data matrices using Swofford's (1989) algorithm, Phylogenetic Analysis Using Parsimony (PAUP), it is common to obtain numerous equally parsimonious trees. So many trees, in fact, that it becomes impossible to examine each of them individually. Furthermore, because all these trees are equally parsimonious, it is impossible to objectively select one tree over all the others. One approach to this stumbling block is to determine how all the trees agree (i.e., calculate a consensus tree). Three different types of consensus trees can be calculated by PAUP:

1. Strict consensus tree. Trees of this sort include only those nodes shared by all the equally parsimonious trees discovered.
2. Adams consensus tree. There are two methods for calculating Adams consensus trees (called Adams 1 and Adams 2 by Rohlf 1982); the second approach is employed by PAUP. A consensus is initially determined from the first two trees amongst the equally parsimonious trees. Next, a consensus is determined from the tree obtained in the first step and the third equally parsimonious tree. Then the tree obtained in this second step is employed along with the fourth equally parsimonious tree to formulate a consensus tree that will be used with the fifth equally parsimonious tree. This procedure continues until all the equally parsimonious trees have been included. The order in which trees are input into the consensus formulation can impact the resultant tree; the first two trees have the greatest impact. Most troubling is that a node (uniting particular taxa) may be obtained that is not shared by any of the trees from which consensus is derived.
3. Majority rule consensus tree. These trees bear nodes shared by the majority of equally parsimonious trees. The minimum acceptable majority is assigned by the investigator prior to the formulation of a consensus tree. The minimum allowable majority is 50% and the maximum majority (100%) produces a consensus tree that should be identical in all respects to the strict consensus tree.

Problems regarding the theoretical basis of consensus trees make their evaluation difficult. Some have criticized them on the grounds that they produce a tree that is not represented, in all details, by any tree from within the set of trees used to calculate consensus in the first place. Once a consensus tree has been calculated, however, it may be necessary to compare how well the consensus tree reflects a fully resolved (i.e., dichotomous) phylogenetic hypothesis. The question becomes: is this consensus tree approaching a resolved phylogeny or are the individual trees from which consensus is determined so different from one another that consensus can only be represented as a largely unresolved bushlike tree?

PAUP provides nine statistical measures that can be used to compare consensus trees of different types to fully resolved trees. These indices are of three types (Rohlf 1982):

1. Indices based on unweighted count of the number of taxa united by each node of the consensus;
2. Indices based on weighted count of taxa per node; and
3. Indices based on probability. Below, I briefly review these measures.

Mickevich's Consensus Information

Mickevich (1978) proposed this parameter to compare the differences between resolved and unresolved (bushy) trees. Calculation was described as follows:

1. Each cluster in a consensus tree is described through an artificial variable assigned a value of 1; 0 for all taxa not in the cluster.

2. Based on step 1, it is determined how many extra steps would be required to allow the artificial variable to evolve on a bush.
3. The total number of extra steps (summed over all clusters) is taken as the difference between the obtained tree and a bush. This number is assigned the parameter, X. The higher the number the further the tree is from a bush.
4. To normalize the value of X, it is divided by the maximum value it may assume, where t = the number of taxa:

   for directed trees:
   $I(t) = (t/2)(t - 1/2)$ = maximum value for X;
   for undirected trees:
   $I(t) = (t - 1/2)(t - 2/2)$ = maximum value for X.
5. Consensus information = $X/I(t)$ (coefficient of similarity between two alternatives—bushy or dichotomous).

This parameter varies between 0 and 1, and 1 indicates that the consensus tree differs greatly from a bushy unresolved tree. Rohlf (1982) identified this index as one based on weighted counts of taxa per node and provided a different method of calculation. He also has noted several problems with this index. First, very large clusters of taxa (nodes uniting many taxa) and very small clusters may have less influence on the value of the computed parameter of consensus information than will intermediate sized clusters. Second, tree shape influences the result (earlier noted by Colless 1981); maximum values of consensus information can only be reached when the consensus tree is maximally pectinate or asymmetrical. A different maximum value for consensus information prevails when a tree is maximally symmetrical (Rohlf 1982).

Consensus Fork Index

Colless (1980) proposed this index to determine how different a consensus tree is from a completely unresolved bush. The basis of this index is an unweighted count (Rohlf 1982) of the nodes in the obtained consensus tree. Colless (1980) described computation as follows:

1. Count number of branching points (excluding basal one).
2. Number will be between 0 and $(n - 2)$, where n = number of OTUs.
3. Dividing by $n - 2$ yields number between 0 and 1. When the value approaches 1, there is great consensus among equally parsimonious trees:

   number of branches/$n - 2$ = normalized consensus fork index.

In PAUP 3.0a, the Normalized Consensus Fork Index is not reported. Instead, a count of the number of branching points (component count) is provided along with a Weighted Consensus Fork Index.

Although Colless suggests that this is the "simplest way" to measure the differences between unresolved bushy trees and a consensus tree, he does not provide a reason for preferring his measure over the earlier proposed measure of Mickevich (1978).

Later, however, Colless (1981) reported that symmetrical and asymmetrical trees are compared differently by the Consensus Information parameter of Mickevich (1978), which was also noted by Rohlf (1982).

Weighted Consensus Fork Index

Colless (1980) also proposed a second parameter to distinguish bushy trees with a certain number of components from other differently bushy trees with the same number of components. He recognized that trees with the same consensus fork index may be bushy in different ways. He then suggested that more undesirable bushy parts of trees are those that include more taxa. Colless then proposed his Weighted Consensus Fork Index as a way to distinguish trees that are bushy in their basal regions from trees that tend to be bushy in their more terminal regions.

Originally, Colless suggested the following formula for calculating his Weighted Consensus Fork Index:

$$\frac{\text{number of taxa joined by each branch point}}{\tfrac{1}{2}(n-1)(n+2)} = \text{weighted CF index}$$

However, Mickevich and Farris (1981) showed that the denominator of this formula was in error and corrected the formula to

$$\frac{\text{number of taxa joined by each branch point}}{\frac{1}{2}(n-2)(n+1)} = \text{weighted CF index}$$

This parameter, like others, also varies between 0 and 1 and, again, 1 indicates that the consensus tree approaches a fully resolved dichotomous tree.

Term Information and Total Information

Nelson and Platnick (1981) suggested two ways to determine the information content of cladograms. Calculation was based on certain observations of the obtained trees; thus,

component information + term information = total information.

Component information is the number of branch points (including basal node). Because basal node is uninformative, however, it is not counted, and the component information becomes a count of the number of informative branching points (total number of taxa joined by a particular branching point minus 1). Term information is the total number of taxa joined by a particular branching point minus 1.

Schuh–Farris Levels Sum

This weighted count (Rohlf 1982) was proposed by Schuh and Farris (1981). It is computed by the following procedures:

1. For each pair of taxa, count the number of components (shared branching points) that include both taxa.
2. Make such a count for all possible pairs of taxa.
3. Sum all such counts for all possible pairs.

This will correspond to the following:

$$\Sigma N_i = \Sigma n_i(n_i - 1)/2 = \text{levels sum}$$

and the maximum value is

$$N_{\max} = t(5-1)(t-2)/6$$

Rohlf (1982) noted that this parameter is even more sensitive to differences in tree shape than the Consensus Information parameter of Mickevich (1978).

Rohlf Consensus Indices (CI_1 and CI_2)

Two separate indices were proposed by Rohlf (1982). One was a recomputation of the Mickevich's (1978) parameter and, therefore, is a weighted index (CI_1). The other parameter is a probability measure (CI_2). In order to correct for two disadvantages of Mickevich's Consensus Information parameter, Rohlf (1982) suggested the following method of calculation for CI_1:

1. To correct for differences in weight between intermediate and large/small clusters the numerator of CI_1 (ΣN_i) will vary from

   $$2[2^k(k-1)+1] + m\mathrm{L}(\log_2(t-1)) \text{ to } (t-1)(t-2)/2$$

   where k = the number of nodes, t = the number of taxa, and $m = t - 2^{k+1}$.

   The first value is when the consensus is maximally symmetrical and fully resolved (i.e., bifurcating). The second value is for maximally asymmetrical trees that are also fully resolved (i.e., bifurcating and pectinate).

2. To correct for the impact that the shape of the tree has on $N_{\max}$, which is the denominator of CI_1, $N_{\max}$ is defined as ΣN_i for totally bifurcating trees. Then the number of corrections required to change a tree that is not completely bifurcating into a fully resolved and bifurcating tree is calculated. Should the consensus tree be fully resolved then no changes will be necessary and CI_1 will equal 1.0 regardless of tree shape. Should any changes be necessary, these are summed over all nodes ($\Sigma\Delta_i$), see Rohlf (1982:138) for the formula.

Thus, Rohlf's modification of the consensus information parameter of Mickevich (1978) is calculated as

$$\Sigma N_i / \Sigma N_i + \Sigma\Delta_i = \text{consensus index}_1.$$

Rohlf (1982) also suggested a second index to determine the probability that the clusters of the consensus tree will be repeated by chance alone. If the consensus tree approaches full resolution, then the probability will approach zero. In PAUP, this parameter is referred to as CI$_2$ and is calculated as follows:

1. List the number of clusters joining at each node (i) which equals f_i.
2. Determine the total number of bifurcating trees containing the clusters in the consensus tree. This is given as

$$N = \Pi B(f_i)$$

calculated from $i = 1$ to $i = t - 1$, where t = the number of taxa and where $B(f) = \Pi(2k - 3)$ = total number of bifurcating trees with the same f objects calculated from $k = 2$ to $k = f$ (k is equal to the number of nodes).

3. Calculate

$$N/B(t) = \text{a probability} = \text{Consensus Index}_2.$$

If the consensus tree is fully bifurcating (i.e., resolved), then the probability that this resolution is due to chance is very low (approaching 0.0). On the other hand, if the consensus tree is a bush, all the possible trees ($B(t)$) will contain the same taxa; the probability will approach 1.0.

Appendix D. Synapomorphies that support relationships among *Gopherus*.

The numbered nodes from Fig. 6 are supported by the following synapomoorphies. Also, node A2 is supported by the same synapomorphies as node B1.

Node A1—Median premaxillary ridge present (Char. 4, State 1→2), triturating ridges represented by uniform keel (Char. 6, State 0→1), dorsal exposure of prootic narrow and rectangular and/or widest posteriorly (Char. 9, State 0→2), ethmoid fissure wide (Char. 14, State 0→1), mental glands absent (Char. 17, State 0→1), intertrochanteric fossa narrow and relatively short (Char. 20, State 0→1), latissimus dorsi scar present (Char. 27, State 0→1), forearm scales smaller usually juxtaposed (Char. 32, State 0→1; reversal in *Hesperotestudo*), hip spines absent (Char. 33, State 0→2; reversal at Node B3), supracaudal scute entire (Char. 35, State 0→1), gular scutes overlap entoplastron (Char. 40, State 0→1).

Node A2 (and B1)—Radix trabeculae short and robust and only slightly converge (char. 2, State 0→1), prefrontal pits present in adults (Char. 5, State 0→1), maxillary apertures absent (Char. 8, State 0→2), os transiliens present (Char. 11, State 0→1), vomerine foramen frequently present (Char. 15, State 0→1; reversal at Node B3), class I mental glands present (Char. 17, State 0→2), crests absent on the postzygopophyses of last cervical vertebrae (Char. 18, State 0→1), phalanx present on fifth toe (Char. 30, State 0→1), anal lip relatively less thick (Char. 38 State 0→1), gular scute longer than wide (Reversal, Char. 39, State 1→0), marginals four through six contact second pleural scute and fourth and sixth marginals enlarged (Char. 41, State 0→1).

Node A3—Two phalanges in all five digits (Char. 23, State 0→2; reversal in the Testudininae), first and second carpals not fused (Reversal, Char. 26, State 1→0), humerus with prominent curvature (Char. 28, State 0→1; reversal in *Hesperotestudo*), narrow and rectangular cervical scute (Char. 34, State 0→1) reduced medial extension of the pectoral scutes (Char. 36, State 0→1; homoplasious in *G. brevisternus*), shell not thin (Reversal, Char. 37, State 1→0).

Node A4—Loss of median premaxillary ridge (Reversal, Char. 4, State 2→0), intertrochanteric fossa of humerus short and deep, but either broad or narrow (Char. 20, State 1→2), fifth and sixth marginals enlarged and contact the second pleural scute (Char. 41, State 0→2; homoplasious in *G. brevisternus*).

Node B2—Somewhat enlarged cavum labyrinthicum containing saccular otolith (char. 3, State 0→1), large f. orbitonasale (Char. 12, State 0→1), posterior maxillary processes present (Char. 13, State 0→1; homoplasious in *Hesperotestudo* and reversal in *G. brevisternus*), pisiform usually absent (Char. 22, State 0→1), inguinal scutes large, sometimes multiple and contact femoral scute (Char. 42, State 1→0).

Node B3—Pterygoid does not underlap the "batagurine" process (Char. 1, State 0→1; reverses in *G. brevisternus*), cavum labyrinthicum greatly enlarged and containing a very large saccular otolith (Chr. 3, State 1→2; reverses in *G. brevisternus*), prefrontal pits present even in juvenile specimens (Char. 5, State 1→2; reverses in *G. brevisternus*), reduced trochlear processes (Char. 10, State 0→1), vomerine foramen lost (Reversal, Char. 15, State 1→0), elongated postzygopophyses of last cervical vertebrae (Char. 19, State 0→1), medial and lateral centralae separate and not fused (Char. 24, State 0→1), first and second distal carpals separate and not fused (Reversal, Char. 26, State 1→0), large hip spines (Reversal, Char. 33, State 2→0).

Validity of the Tortoise *Xerobates lepidocephalus* Ottley and Velazques in Baja California

by

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Abstract. A previously unknown population of tortoises from the Cape region of Baja California Sur, Mexico, was described as *Xerobates lepidocephalus* (Ottley and Velazques 1989). The description is based on a single living female and fragmented skeletal remains. The defining characters are subject to variation in *Gopherus* and are present in *G. agassizii*, including raised scales of the posterior head and anterior neck, fragmented scales on the frontal and prefrontal areas, the fusion of the fourth and fifth carpals, and the absence of the pisiform. We consider *X. lepidocephalus* a synonym of *Gopherus agassizii* and the tortoise on the Baja peninsula evidence of either an important range extension or an introduction of *G. agassizii*.

Key words: Baja California, biogeography, fossil, *Gopherus agassizii*, synonym, tortoise, *Xerobates lepidocephalus*.

The living tortoises (family Testudinidae) of North America include four allopatrically distributed species in the genus *Gopherus* (Crumly 1987, 1989, 1994; Iverson 1986). The fossil record of this group extends back to the Middle Oligocene (Bramble 1982). Ottley and Velazques (1989; Table) described a new species of North American tortoise, *Xerobates lepidocephalus*, from one adult and a partial, reconstructed shell about 20 km south of La Paz, Baja California Sur (Figure).

When first discovered, new taxa are often represented by only one or few specimens. To avoid disagreements about the validity of new forms, it is important that the distinguishing features or the unique combination of features be verified in comparisons with series of specimens of related taxa. These steps help new descriptions survive an initial period of skepticism. Usually, additional specimens either further validate or question the original descriptions. An example of this process was the description of the Bolson tortoise, *Gopherus flavomarginatus* (Legler 1959), the initial acceptance of which was reluctant (Grant 1960).

We reviewed the evidence for the recognition of *Xerobates lepidocephalus*, evaluated the taxonomic procedures of Ottley and Velazques (1989), and determined the probable occurrence of *Gopherus agassizii* in Baja California.

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Table. The distribution of the characters used to define *Xerobates lepidocephalus* (Ottley and Velazques 1989).

Character	In *Xerobates lepidocephalus*	Among *Gopherus*	Among other tortoises
Frontal and prefrontal scales	Indistinct/not large	Indistinct/not large	Usually distinct and large
Parietal and temporal scales	Thickened	?	?
4th and 5th carpals	Sometimes fused	Sometimes fused	Not fused
Pisiform	Absent	Usually absent	Frequently absent

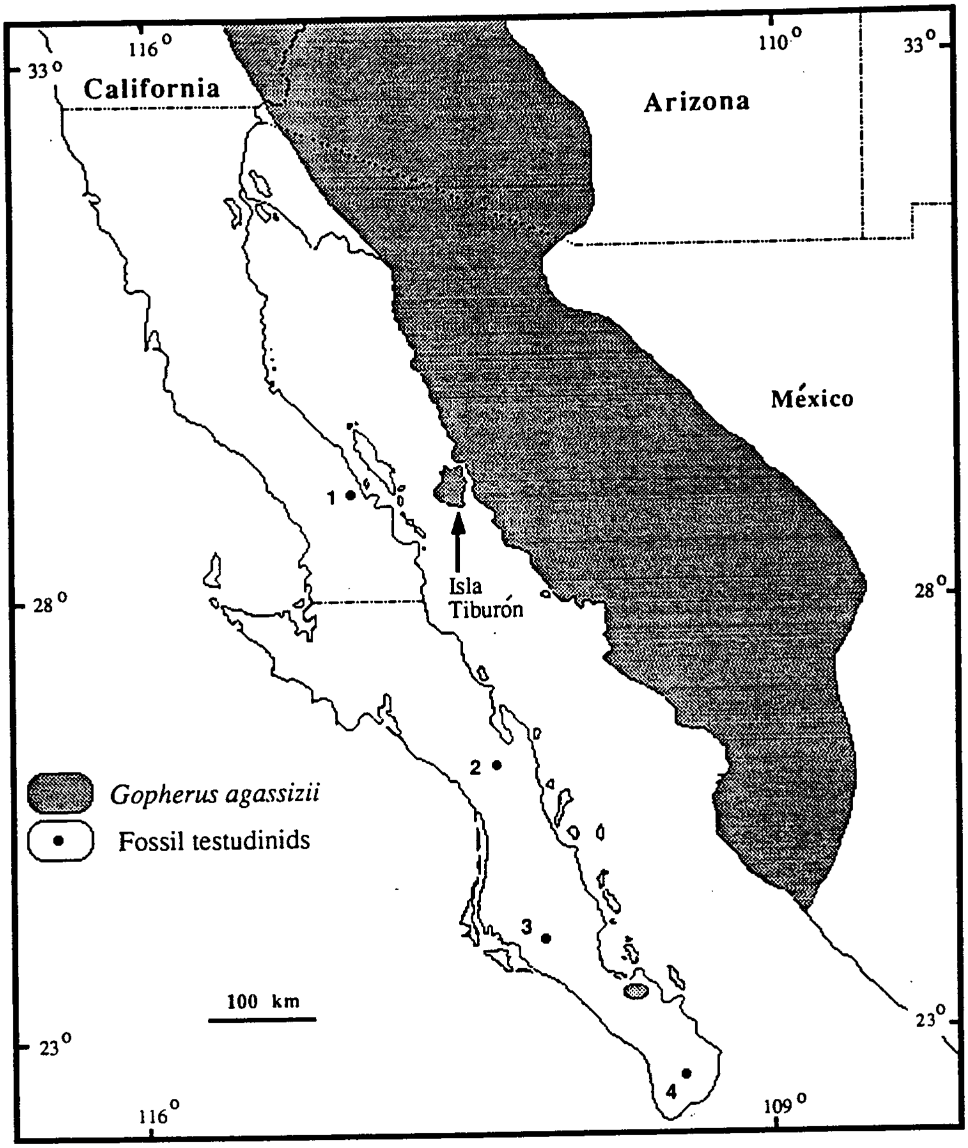

Figure. The southern portion of the distribution of *Gopherus agassizii*. *Solid circles* indicate where fossils of testudinids were recovered: (1) Agua Higuera; (2) 23 km southeast of San Miguel de Comondu; (3) Santa Rita; and (4) Las Tunas. The *shaded area* in Baja California Sur is the range of tortoises from the account of Ottley and Velazques (1989).

Results

Origin of Material

The holotype of *Xerobates lepidocephalus* was collected by a local rancher, Eusebio Villalobos, near the Buena Mujer Dam about 20 km south of La Paz, Baja California Sur. Ottley and Velazques (1989) stated they had heard rumors of the existence of a terrestrial turtle, but no one with whom they spoke had actually seen one or could accurately describe where such sightings had been made. In their closing paragraphs on the seasonal activity of this population, however, they stated that several local ranchers provided them with data.

Ottley and Velazques (1989) described this form on the basis of one complete and one incomplete specimen. The holotype (BYU 39706) was an adult female (live at the time) with a 229-mm-long carapace, and the paratype was a reconstructed partial shell of a female for which no measurements were provided.

Absence of Enlarged Frontal and Prefrontal Scales

Ottley and Velazques (1989:497) cited these enlarged frontal and prefrontal scales as one of the main diagnostic characters, stating that *Xerobates lepidocephalus* "is distinguished from all other North American tortoise species...as well as virtually all testudinids in lacking enlarged scales on the frontal and prefrontal regions."

However, specimens we examined (CAS 13190, MVZ 38585–86) from Isla Tiburón, Sonora, Mexico, had small scales in the frontal and prefrontal regions (L. Grismer, personal observation). Furthermore, C. H. Lowe (University of Arizona, personal communication) stated that this is a common condition of this island population. Thus, fragmented head scales are not diagnostic because such scales are found in other populations of *Gopherus agassizii*.

Thickened and Raised Parietal and Temporal Scalation

Although used as a distinct feature by Ottley and Velazques (1989), parietal and temporal scalation has not been examined in a broad range of testudinids. Its appearance in a single specimen, therefore, cannot be evaluated. We examined the holotype when it was alive, and the thick, raised parietal and temporal scales did not seem to be different from those in other *Gopherus* species.

Fused Fourth and Fifth Carpals

Ottley and Velazques (1989) stated that the fusion of the fourth and fifth carpal elements occurs in only *Xerobates lepidocephalus* and *Gopherus laticunea* (Oligocene fossil). However, we observed this condition in a specimen of *G. agassizii* (MVZ 58187) from the Isla Tiburón, Sonora, Mexico. Thus, the fusion of the fourth and fifth carpals cannot be regarded a diagnostic character because it also occurs in *G. agassizii*. Furthermore, such fusion has been observed in many turtles including emydines, batagurines, and even some pleurodires (Bramble 1982; Crumly 1984). Bramble (1982) suggested that this condition was ancestral of testudinids.

Absent Pisiform

Bramble (1982) and Crumly (1984) noted that the presence of the pisiform is probably symplesiomorphic of tortoises. However, the pisiform is absent in living *Gopherus* and *Manouria* and in many *Geochelone*. Because all other species of *Gopherus* lack a pisiform, its absence in *Xerobates lepidocephalus* is not diagnostic.

Discussion

Ottley and Velazques (1989:499) stated that generally "shared primitive characters strongly suggest monophyly [of *Xerobates*]." Only shared derived character states are evidence of monophyly (Eldredge and Cracraft 1980; Wiley 1981). They used this erroneous logic to recognize *Xerobates* when they argued that the recognition of two genera more fully conveys the unique adaptive history of each group. Ottley and Velazques (1989) further reported that similarities in shell meristics suggested that the closest living relative of *Xerobates lepidocephalus* is *Gopherus agassizii*. However, this assertion cannot be evaluated because no meristic data were provided.

Ottley and Velazques (1989:496) also stated that *Xerobates agassizii* "has been reported from the...extreme northeastern corner of Baja California, Mexico" and cited Van Denburgh (1922), Carr (1952), Stebbins (1966), and Auffenberg and Franz (1978a, 1978b) as sources of this information. However, Van Denburgh (1922) and Stebbins (1966) made no mention of this taxon in Baja California, and Stebbins' (1966) distribution map shows it well outside the peninsula. Auffenberg and Franz (1978b) stated, "Smith and Taylor (1950) mentioned the presence of this tortoise in northwestern Baja California, but we are unaware of any specimens from this area." Auffenberg and Franz (1978a) and Carr (1952) show the range in only the northeasternmost corner of Baja California, and the range limits are east of the Colorado River. Furthermore, Fritts and Jennings (1994) reviewed the occurrence of desert tortoises in northern Baja California and reported that statements and observations of tortoises are not supported by any specimens.

Although not mentioned by Ottley and Velazques (1989), Clavigero (1789 *in* Lake and Gray 1937) discussed the turtles of Baja California, stating that two species of large sea turtles exist besides the common land variety and the freshwater turtles.

Another question remains: Have there been fossils of tortoises in southern Baja California? Ottley and Velazques (1989) reported that no fossils of tortoises have been found in the Baja California Cape or in the region of Jalisco, Mexico, the origin of the cape land mass. However, there are some records (Figure). Miller (1977) reported a Pleistocene tortoise from near Santa Rita and 23 km southeast of San Miguel de Comond, Baja California Sur. Later, Miller (1980) reported several specimens of *Geochelone* sp. [probably not "*Geochelone*" sensu Crumly (1984)] from the Late Pliocene (Las Tunas Local Fauna) in the Cape Region of Baja California. One of us (Grismer) found fossil testudinid material at Agua Higuera, about 15 km west of Bahia de Los Angeles, Baja California. This material was tentatively identified (by Crumly and independently by J. H. Hutchinson, University of California, Berkeley) as *Gopherus* and, thus, represents the first record of this genus in northern Baja California.

We conclude that the chosen characters for the new description of *Xerobates lepidocephalus* are not diagnostic or unique and, thus, recommend that *X. lepidocephalus* be relegated to the synonymy of *Gopherus agassizii*.

The rarity of material and the lack of morphological differences suggest that *X. lepidocephalus* are introduced *Gopherus agassizii*, probably from Sonora (C. H. Lowe, University of Arizona, personal communication). Separate anecdotal evidence (F. Reynoso, local resident, personal communication) reported to one of us (Grismer) suggested that La Paz tortoises were from an introduction. If the tortoise proves to be native to the cape region, however, this status is important for biogeographic reasons and for other research and conservation interests.

Acknowledgments

The comments of A. Berta, R. Estes, R. Etheridge, and M. Simpson improved earlier drafts of the manuscript. R. B. Bury and D. J. Germano were instrumental in stimulating the completion of this project. Financial assistance for some parts of this work are from the National Science Foundation (DEB 81–14467 to Crumly) and from the U.S. Fish and Wildlife Service, National Ecology Research Center. J. Ottley generously allowed access to the holotype, to 35-mm slides of the type locality, and to original X-rays. We take full and exclusive responsibility for the expressed viewpoints. We thank the California Academy of Sciences (CAS) and Museum of Vertebrate Zoology (MVZ) for use of material.

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*Asterisk denotes unpublished work.

Controlled fire to open the understory in sandhill habitat of the gopher tortoise (*Gopherus polyphemus*). Ecology Research Area of the University of South Florida. *Photo by H. R. Mushinsky.*

Comparison of Gopher Tortoise Populations on Islands and on the Mainland in Florida

by

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Abstract. We surveyed gopher tortoises (*Gopherus polyphemus*) on 20 relatively undisturbed sites in Florida, 10 on true islands and 10 on the mainland. At each site, we used the number and condition of burrows as indicators of tortoise abundance. On the mainland and on islands, the number of active and inactive burrows increased with area of habitat. On the mainland, the density of tortoise burrows decreased with area of habitat; on islands, the density of burrows was not related to area. On the mainland, the ratio of inactive to active burrows increased with area of habitat and burrow density increased with herbaceous ground cover, but neither of these relations could be demonstrated on islands. We suggest that tortoises have a greater selection of suitable habitats on the mainland than on islands. Tortoises on islands are confined and thus are forced to live in less-than-ideal conditions. Human development fragmented tortoise habitat on mainlands, creating habitat islands from which tortoises cannot disperse easily. Thus, we suggest that tortoises on these habitat islands also will be faced with less-than-ideal conditions. Without protection and management of habitat, the long-term survival of these isolated tortoise populations is uncertain.

Key words: Burrow abundance, Florida, *Gopherus polyphemus*, habitat fragmentation, habitat selection, islands, mainland.

Knowledge of the life history of *Gopherus polyphemus* (Daudin), especially the demography and social factors that influence density and moves of individuals between populations, is incomplete. Most of the 600 publications on tortoises of the genus *Gopherus* (Douglass 1975; Diemer 1986) are anecdotal observations.

Briefly, the life history of gopher tortoises in Florida conforms to the following pattern: Males court females in the spring of the year and again in fall. Females deposit eggs during May and June, often in the spoil mounds outside their burrows. Following an incubation of 97–106 days, eggs may hatch from mid-August through September (Landers et al. 1980). Females achieve sexual maturity at 12 to 15 years of age when their carapace lengths are 19 to 21 cm (Auffenberg and Iverson 1979; Alford 1980). Each female may produce a single clutch per year with a mean of five (Iverson 1980) to eight (Linley and Mushinsky 1994) eggs. Gopher tortoises grow more rapidly before sexual maturity than after sexual maturity and may live to an age of more than 60 years (Landers et al. 1982).

Survivorship of nests and young is low. Predation on eggs is severe (Auffenberg and Iverson 1979; Landers et al. 1980) and profoundly reduces the effective rate of reproduction. For example, fewer than 6 hatchlings/mature female/decade may be produced in a population in southern

Georgia (Landers et al. 1980). Survival of juvenile tortoises is low throughout the first year of life (e.g., only about 6% of the eggs in a population in central Florida yielded 1-year-old tortoises; Alford 1980). Soft shells and small sizes render gopher tortoises vulnerable to predation until they are 5 or 6 years old (Diemer 1986; Wilson 1991).

Throughout their range, tortoises are becoming increasingly rare because of the extensive mortality and displacement from a reduction of the number of places where they can live (Auffenberg 1978). The gopher tortoise prefers habitats with a sandy substrate suitable for construction of extensive burrows, which average about 4.5 m in length (Hansen 1963). Gopher tortoises are typically in open upland habitats (Campbell and Christman 1982; Diemer 1986); hence local abundances of the tortoises change through time because forest succession causes closure of the tree canopy in areas protected from fire.

Their preference for upland habitats brings gopher tortoises in direct conflict with human interests. In Florida, for example, prime tortoise habitats of longleaf pine (*Pinus palustris*)–turkey oak (*Quercus laevis*) uplands (sandhill) and coastal dunes were destroyed or fragmented for development, recreation, and other uses (Peroni and Abrahamson 1985a, 1985b; Diemer 1986; Diemer and Moore 1994). Another upland habitat of tortoises, formerly common along the ancient coastal ridges of peninsular Florida, is sand pine (*Pinus clausa*) scrub. About 66% of the original extent of this habitat was altered by development, primarily for agriculture (Christman and Judd 1990).

Alteration of upland habitat fragmented formerly large populations of tortoises into smaller, isolated populations in habitat islands surrounded by developed land. Based on the theory of island biogeography (MacArthur and Wilson 1967), extinction rates are most influenced by the population size of a species (large populations are less prone to extinction); and population size, in turn, is most influenced by island size (Connor and McCoy 1979). Understanding the relation between island size, habitat quality, and tortoise demography has applications to the design and maintenance of nature refuges.

Because they provide an opportunity for the necessary level of replication of bona fide tests of hypotheses about demography, publicly owned lands have high value to population ecologists (Eberhardt 1988). In Florida, the gopher tortoise inhabits many state and federal lands. Although none of these lands was obtained by governmental agencies primarily for the well-being of tortoises, resident tortoises are protected by virtue of public ownership. However, gopher tortoises have not successfully maintained populations on all state and federal lands.

Possible explanations for the lack of success on some lands include isolation (McCoy and Mushinsky 1992a) and vegetation structure (Mushinsky and Gibson 1991). Vegetation influences gopher tortoise populations because the tortoise's habitats typically are fire-dependent; the absence of fire for a few decades can influence the vegetation structure and reduce the abundance of tortoises. Because 10 of our sites are on islands and 10 are on the mainland, we can evaluate the effects of isolation on tortoise populations. Likewise, because vegetation structure differs among sites, we can evaluate its effects on tortoise populations. We will use the results of our evaluations to speculate about the reasons for observed success or failure of tortoise populations.

Sites and Methods

We searched 20 public tracts (Figure) for gopher tortoises in 1987–88: 10 sites on true islands and 10 on the mainland. We searched all small areas (<10 ha) and used 7-m-wide belt transects of variable length for surveys of moderately sized areas (between 10 and 120 ha) and 7-m × 150-m belt transects for large areas (>120 ha; Table 1). We searched the entire widths of all transects to eliminate potential bias introduced by this method (Burnham and Anderson 1984; Burnham et al. 1985). Surveys at transects were made by three researchers walking side by side about 2 m apart to locate and measure each burrow along the transect.

We classified each distinctive tortoise burrow as *active*, *inactive*, or *abandoned*. Active burrows showed evidence of recent tortoise activity, such as footprints around the entrance or scrape marks from the plastron abrading the sand in the burrow. Inactive burrows potentially could be used by a tortoise but lacked evidence of recent activity.

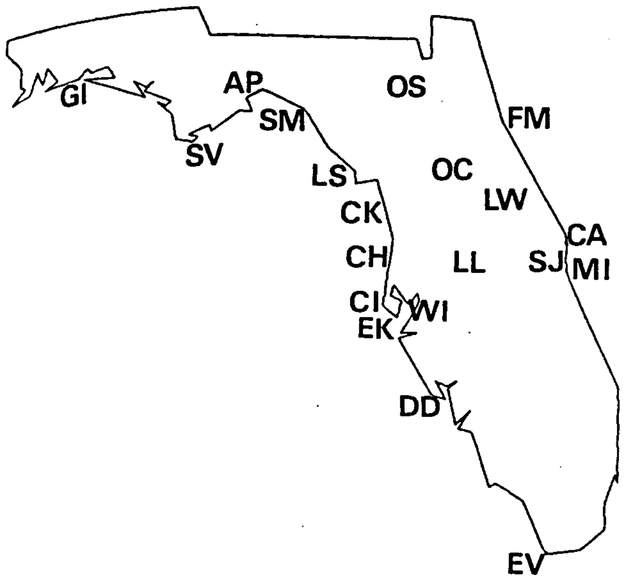

Figure. The 20 state and federal lands in Florida searched for gopher tortoises in 1987–1988. Abbreviations are listed in Table 1.

Abandoned burrows could not be used without modification because the burrow mouths were overgrown with vegetation or damaged.

We measured burrow widths to the nearest 0.5 cm with a pair of metersticks fastened together at the 50-cm mark to form a connected pair of calipers. The metersticks were placed into a burrow to a depth of 50 cm and spread open so that one stick touched each side of the burrow, allowing the width of the burrow to be measured across the opposite ends of the sticks. Occasionally, abandoned burrows were measured at a depth of 10 cm because the burrow had collapsed. We measured burrow widths because they correlate strongly with the carapace lengths of resident tortoises (Alford 1980; Martin and Layne 1987), and the size distribution of usable (active and inactive) burrow widths accurately reflects the size distribution of carapace lengths of resident gopher tortoises (Auffenberg and Franz 1982).

The areal extent of gopher tortoise habitat was determined by the occurrence of tortoises, not by our subjective evaluation of habitat suitability. Furthermore, the areal extent of tortoise habitat was

Table 1. Surveys of gopher tortoises (*Gopherus polyphemus*) on 20 state and federal lands in Florida in 1987–1988 and the applied survey method at each site. Site abbreviations are in parentheses.

Site (abbreviation)	Survey method
Gulf Island National Seashore (GI)	—
Saint Johns National Wildlife Refuge (SJ)	Complete
Cedar Keys National Wildlife Refuge (CK)	Complete
Chassahowitzka National Wildlife Refuge (CH)	Complete
Weedon Island State Park (WI)	Complete
Lower Suwannee National Wildlife Refuge (LS)	7 m × 150 m
J. N. "Ding" Darling National Wildlife Refuge (DD)	Complete
Fort Matanzas National Monument (FM)	Complete
Saint Vincent National Wildlife Refuge (SV)	Complete
Lake Woodruff National Wildlife Refuge (LW)	7 m × variable
Osceola National Forest (OS)	7 m × 150 m
Lake Louisa State Park (LL)	7 m × variable
Canaveral National Seashore (CA)	7 m × variable
Everglades National Park (EV)	7 m × variable
Egmont Key National Wildlife Refuge (EK)	7 m × variable
Caladesi Island State Park (CI)	7 m × variable
Saint Marks National Wildlife Refuge (SM)	7 m × 150 m
Merritt Island National Wildlife Refuge (MI)	7 m × 150 m
Ocala National Forest (OC)	7 m × 150 m
Appalachicola National Forest (AP)	7 m × 150 m

estimated in different ways, depending on the size of the site. In large sites that we searched by 7 × 150-m belt transects, any evidence (burrows, scat, footprints, sightings) of tortoises on a transect or in the vicinity of a transect were included as part of the tortoises' habitat. To determine the areal extent of tortoise habitat at each large site, we plotted the location of each transect with signs of tortoises on a topographic map and then estimated the area of tortoise habitat by connecting the peripheral transects with evidence of tortoise occurrence. Some of these sites are so large that we were able to sample only small percentages of them, and our estimates of area occupied by tortoises at these sites are crude.

For moderately sized sites that we searched by 7-m-wide transects of variable length, the positions and lengths of transects with evidence of tortoises again were plotted. The area occupied by tortoises was derived by connecting the peripheral transects with evidence of tortoise occurrence. Because we sampled in much larger percentages of these sites, we could more accurately delineate the periphery of tortoise habitat. Our estimates of area occupied by tortoises on moderately sized sites are, therefore, more accurate than our estimates on large sites.

On small sites that we searched completely, we marked the position of each burrow with a 1.5-m-long PVC pipe. After all burrows were marked, we measured the area occupied by tortoises by locating the approximate center of the habitat occupied by a tortoise population and measuring the distance from the center along eight major compass directions to the edge of a polygon derived by laying straight lines between peripheral burrows.

We calculated the total number of active, inactive, and abandoned burrows at each site (Table 2) by two methods. On sites that were searched by belt transects, we derived estimates of the number of burrows by multiplying the estimated areal extent of habitat by the density of burrows on transects. On sites that were searched completely, the numbers of burrows were known directly from the survey data.

A computed ratio of inactive burrows to active burrows (INACT/ACT) on each site allowed the evaluation of the relative number of burrows used per individual at each site and the comparison of the ratio among sites. The higher the ratio, the more individuals tended to construct new burrows, given the assumptions that (1) each active burrow was used by a single tortoise and (2) each tortoise had caused only one burrow to appear active on the day of our survey. During our surveys, we rarely found nearby active burrows of the same size. We did find nearby active and inactive burrows of the same size, which leads us to believe that these two assumptions are reasonable.

Population sizes of gopher tortoises often are estimated from the number of burrows (Auffenberg and Franz 1982) by multiplying the sum of active and inactive burrows by 0.614. The researchers derived this method from monitoring a single tortoise population with 122 burrows for longer than a decade and finding that an average of 38.6% of the burrows were unoccupied. Most methods of estimating tortoise population size are based on the number of active and inactive burrows, thus we combined these two types of burrows (called ACTIN) for most of our analyses.

Our data (McCoy and Mushinsky, unpublished) from trapping on 15 sites (none of the 20 sites in this study) indicate that a more accurate estimate of tortoise number is obtained by multiplying the sum of active and inactive burrows by 0.33. The range of occupied active and inactive burrows on these 15 sites was 0.22–0.47. We think the use of this proportion and this range is to be preferred over the use of a single value of 0.614 but note that alternative methods have been developed (McCoy and Mushinsky 1992b). We multiplied the sum of active and inactive burrows, either counted (at small sites) or estimated from transect surveys (at medium and large sites), by our calculated proportion (0.33) and range (0.22–0.47) of occupied active and inactive burrows (Table 2).

We also quantified the vegetation structure of habitats with tortoises at 13 of the 20 sites by a method similar to James and Shugart's (1970). Four sites with measured vegetation structure were on the mainland and nine were on islands. We visually estimated the density of plant cover at three levels: from the ground to 1 m aboveground, between 1 and 3 m aboveground (low canopy), and more than 3 m aboveground (high canopy). At the lowest level, we determined vegetation structure from a standing position as (1) the percent of ground surface area occupied by legumes, other herbs, and grasses (collectively called herbaceous vegetation); (2) leaf litter and woody vegetation (litter–wood); or

Table 2. Data on 20 gopher tortoise (*Gopherus polyphemus*) populations in Florida, 1987–1988. See Table 1 for a list of abbreviations.

Site	Area (ha)	Number of burrows			Estimated density	
		Active	Inactive	Abandoned	Mean	Range
GI (I)[a]		0	0	0	0	0
SJ (M)	0.10	5	2	7	23.1	15–33
CK (I)	0.21	21	2	1	36.1	24–51
CH (M)	1.52	43	18	4	13.2	9–19
WI (I)	2.67	40	84	21	15.3	10–22
LS (M)	8.16	73	18	21	3.7	2–5
DD (I)	10.11	13	43	68	1.8	1–3
FM (I)	10.97	122	70	47	5.9	4–8
SV (I)	12.64	18	3	5	0.6	0.4–0.8
LW (M)	19.50	90	36	4	2.1	1–3
OS (M)	64.75	171	23	20	0.9	0.6–1.4
LL (M)	65.12	3,697	2,572	615	31.7	21–45
CA (M)	68.31	886	258	115	5.5	4–6
EV (I)	84.90	1,274	478	173	6.8	5–10
EK (I)	91.93	3,085	381	139	12.4	8–18
CI (I)	107.89	2,017	1,076	1,076	9.5	6–13
SM (M)	732.90	2,765	2,890	1,438	2.5	2–4
MI (I)	6,977.00	22,970	69,084	23,299	4.4	3–6
OC (M)	10,295.00	29,760	34,170	18,738	2.1	1–3
AP (M)	34,150.00	84,009	50,542	22,539	1.3	0.9–1.9

[a] I = island, M = mainland.

(3) bare ground. Above 1 m, the simple presence or absence of vegetation was noted in each of the two levels. These visual estimates of the vegetation structure were made in a series of haphazardly placed 4-m^2 quadrats.

We sampled in at least 20 quadrats in each site that supported tortoises and in more where tortoise habitat was extensive. We used the mean percentages of herbaceous vegetation, litter–wood, and bare ground as estimates of the percentages of these cover types in an entire site. We used the percentage of samples in which ground and low canopy was present as an estimate of these canopy covers over an entire site.

We focused on the relative amount of herbaceous vegetation at each site as representative of habitat quality because (1) gopher tortoises eat a wide variety of the plants we included in herbaceous vegetation (Macdonald and Mushinsky 1988), and (2) tortoise densities and moves are related to the structure of the herbaceous vegetation (Auffenberg and Franz 1982; Diemer 1986). Statistical significance for all analyses was set at $P < 0.05$.

Results

The number of all three types of burrows increased with area of habitat: active (Spearman's $r = 0.937$, $n = 19$), inactive ($r = 0.895$, $n = 19$), and abandoned burrows ($r = 0.868$, $n = 19$). We found no burrows at the Gulf Islands National Seashore, and the site was excluded from all analyses.

The relation between ACTIN and area ($r = 0.910$, $n = 19$) was strong but inflated because the total number of burrows at 12 of the 19 sites was calculated by multiplying the density of burrows in the area encompassing transects by the estimated areal extent of habitat. When sites in which we sampled by either of the two transect methods were removed from the analysis, the resulting correlation coefficient no longer demonstrated a strong relation between ACTIN and area ($r = 0.357$, $n = 7$).

The mean INACT/ACT burrow ratio was 0.82 (0.95), and 55% of the burrows were active on all 19 sites combined. The number of active burrows exceeded the number of inactive burrows in 14 of the 19 sites, and on average we found no relation between the INACT/ACT burrow ratio and area ($r = 0.280$, $n = 19$).

We found no difference in area occupied by tortoises on the mainland and islands (Wilcoxon Signed Rank Test, $T = 14$, $n = 19$) or in density of burrows ($T = 17$, $n = 19$) on the mainland and islands; comparisons between island and mainland tortoise populations are not a function of the location of the site (island vs. mainland). We found a strong relation between ACTIN and area on the mainland ($r = 0.964$, $n = 10$) and on islands ($r = 0.800$, $n = 9$). The density of tortoises on the mainland decreased as area increased ($r = -0.515$, $n = 10$), but the density of tortoises on islands was not related to area ($r = -0.317$, $n = 9$).

The INACT/ACT burrow ratios did not differ between the mainland and island sites ($T = 18$, $n = 9$). The INACT/ACT burrow ratio increased with area on the mainland ($r = 0.535$, $n = 10$) but not on islands ($r = 0.100$, $n = 9$). As the area of mainland habitat increased, the INACT/ACT burrow ratio increased, but the same relation did not hold for islands.

Intercorrelations among many of the vegetation variables are strong (Table 3). On the 13 sites with vegetation data, ACTIN increased with area ($r = 0.829$, $n = 13$); density tended to decline with area, but the relation was weak ($r = -0.264$, $n = 13$); and the INACT/ACT burrow ratio was not related to area ($r = 0.044$, $n = 13$). ACTIN did not correlate with herbaceous vegetation ($r = 0.209$, $n = 13$), but tortoise density increased with herbaceous vegetation ($r = 0.461$, $n = 13$). The INACT/ACT burrow ratio was not related to herbaceous vegetation ($r = -0.163$, $n = 13$).

At the mainland sites with vegetation data ($n = 4$), ACTIN increased with area ($r = 0.800$), but density was not related to area ($r = 0.001$). These relations were the same in all 10 mainland sites. The INACT/ACT burrow ratio was not related to area ($r = -0.400$). At the four mainland sites, ACTIN ($r = -0.200$) and the INACT/ACT burrow ratio ($r = 0.600$) were not related to herbaceous vegetation; density increased with herbaceous vegetation ($r = 0.800$). On the nine islands, neither ACTIN ($r = 0.200$) nor density ($r = 0.117$) or the INACT/ACT burrow ratio ($r = -0.383$) was related to herbaceous vegetation.

Table 3. Relations among the five aspects of measured vegetation structure at Florida sites in 1987–1988.

Structure	Bare ground	Litter–wood	Herbaceous vegetation	Low canopy
Bare ground				
Litter–wood	–0.31			
Herbaceous vegetation	–0.08	–0.82[a]		
Low canopy	0.03	0.50[a]	–0.67[a]	
High canopy	–0.18	0.58[a]	–0.54[a]	0.41

[a] $P < 0.05$.

Discussion

We found an increase in the number of gopher tortoise burrows with increases in area occupied by tortoises and a decrease in the density of burrows with area occupied by tortoises on 19 state and federal lands in Florida (Gulf Islands National Seashore excluded). These results suggest that, in general, tortoises disperse into suitable available habitat. We suspect that as area increases, patchiness of the habitat also increases, and thus relatively less habitat is available to tortoises in large areas.

We have other data (McCoy and Mushinsky, unpublished), collected on 33 sites (including 7 state and federal lands) with the complete method of sampling relatively small sites, that demonstrate a positive relation between ACTIN and the size of habitat ($r = 0.620$, $n = 33$). In general, a positive relation exists between ACTIN and area. ACTIN density (number/area) negatively correlated with area ($r = -0.412$, $n = 19$), revealing that smaller sites tend to support proportionately more tortoises than larger sites.

Tortoises may disperse in the manner suggested by our results because of the dynamic nature of upland ecosystems. In just a few decades without fire, a site can change from relatively open habitat with a dense herbaceous ground cover to forest with a dense canopy and scanty herbaceous vegetation (Mushinsky 1985, 1986).

Tortoises may abandon densely canopied areas for several reasons. First, a reduction of direct sunlight on the ground may hamper tortoises from reaching minimum thermal requirements for normal daily activities or hinder the development of eggs, which females often deposit just outside burrows. Second, an increase in canopy is accompanied by a decrease in the herbaceous vegetation essential for normal growth, development, and reproduction of this herbivorous reptile (Auffenberg and Franz 1982; Mushinsky et al. 1994).

Some of the highest densities we found were on small sites (<70-ha area) with moderate to dense canopies. We suspect that high densities of tortoises occur where populations are sometimes confined (e.g., on true islands). Also, the development of the land around mainland populations creates small habitat islands for tortoises.

We found no difference in densities of gopher tortoise populations between islands and the mainland; thus, location does not cause unusually high density. The density of tortoises at mainland sites decreased as area increased, but the density of tortoises at island sites did not decrease in a similar manner. Furthermore, the INACT/ACT burrow ratio increased with area on the mainland but not on islands. On the mainland, some tortoises can move relatively freely to new locations as the quality of their habitat degenerates, but tortoises on islands cannot.

Tortoises may prefer to avoid areas of dense tree canopy, but we suggest that in certain circumstances they cannot. We suggest that where tortoises are increasingly confined to smaller and smaller patches of suitable habitat, such as on an island where canopy cover is increasing, they probably become densely packed. Intraspecific interactions increase as a result of increased density (McRae et al. 1981), causing individuals to move about inside and between patches, constructing new burrows. This conclusion, if valid, has far-reaching implications for the management and conservation of tortoises. Finding high densities of active and inactive burrows could indicate that a population is healthy. If our interpretations are correct, high densities of these types of burrows may indicate just the opposite: that tortoises are confined, forced to move frequently, and constructing burrows at a relatively high rate.

The use of a standard method based on the number of active and inactive burrows may not be the best to estimate tortoise populations. For example, our data also suggest that the widely used 0.614 correction factor (Auffenberg and Franz 1982) automatically results in overestimates of population sizes on true islands and on small habitat patches on the mainland.

In the 13 sites (mainland and island sites combined) with data on vegetation structure, the tortoise density increased with herbaceous vegetation. When considered separately, however, populations on the mainland—but not on islands—reached high densities in areas with relatively large amounts of herbaceous vegetation. We view these findings as further evidence that island populations of tortoises have less selection of habitats than mainland populations. For example, relatively large amounts of high and low canopy and small amounts of herbaceous vegetation are on the Egmont Key National Wildlife Refuge (Table 4). The island may support a low density of gopher tortoises because density often decreased as herbaceous vegetation decreased. However, the estimated density of 12.4 tortoises/ha on the Egmont Key National Wildlife Refuge was greater than the mean tortoise density (9.4 tortoises/ha) in all 19 study sites.

The inconsistency between predicted and actual densities of tortoises on the Egmont Key National Wildlife Refuge may be explained by a pattern of local distribution. Many tortoises were tightly packed around the periphery and near the ends of the oval-shaped island; these areas lacked the dense canopy of the island interior, which was void of tortoises.

Previous studies of gopher tortoises on island sites that we also searched provided a basis for a greater understanding of the responses of tortoises to vegetation structure. Kushlan and Mazzotti (1984) surveyed the same tortoise population in the Everglades National Park as we did. This population inhabits an isolated near-island with sparse canopy and large amounts of herbaceous vegetation, probably because the region is subject to natural fires, hurricanes, and drought. The tortoise population at this site seems to be healthy. McCoy and Mushinsky (1992a) found 11% more active burrows than Kushlan and Mazzotti (1984), which suggests an increase in the number of tortoises during the 6 years between the surveys.

In contrast, the J. N. "Ding" Darling National Wildlife Refuge on Sanibel Island supports dense high and low tree canopies and small amounts of herbaceous vegetation. We found a 33% decrease in

Table 4. Data on five aspects of vegetation structure at 13 of the 19 sites searched for gopher tortoises (*Gopherus polyphemus*). Values are densities of plant cover (percent). See Table 1 for a list of abbreviations.

Site	Bare ground	Litter-wood	Herbaceous vegetation	Low canopy	High canopy
LW	0	98.4	1.5	75.0	100
WI	43.5	52.6	3.8	61.0	54.6
DD	15.5	69.8	14.7	70.0	57.0
EK	23.6	60.1	15.7	63.0	58.0
SV	17.6	65.8	17.5	5.0	38.0
MI	33.0	44.0	23.0	64.6	16.5
FM	57.5	11.7	30.7	32.0	15.0
CA	19.5	49.1	31.4	38.0	0
CK	21.0	47.0	32.0	20.0	60.0
CI	26.7	40.9	32.4	21.0	41.0
LL	16.2	24.2	59.6	4.5	0
EV	19.4	20.6	60.5	56.0	11.0
CH	4.5	18.0	77.5	20.0	50.0

the number of active burrows between our survey and those of T. Logan (unpublished) during 1978–79, which suggests a substantial decline in the number of tortoises. Tortoises were larger on average during our survey in the late 1980's than during Logan's study (unpublished), reflecting growth of individuals. However, young adults (carapace length 15–21 cm) were fewer, and juvenile tortoises were absent in our survey. In other words, there was little or no evidence of recruitment between surveys.

These two contrasting examples indicate that much could be learned about gopher tortoises through demographic studies on true islands. Such studies could provide a better understanding of population dynamics of tortoises in confined areas and have direct application to habitat islands that fragmentation and isolation of existing tortoise habitat created on the mainland. The current practice of setting aside small habitat islands of land for gopher tortoises in urban developments and elsewhere may accomplish little more than prolonging local extirpation for a short time.

Acknowledgments

We thank T. Logan for supplying copies of his reports on the status of gopher tortoises on federal lands in Florida and D. S. Wilson for assistance with all surveys and the review of the manuscript. Many persons connected with the state and federal lands in Florida provided us with assistance, information, and logistical support. J. Stevenson of the Florida Department of Natural Resources gave us the opportunity to survey state parks in Florida; we thank him for his cooperation. Our research was supported by a grant from the Nongame Wildlife Research Program of the Florida Game and Fresh Water Fish Commission.

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Sinaloan thornscrub approximately 8 km northeast of Ures, Sonora, Mexico. *Photo by D. J. Germano.*

Distribution, Habitat Use, and Status of the Desert Tortoise in Mexico

by

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Abstract. We recorded 17 new localities of the desert tortoise (*Gopherus agassizii*) in Mexico based on specimens and 10 additional sight records, increasing the known range by about 48%. The range includes most of Sonora except the northwestern corner and parts of the Sierra Madre Occidental and northern Sinaloa (south as far as El Fuerte). The northern and eastern limits of the range in Sonora are generally defined by the 800-m contour, but occupied habitats in southern Sonora and northern Sinaloa are only as high as 300 m. Tortoises seem to be absent between Guaymas and Alamos, Sonora. We do not consider Baja California a part of the tortoise's range. In Mexico, desert tortoises occur on slopes, bajadas, and the sides of arroyos and seem to be absent from valley floors and other flat areas. Tortoises may be more abundant and have a less patchy distribution at intermediate elevations (300–500 m) than at lower elevations and on coastal mountains. Only in two areas does human use of tortoise meat seem to have reduced the abundance of tortoises. The wide expanse of tortoise habitat, the largely inaccessible area, and the difficulty of finding tortoises on steep and densely vegetated slopes deter human use of this species. Steep rocky slopes also protect the tortoise and its habitats from intensive agriculture and vehicular traffic.

Key words: Anthropogenic effects, biogeography, *Gopherus agassizii*, habitat use, Sinaloa, Sonora, desert tortoise.

Although as much as one-third of the desert tortoise's (*Gopherus agassizii*) range is in Mexico (Patterson 1982), the distribution and ecological requirements of this tortoise are poorly documented. The distribution of desert tortoises in Mexico was summarized by Auffenberg and Franz (1978; 22 localities), Smith and Smith (1979; 43 localities), and Patterson (1982; 28 localities). Based on these reports, the distribution in Mexico includes extreme

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northern Sinaloa and most of the state of Sonora except the northwestern corner and parts of the Sierra Madre Occidental immediately adjacent to the Chihuahua border. The only extensive ecological observations of desert tortoises in Mexico were made on the large gulf island of Tiburon (Bury et al. 1980; Reyes Osorio and Bury 1982).

In response to concerns for the protection and management of the species, we initiated a field study of the desert tortoise in Mexico. Here we describe the geographic distribution, characterize the use of habitats, estimate the population status from observed relative abundances, and comment on the human use of the desert tortoise in Mexico.

Nomenclature

We retain the customary use of *Gopherus* as the genus of all gopher tortoises. Although Bramble (1982) presented a strong argument for the use of a new generic name, *Scaptochelys*, for *Gopherus agassizii* and *G. berlandieri*, it is not clear that these two species are more closely related to each other than to other taxa (Crumly 1987, 1994). Thus, we also refrain from the use of *Xerobates*, a senior synonym of *Scaptochelys*, as suggested by Bour and Dubois (1984). Until this point is resolved and the importance of Bramble's distinctions are further evaluated, we prefer the conservative approach of grouping all four living tortoises in North America in the genus *Gopherus*. We also use the *-ii* termination for *agassizii* following the original description (cf. Auffenberg and Franz 1978). This is in accordance with the ruling in the International Code of Zoological Nomenclature (International Union of Biological Sciences 1985).

Materials and Methods

We obtained museum records from summaries by Smith and Smith (1979) and Patterson (1982) and previously unreported records from collections (Arizona State University and the Museum of Southwestern Biology, University of New Mexico). We plotted localities on maps by hand. Several undocumented sight records in the literature—for example, those in Patterson (1982)—do not add appreciably to the distribution of the tortoise and were not plotted. The sight record by Ives (1964) was imprecise and was not used. Literature records by Van Denburgh (1922) and Reyes Osorio and Bury (1982) were included as valid sight records.

We searched beyond the known distributional limits and corroborated our findings with local residents. We conducted fieldwork in northwestern Mexico in August–September 1983 during summer rains and the anticipated period of maximum tortoise activity. Searches for tortoises and their signs were made with and without the help of local residents by walking in habitats with 2–5 people spaced 5–10 m apart. We spent short periods (1–8 person-hours) at any one locality.

When possible, we examined recent kitchen middens near dwellings for tortoise remains and interviewed local residents. Interviews were generally unstructured and leisure and mostly in Spanish. We focused on information about the presence, habits, and abundance of tortoises and the local use of tortoises as food and pets. We used information only from people who could distinguish tortoises from the local aquatic turtles (*Kinosternon* and *Trachemys*), box turtles (*Terrapene*), and forest terrapins (*Rhinoclemmys*). Some people were initially evasive but cooperated once they understood we wanted information rather than an enforcement of regulations. Most were aware of the Mexican government's ban on taking tortoises.

Some tortoise signs, such as bones, scats, and clear tracks, are unequivocal evidence of tortoises. Burrows and pallets are less certain indicators of tortoises, although their shapes and positions in the habitat are often distinctive (Luckenbach 1982; Germano et al. 1994). In our work, bones were collected and cataloged as museum specimens; other types of signs were recorded.

Results

Distribution

Smith and Smith (1979), in the most complete summary of desert tortoise distribution in Mexico, cited records from 26 quadrats formed by trapezoids that are 30′ of latitude or longitude on a side.

Patterson (1982) added one more reliable record in another quadrat. We found tortoises in an additional 13 quadrats, largely in the outer limits of the known range. Desert tortoises or their signs have now been found at 74 sites in Sonora and Sinaloa, Mexico (Figure).

The Mexican range of the desert tortoise is contiguous to the occupied range in Arizona along approximately 150 km of the United States–Mexico border in northern Sonora (Figure). The northeastern range limits in Sonora are roughly defined by the 800-m contour, and contact with southern Arizona populations occurs in the low hills around and west of Sonoyta, Sonora, and the Organ Pipe Cactus National Monument, Arizona. High montane outliers of the Sierra Madre Occidental cover much of north-central and northeastern Sonora, and this area is not inhabited by the desert tortoise. Tortoises generally occupy the foothills to an elevation of 800 m, although they have been recorded as high as 1,050 m at Rancho La Palma northeast of Vaviacora, Sonora.

The eastern limits of desert tortoises in Mexico are sharply defined by the abrupt change from lowland Sinaloan thornscrub to Madrean evergreen woodland at about 800–1,000 m (Figure). Tortoises may occasionally be found in the lower margins of this woodland vegetation zone. The westernmost locality in Sonora is in the Pinacate lava flow, 135 km east of the Baja California border with Sonora.

Distributional limits defined by elevation and topography were identified between Moctezuma and Nacozari de García (about 800 m elevation),

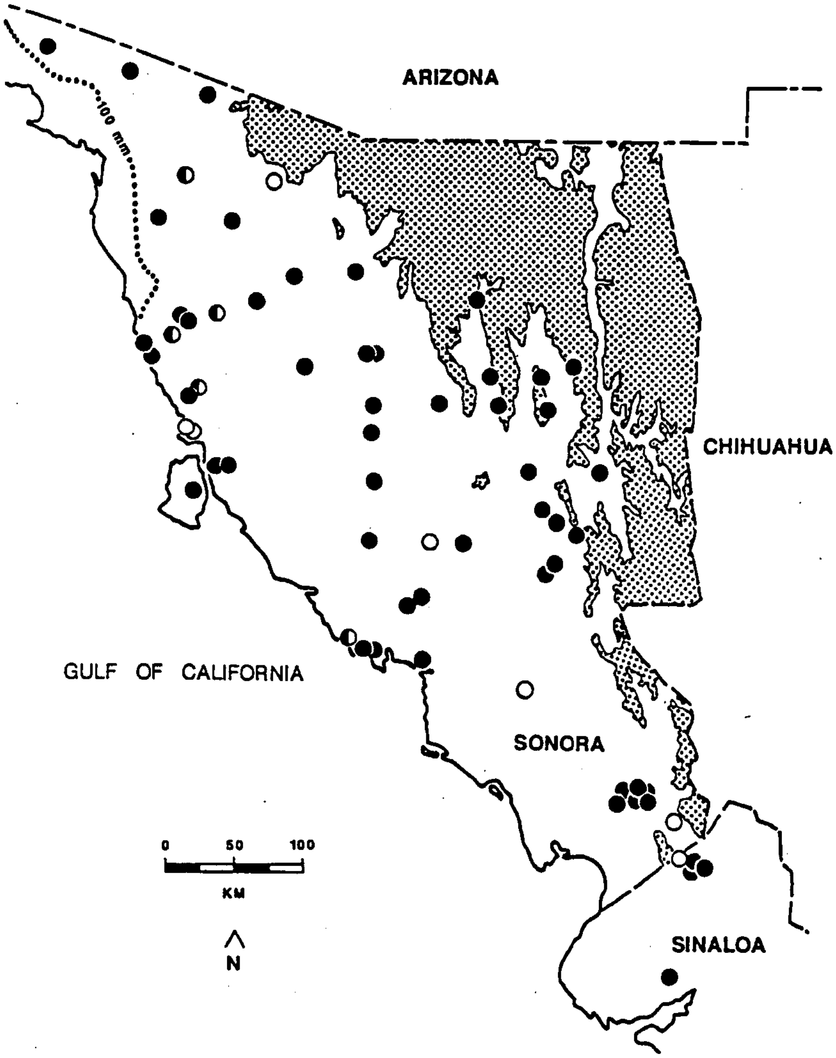

Figure. Northwestern Mexico and the range of *Gopherus agassizii* as defined by published records and new observations. The 100-mm annual rainfall isopleth is shown in the northwest. *Stippled areas* in Sonora are zones of upland vegetation (Brown and Lowe 1980), including semidesert, plains, Great Basin grasslands, Madrean evergreen woodland, and Petran montane conifer forest. *Open circles* = tortoise sign (scat, burrows, tracks) but no tortoises; *half-open circles* = tortoise sightings unsupported by specimens; and *closed circles* = new and historic specimen records.

between Huásabas and El Coyote (1,000 m), north of Arispe (800 m), and between El Fuerte and Estacion Loreto (300 m), Sonora. There is an apparent gap in the range between Guaymas and Alamos, and the only sign we found was a burrow tentatively attributed to tortoise activity. Desert tortoises range at least as far south as the region of El Fuerte, Sinaloa, in the foothills of the Sierra Madre Occidental (Figure).

Habitat Use

Although tortoises were widespread in Sonora and northern Sinaloa, they seemed to be restricted to arroyos, slopes, and bajadas. Throughout the occupied areas of Mexico, we found that desert tortoises were conspicuously absent from valley floors and other flat areas. At a few sites (especially near Ortiz and Santiago, Sonora), residents reported that tortoises were absent from the immediate vicinity but present on nearby mountain slopes. Desert tortoises in Mexico range from xeric habitats near sea level to the lower edges of evergreen oak (*Quercus*) and juniper (*Juniperus*) woodlands at about 800 m elevation.

Based on the number of localities where we found tortoises or evidence of their presence during short searches, fewer animals seemed to be in coastal mountains and low elevations (e.g., Navojoa or vicinity of Guaymas) than at intermediate elevations of 300–500 m. At elevations above 500 m, densities seemed to vary with local features of vegetation, soil, and exposure.

Frequency of Occurrence

In 30 timed searches totaling 88.5 h ($\bar{x}$ = 2.95 h), we found live tortoises in 24% of the sampling periods, skeletal remains in 15%, and tortoise signs in 56%. We found some evidence of occurrence in 60% of the timed searches. We spent about 53.5 h at sites where we saw tortoise or their signs and 36 h at sites where there was no evidence of tortoises.

Human Use of the Desert Tortoise

We documented the human use of tortoises by shells and bones in trash piles and tortoises held in patios and gardens. In interviews with residents, many people reported consuming tortoise meat, albeit infrequently. Only in the vicinity of two moderate-sized settlements (Ures/Santiago and Ortiz/La Misa, Sonora) had tortoise populations probably been reduced by exploitation for food. In these areas, the few people we interviewed had consumed tortoises recently or knew of someone who had. Residents considered tortoises to have been reduced in numbers in recent years but to still be important food sources.

People of the small towns of Santiago and nearby Guadalupe were open and frank in discussing their use of tortoise meat. In their view, other meat was expensive, and tortoises, when available, were suitable for domestic use. They reported that tortoises provided limited quantities of meat and were only irregularly available.

Discussion

In Mexico, the desert tortoise occurs throughout the Sonoran and northern extremes of the Sinaloan biogeographic provinces (Lowe and Brown 1982) but not in the Madrean province. Tortoises occur in four subdivisions of the Sonoran desert–scrub biotic community—Arizona upland, Lower Colorado River Valley, plains of Sonora, and Central Gulf Coast—categorized by biotic differences associated with latitude and altitude (Turner and Brown 1982). Many areas in these subdivisions, especially the hills and mountain slopes occupied by tortoises, are in Sinaloan thornscrub (Turner and Brown 1982) because they have rainfall at the upper limits of desert scrub and exhibit related differences in vegetation. Lowland vegetations include several subdivisions of Sonoran desert scrub, Sinaloan thornscrub, Chihuahuan desert scrub, Sinaloan deciduous forest, and Sonoran savanna grassland (Brown 1982a, 1982b).

In a north–south direction, Sinaloan thornscrub is increasingly prevalent as tortoise habitat, and in extreme southern Sonora and northern Sinaloa desert tortoises occupy mesic and luxuriant habitats in Sinaloan deciduous forest. These communities and their subdivisions reflect latitudinal (north–south) and altitudinal gradients (predominantly west–east) of increasing moisture and moderated temperatures.

Rainfall in the Sonoran desert scrub varies by an order of magnitude (40–400 mm annually), but most areas receive between 100 and 300 mm (Turner and Brown 1982). Desert tortoises are not found in areas receiving less than 100 mm of rain. Presumably, tortoises occur on slopes and in montane habitats because of the local increased rainfall and potentially moderated temperatures. The surrounding habitat is generally inhospitable.

In northwestern Sonora, the boundary of the tortoise coincides closely with the 100-mm annual precipitation isopleth (Figure). The only coastal-plain record south of the Guaymas area is near Los Mochis in Sinaloa; this record is on a major highway and should probably be viewed with skepticism because it may have been a transplant. Further surveys are needed in the area.

Desert tortoises occupy narrow ribbons and disjunct patches of Sinaloan thornscrub associated with hills, isolated mountains, and mountain ranges in northern and central Sonora. Larger, more continuous expanses of habitat occur in eastern and southern Sonora, which probably support the highest density of desert tortoises in Mexico (based on information from interviews and frequency of our encountering tortoises and tortoise sign).

This habitat use is in marked contrast to the valley floor habitats typical of tortoises in the Mojave Desert (Berry 1989). Desert tortoises frequent rocky slopes and higher elevations in the eastern Mojave Desert (Bury et al. 1994) and in the Sonoran Desert in Arizona (Germano et al. 1994). Failure to survey mountain slopes and arroyos in Mexico would have resulted in few sightings and markedly different conclusions than those reported here.

The gap of about 150 km between the Guaymas and Alamos regions in the known range of the tortoise seems to be real because the highway and adjacent roads traverse a flat agricultural area. However, the sparse foothills in this region have not been well surveyed.

Repeated statements that the desert tortoise occurs naturally in Baja California (Cuesta Terron 1920, 1921; Schmidt 1922; Smith and Taylor 1950; Ernst and Barbour 1972) are not supported by specimens and are probably unwarranted (Auffenberg and Franz 1978; Smith and Smith 1979). The combination of aridity and sandy soils in the Colorado River delta seems to delineate the western distribution of the species in this area. Across the United States–Mexico border in southwestern Arizona and extreme southeastern California, desert tortoises are restricted to isolated colonies in small desert mountain ranges (Patterson 1982).

Recently, Ottley and Velazques (1989) described a new tortoise from near La Paz, Baja California Sur. However, Crumly and Grismer (1994) question the distinctiveness of this form and suggested that current evidence of the tortoise in the lower peninsula was either an important range extension or an introduction of *G. agassizii*.

The Sinaloan deciduous forest extends much farther south than the range of the desert tortoise as presently understood, and a narrow band of tortoise habitat may exist along the foothills for much of the length of Sinaloa. In the deciduous forests, however, the nearly continuous vegetative cover—including trees, vines, forbs, and low shrubs—is a deterrent to locating tortoises and signs. Further surveys of tortoises are needed south of the Rio Fuerte and northeast of Los Mochis in Sinaloa where suitable habitat may occur in some of the isolated mountain ranges on the coastal plain.

Tortoises seem to be absent from areas without topographic diversity, which may explain some voids in the distribution of the tortoises and provide a guide for future searches. Higher elevations are probably not limiting in Sonora because the tortoises reach an elevation of 1,300 m in central Arizona (Burge 1979) and 1,500 m in eastern California (Luckenbach 1982) and southern Nevada (Bury et al. 1994). Exposure, aspect, and soils probably influence altitudinal limits for the species. The factors that limit the tortoises to markedly lower elevations in the southern portions of the range are unclear.

Previous studies revealed desert tortoises as common in foothills and in arroyos on the Isla Tiburón (Reyes Osorio and Bury 1982) in contrast to conclusions that tortoises faced extinction there (Smith and Smith 1979). Our surveys increased the known range of the desert tortoise in Mexico by about 48% and highlighted the association of tortoises with mountain slopes.

Our success in finding tortoises (24% of surveys) and tortoise sign (56%) was remarkably similar to the results of Burge (1979) in upland habitats in Arizona: tortoises at about 24% and sign at 55% of the transects. Burge's overall success in finding any sign of tortoises (44% in Arizona) was slightly lower than ours (60% in Mexico).

Human Use of Tortoises

Tortoise populations adjacent to large population centers such as Hermosillo, Guaymas, and Caborcas probably have experienced long-term harm, including direct human exploitation, habitat degradation, road kills, predation by domestic dogs, and use as pets. However, we found evidence of tortoise populations on hillsides and mountain slopes near each of these cities, which suggests that some tortoise populations have survived despite perturbations by humans. For example, we found tortoises on a small isolated mountain beside the main highway 48 km north of Hermosillo, Sonora. The area is a popular rest stop for truck drivers and other motorists between Hermosillo and the border towns to the north. The continued existence of the tortoise in such an accessible location suggests that hillsides present a significant deterrent to the capture of tortoises or that hunting pressure is not great.

Clearly, some tortoise populations in rural areas with extensive human activity declined more than tortoise populations in rural areas with less human traffic. Tortoises near villages, large ranches, and roads may be vulnerable to capture, but populations farther from settlements come in less contact with hunters and people searching for livestock.

Near Santiago, local residents captured tortoises opportunistically (usually tortoises were found crossing roads or by ranch hands on nearby ranches). Much of the surrounding area was sparsely populated or unpopulated, and much tortoise habitat remained on steep slopes at considerable distances from ranches, roads, and villages. Thus, even if tortoises were extirpated in localized areas by human activity, other tortoise populations may persist in the immediate vicinity.

No residents we interviewed knew of anyone who gathered tortoises as a principal activity, although some men apparently had more interest and ability in collecting tortoises than others. Thus, the capture and use of tortoises remain opportunistic and limited by local economics, customs, and the proximity of tortoises to areas of human activity. When tortoises become scarce, people cease hunting them. The steep, rocky slopes inhabited by tortoises in the Sonoran Desert and in Sinaloan thornscrub increase the energy and time of the search for tortoises and reduce the harm to tortoises by hunters.

We were told that some residents of Alamos, Sonora, collect desert tortoises for sale to foreign tourists and for direct shipment to the United States and Europe. These activities are illegal. However, such collections may reduce local populations (i.e., those next to roads) because of the high economic incentives offered by foreign pet markets.

Locality Records

We do not repeat the localities given in Smith and Smith (1979) and Patterson (1982). Museum acronyms are ASU (Arizona State University, Tempe) and MSB (Museum of Southwestern Biology, University of New Mexico, Albuquerque).

Sinaloa

Specimens. MSB: Jipago, 3 km E Presa Miguel Hidalgo; Rancho San Pedro, 20 km NE El Fuerte.

Tortoise sign. 10 km N El Fuerte (burrow).

Sonora

Specimens. MSB: 3 km N Noria Agualareña; Cerro Carrizal near Santiago; 48 km N Hermosillo; Mina Mendosa, 3 km NE La Aurora; Mina Esmeralda, Tehuibabi; 8 km N, 3 km W Guaymas; Ortiz; Rancho Seco, 13 km N La Misa; 42 km S Hermosillo; Agua Caliente, 23 km N Tasajera; Ejido San Ignacio, 118 km N Kino–Hermosillo Highway on road to La Libertad; 55 km NE La Libertad; 17 km N Highway 2 on El Arenoso road; La Cienega, 60 km SE Caborca; 1 km N Minas Nuevas, 9 km NE Alamos. ASU: Agua Marín, 11 km W Alamos; 19 km W Alamos; 4 km NW Alamos; Tepustete, 11 km NW Alamos.

Sight records of tortoises. 37 km NE of La Libertad; 75 km NE La Libertad; 54 km NW Caborca; San Pedro Bay (Van Denburgh 1922); Rancho Los Mochos, 10 km NE San Ignacio.

Tortoise sign. Moradillas, N La Misa (burrow); Cerro Blanco, 22 km SE Desemboque del Seri (tracks, pallet ?); 33 km S Desemboque del Seri, 3 km E coast road (scats); 4 km W cerro Noche Buena, 15 km N Punta Chueca (tracks); 46 km NE Altar (burrows); near Guirocoba, 37 km SE Alamos (burrows); Agua Caliente, 17 km N, 5 km E Esperanza (burrow).

Acknowledgments

We thank P. R. Fritts, S. Reyes Osorio (Dirección General de Flora y Fauna Silvestre), J. M. Scott, and N. J. Scott, Jr., who helped us in the field. R. E. Robino typed the manuscript, and N. J. Scott, Jr., prepared the figure. We gratefully acknowledge support by D. B. Bowman and other personnel in the U.S. Fish and Wildlife Service. D. J. Germano secured the specimen records from the Arizona State University Museum. Field work was undertaken at the requests of the U.S. Fish and Wildlife Service and the Dirección General de Flora y Fauna Silvestre de México that also provided permits.

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Agonistic behavior between two female desert tortoises (*Gopherus agassizii*) in southwestern Utah. Fights between females are rarely observed in the wild. *Photo by T. C. Esque.*

Distribution, Habitat Use, and Protection of the Desert Tortoise in the Eastern Mojave Desert

by

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Abstract. The range of the desert tortoise (*Gopherus agassizii*) is widespread across the eastern Mojave Desert (southern Nevada, the Arizona Strip, and southwestern Utah). It occupies many habitats from flats and bajadas (hillsides) dominated by creosotebush at lower elevations (below 1,200 m elevation) to rocky slopes that border on blackbrush and juniper woodland at higher elevations (as high as 1,600 m). High mountain ranges, cold deserts, and playas (dry lake beds) are usually unsuitable habitat for tortoises. In winter, tortoises opportunistically use shallow burrows or deep caves, caliche overhangs, and rock crevices for cover. Although small isolated populations in the northern limits of the range may be prone to extirpation from cataclysmic stochastic events, deleterious effects of inbreeding depression may be mitigated by long generation times and relatively large home-range sizes of tortoises. Urbanization, roadways, habitat fragmentation, and other perturbations reduce wild populations. Because they may have unique local adaptations, small and peripheral populations of tortoises merit special protection. They are also protected by state and federal laws. We also urge protection of the tortoise in the eastern

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Mojave Desert because several large populations and many low- to moderate-sized populations still exist in remote areas and rugged terrain.

Key words: Distributional patterns, eastern Mojave Desert, *Gopherus agassizii*, habitat use, isolated populations, management, seasonal behavior.

Several studies addressed the ecology and conservation of desert tortoises (*Gopherus agassizii*) in the Mojave Desert—for example, at the Beaver Dam Slope in southwestern Utah (Woodbury and Hardy 1948), in southern Nevada (Burge and Bradley 1976; Turner et al. 1987; Germano and Joyner 1988), and in California (Luckenbach 1982; Berry 1986a). No synthesis is available, however, for the occurrence and habitat use of desert tortoises in the eastern Mojave Desert.

Desert tortoises in the eastern Mojave Desert are more vulnerable to stochastic events (freezing temperatures in winter, prolonged drought) than tortoises in the Sonoran Desert and Sinaloan thornscrub where freezes are rare and rainfall is more predictable (Germano 1994). The threat of extirpation is generally highest in populations at the periphery of a species' range and in small isolated populations (MacArthur 1972; Gilpin and Soule 1986). Furthermore, large distances between core and peripheral populations can limit or block gene flow. These processes may lead to genetic drift that may be part of natural speciation (Mayr 1970) or have deleterious effects on populations (Gilpin and Soule 1986). However, genetic drift may be low in tortoises because of their long generation time and relatively large home ranges (Bury et al. 1994).

Fragmentation of tortoise habitats from human perturbations results in smaller populations that become increasingly vulnerable to declines or extirpation (Dodd 1986). To understand the effects of habitat loss and fragmentation, we must accurately delineate the distributions and abundances of tortoise populations as well as dispersal corridors where gene flow may or may not be occurring as a result of management.

Toward a resolution of these issues in the eastern Mojave Desert, our objectives were (1) to determine the distribution of desert tortoises; (2) to describe the desert tortoises' use of heterogeneous habitats; and (3) to examine the special conservation needs of isolated tortoise populations.

Definition of Population, Range, and Distribution

Biologists use the term *population* to refer to an entire species or to local groups of a species. Here, we restrict the term to the local population or deme (Mayr 1970), which Schonewald-Cox et al. (1983) define as a breeding unit of individuals that essentially mate at random. Thus, we consider populations to comprise individuals that interbreed and occupy habitat unbroken by physical or biological barriers.

The *range* of a species is the geographic area of occurrence and usually includes many areas that are not occupied (e.g., unsuitable habitats).

The *distribution* denotes the known geographic localities of the species and is usually described by detailed maps or lists of localities, which help identify the elevational limits and habitat type (soil and vegetation) used by the species. It is important to obtain many positive and negative locality records because they best describe a species' patterns of occurrence or absence: areas with high frequency of records may indicate preferred habitats and corridors between populations, and areas with an absence of tortoises may be unsuitable habitat or barriers to gene flow.

Material and Methods

We used several sources of information to document the distribution of the desert tortoise in the eastern Mojave Desert. The largest data set was compiled from survey transects sponsored by the Bureau of Land Management (BLM). Bureau of Land Management transects are about 9.1 m wide by about 2.4 km long and in the form of an equilateral triangle (Minden 1980; Karl 1981; Turner et al. 1985; Berry 1986a). Recorded sign were live tortoises, shells, scats, tracks, and shelter sites. Cover and shelter included pallets (depressions that cover the shell of a tortoise), burrows (constructed underground holes about 0.5–2 m deep) and dens (2–10 m long). Although total sign on transects is used to estimate the density of tortoises (Berry 1986a), we mostly used these data to document the presence or absence of tortoises.

Besides the BLM transects, we include our observations in the Dixie Valley in southwestern Utah, Nevada Test Site, and other field surveys in the region. Several biologists familiar with tortoises added many new locality records in the periphery of the tortoise's range. We also summarized the literature and unpublished reports.

Study Area

Our scope of coverage is the eastern Mojave Desert in Utah, Arizona, and Nevada east of the Nevada–California border. We chose the Nevada state line as our western limit because survey data are usually collected by administrative units based on country and state borders. Furthermore, there are some differences in vegetation across this state line (Rowlands et al. 1982).

The morphology and genetics of desert tortoises is also somewhat different in Nevada and California. Desert tortoises of several different geographic groups have been differentiated: western Mojave Desert (most of the California Desert), eastern Mojave Desert (Nevada, Utah, northwest Arizona, and easternmost California), Sonoran Desert (Arizona and Mexico), and Sinaloan habitats (Mexico). These populations differ from each other in electrophoretic patterns of proteins (Jennings 1985; Glenn et al. 1990), mitochondrial DNA (Lamb et al. 1989), and shell morphology (Germano 1993). Also, minor differences exist in electrophoretic patterns of tortoises in the Mojave Desert in California (Rainboth et al. 1989).

In the past, the tortoises in the Mojave Desert may have been separated from those in the Sonoran Desert by the lower Colorado River, which earlier had extensive inland intrusions by the sea (Lamb et al. 1989). To a lesser degree, there may be a differentiation between tortoises in the western and eastern Mojave Desert. Here, we focus on a group of tortoises in the eastern Mojave Desert that (1) is distinct from other populations to varying degrees and (2) represents a large portion of the tortoise's range in the United States.

Utah and Northwestern Arizona

Dixie Valley, Utah

Desert tortoises occur in the Dixie Valley (east of the Beaver Dam Mountains) of southwestern Utah, which is the northeastern limit of the species' range. Tortoises occupy a broken band of sandstone and dune habitats across the northern foothills of the Dixie Valley and parts of the adjacent valley floor.

Several reports and museum records indicate that the desert tortoise occurred near St. George (the largest town in the Dixie Valley) more than 60 years ago. The Utah Division of Wildlife Resources (unpublished report, undated) stated

> ...several other scattered but fairly dense populations exist around Bloomington, St. George, Washington City, Snow Canyon, and LaVerkin, Utah. Some of these populations may be introduced but recent work indicates that even early pioneers observed tortoises in these areas so they probably now represent mixed populations of native and formerly captive animals from the entire range including California, Nevada and Arizona.

To our knowledge, the first specimen of the tortoise in Utah (Van Denburgh 1922:989) was an individual "taken on the mesas south of the Shivwits Indian Reservation, about 14 miles west of Saint George, Washington County." However, no museum number was provided. Patterson (1982) reported the Shivwits record as a literature citation and one museum specimen from St. George (California Academy of Sciences [CAS] 54190, collected in July 1921). We were informed that there is only one Utah specimen (CAS 54190) from that period and it is from St. George. Possibly, Van Denburgh's report (1922) of a tortoise from Shivwits was cataloged as having been from St. George, the nearest large town. In either case, one or two tortoises were obtained about 70 years ago in or near St. George. Also, Tanner (1927) reported tortoises near St. George, Utah. Woodbury (1931:123) recorded these localities and records from the Beaver Dam Slope and St. George where "...B. Jarvis found a juvenile freshly hatched from the egg."

Recently, many desert tortoises have been reported near St. George and elsewhere in the Dixie Valley, Utah (Fig. 1), as far east as Springdale, LaVerkin, and Hurricane in the eastern Dixie Valley. Coffeen (1990) reported 29 tortoises near Hurricane. In 1990, we observed three tortoises in a basalt cave 2–3 km west of Hurricane.

Other isolated pockets of tortoises occur west of St. George, Utah: a local resident told us that he has observed tortoises around Gunlock (26 km northwest of St. George) for the last 50 years. In June 1989, we found one adult tortoise, parts of a shell and scats during a 2-h search in a foothill 3–4 km northwest of Gunlock (Table 1). The terrain is steep, south-facing slopes and is dominated by blackbrush (*Coleogyne ramosissima*).

Southwest of St. George, tortoises occur in parts of the Virgin River Gorge (T. Duck, Bureau of Land Management, Arizona, personal communication), which is a narrow canyon through the Beaver Dam Mountains. A major gap in the known distribution of the tortoise is the Shivwits Indian Reservation and vicinity (15–20 km west of St. George) along the eastern flanks of the Beaver Dam Mountains (Fig. 2).

The desert tortoise is not known in the Dixie Valley south of St. George in Arizona. This area has

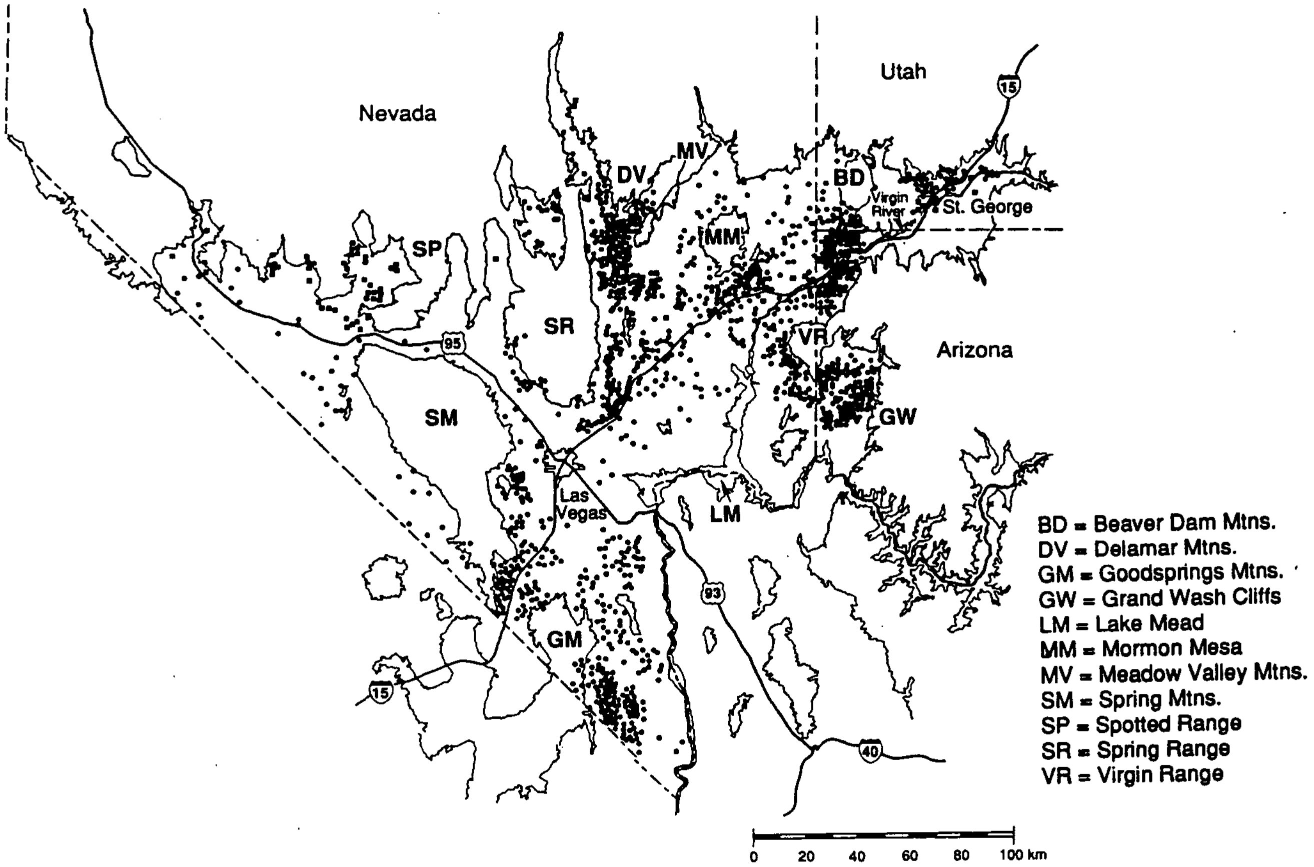

Fig. 1. Distribution of the desert tortoise (*Gopherus agassizii*) in Nevada, northwestern Arizona, and southwestern Utah. *Solid circles* indicate records of one or more signs at transects by the Bureau of Land Management; and *solid squares* are our observations or those of colleagues. *Irregular lines* indicate elevations of 1,220 m.

Table 1. Elevation records of desert tortoises (*Gopherus agassizii*) in the eastern Mojave Desert.

Location	Elevation (m)	Observer or reference
Utah		
Gunlock, 26 km northwest of St. George	1,250	Our record
Nevada		
East Pahranagat Range	1,520	C. Stevenson *in* USFWS[a](1993)
Joshua Forest, Desert NWR[b]	1,600	Our record
Nellis Air Force Base	1,400	Revegetation Innovations (unpublished data)
Jackass Flats, hill in NTS[c]	1,320	Our record
Yucca Mountain, NTS[c]	1,530	Collins et al. (1986)
Goodsprings Mountains	1,460	R. Marlow *in* USFWS[a](1993)
Springdale (22–28 miles northwest Las Vegas)	1,250–1,300	D. Baepler, Univ. Nevada,
Mount Charleston	as high as 2,130	Anecdotal *in* USFWS[a] (1993)
California		
Death Valley National Monument	1,120–2,235	Luckenbach (1982)

[a] U.S. Fish and Wildlife Service.
[b] National Wildlife Refuge.
[c] Nevada Test Site.

tortoise habitats typical of the Mojave Desert; they are relatively flat (i.e., 3–5% slope) and dominated by creosotebush (*Larrea tridentata*). Extensive general surveys in this area (T. Duck, Bureau of Land Management, Arizona, personal communication) revealed only a few tortoises, all of which were near highway rest areas, suggesting they were released captives. The lack of tortoises in the lowlands of the

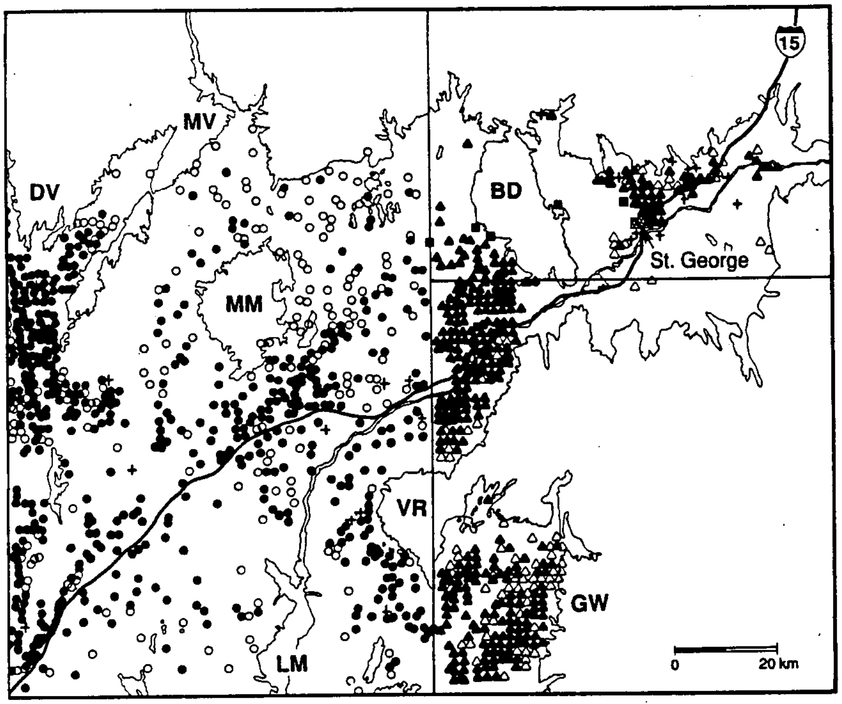

Fig. 2. Occurrence of the desert tortoise (*Gopherus agassizii*) in the northeastern portion of its range. *Solid symbols* are sites with tortoises or their sign; *open symbols* indicate that no tortoises and no sign were observed. *Circles* indicate transects based on records at the Bureau of Land Management, Las Vegas, Nevada; *triangles* indicate transects on file at the Bureau of Land Management, Dixie, Utah, and at the Arizona Strip District offices in St. George, Utah; *squares* indicate records from the literature; and *crosses* indicate our observations. Abbreviations are the same as in Fig. 1. Elevations at 1,220 m are indicated by *irregular lines*.

Dixie Valley may be a result of livestock bedding grounds and sheep pens used in the past. The area may have become devoid of palatable vegetation, and livestock herders may have taken tortoises for food. However, there are no data to support this hypothesis.

North St. George, Utah

Recently, many tortoises have been found in the Red Hills area, north of St. George. In the Red Hills are several pockets of tortoises at high density (>77/km^2), surrounded by pockets of medium density (8–20/km^2; Coombs 1977; Coffeen 1990). In 1988, more than 230 desert tortoises were marked in one 2.6-km^2 study area (Coffeen et al., unpublished data). We found similar high numbers of desert tortoises in 1989–90 (Esque et al., unpublished data). This is one of the highest recorded densities of the desert tortoise in any part of the Mojave Desert (Luckenbach 1982; Berry, unpublished data).

Desert tortoises north of St. George inhabit a mosaic of sandy valleys, sandstone outcrops, and ridges with basalt caps (mostly old cinder cones). Most of the sandstone outcrops have a southern exposure that may provide a warmer environment for tortoises during winter. The basalt caps and tops of ridges have worn rock or shallow soils that are unsuitable for burrow construction by tortoises, but there are many caves below the ridges where the basalt strata meet sandstone. Tortoises in this rocky terrain mostly use caves for shelter and forage on the rugged basalt slopes and ridges or adjacent sandy valleys (Esque et al., unpublished data). Ridges that are wider than 500 m may be a partial barrier to tortoise dispersal because of a lack of cover, especially where anthropogenic disturbances (i.e., paved roads, off-highway vehicle use, and garbage dumps) further reduced vegetation. However, this hypothesis needs further study.

Adjacent to sandy valleys, tortoises frequent sandstone outcrops that offer shelter (Esque et al., unpublished data). Sandy soils retain rainfall and often have much forage. Tortoises are less common in the middle of large expanses of aeolian sands (these can be as wide as 3 km near St. George), probably because the low clay content of the soils (<8%) does not provide adequate cohesiveness to maintain the structure of burrows.

Beaver Dam Slope and Vicinity, Utah and Arizona

There are about 60 tortoise localities on the Beaver Dam Slope in Utah (Minden 1980), and most are near Big Wash (1.0–2.4 km north of Arizona). Field studies have continued intermittently on the Big Wash of the Beaver Dam Slope since the late 1930's (Woodbury and Hardy 1948; Coombs 1977; Minden 1980; Minden and Keller 1981; Coffeen and Welker, unpublished data).

Woodbury and Hardy (1948) reported about 100 tortoises/km^2 in Big Wash, but this estimate is dubious because tortoises were mostly counted in winter dens and not on plots. Recently, the estimated density of the tortoises was 13–18/km^2 (Coffeen and Welker, unpublished data), which apparently is a decline from the former density. If this population declines further, then recolonization of this area could occur naturally by moves of tortoises from the west in Nevada or south on the Beaver Dam Slope in Arizona. For example, tortoises are widely distributed along the Utah–Arizona border (Fig. 1), and most habitat features occur across this broad valley (Hohman and Ohmart 1978; Minden 1980; Sheppard 1980; T. Duck, Bureau of Land Management, Arizona, personal communication).

Several records of tortoises occur west and northwest of the Big Wash area (Minden 1980). The northernmost site was the Jackson Wash (8 km east of Nevada; 27 km north of Arizona), where tortoise scats and winter dens have been observed (Minden 1980; D. J. Germano, personal communication). The Jackson Wash is a probable dispersal route for tortoises around the north end or through passes of the Beaver Dam Mountains. This is another route that tortoises may have used to reach the Dixie Valley to the east.

Habitats used by tortoises on the Beaver Dam slopes vary considerably but are mostly rocky uplands (foothills of the Beaver Dam Mountains) and upper bajadas dissected by steep-sided, rocky washes (Woodbury and Hardy 1948). Elevations decrease to the south toward Arizona where tortoises frequent areas of cobble on lower bajadas and broad washes with coarse sand and gravel (Hohman and Ohmart 1978).

There are many records of the desert tortoise west of the Beaver Dam Mountains in southwestern Utah and northwestern Arizona (Fig. 1). We believe that the Beaver Dam and adjacent populations are connected to other Mojave Desert populations: (1) east—to tortoises in the Dixie Valley, Utah, (2) west—to tortoises in the Terry Benches and Tule Desert of eastern Nevada, and (3) southwest—to tortoises along the north slopes of the Virgin Mountains in northwestern Arizona and the Pakoon Basin in northwestern Arizona and eastern Nevada.

Northwestern Arizona and Nevada

Virgin Mountains, Arizona

The Virgin River Valley and the Virgin Mountains in the northwestern corner of Arizona have some friable soils, but much of the area is rocky with large expanses of cobbles. Because it is difficult for tortoises to dig in rock and cobbles, rocky substrates create a patchy habitat mosaic for desert tortoises. However, tortoises may on occasion dig burrows at the edges of rocky aprons and cobble areas or use natural caves or crevices in the hard substrates for cover. Transects on bajadas along the Virgin Mountains revealed many localities (Fig. 2), but tortoises mostly occur in patches or at low densities. This pattern may create an incomplete corridor or weak connection to tortoises in adjacent areas to the west near Gold Butte in eastern Nevada and to the southwest in the Pakoon Basin of westernmost Arizona and eastern Nevada.

Pakoon Basin and Gold Butte, Arizona and Nevada

This is a large and remote region, bounded by the Grand Wash Cliffs on the east, Lake Mead to the south, the Virgin Mountains on the north, and the Virgin River and Overton Arm of Lake Mead on the west. We believe that this region is partially connected to other tortoise populations in the Mojave Desert through the Beaver Dam slope. However, before the placement of dams, the Virgin River had a seasonal flow (or was ephemeral) that may have posed an incomplete barrier to tortoises. Because of the constant flow from flood control and irrigation along the drainage, the river now represents a barrier to dispersal by tortoises.

The distribution of tortoises in this region seems to be widespread (Fig. 2), but the animals mostly occur in low to moderate numbers and in some pockets of higher numbers. The principal land use of the region is livestock grazing, which is dispersed over the basin; most livestock is concentrated in areas with water (stock tanks) and springs.

Nevada

Statewide Records

Linsdale (1940) denoted 6 and Patterson (1982) reported 18 locality records of desert tortoises in Nevada. During the last decade, the Bureau of Land Management identified more than 700 localities of tortoises (Fig. 1) in southern Nevada.

Mormon Mountains and Vicinity

The Mormon Mountains in eastern Nevada are bordered by the Mormon Mesa (to the south), Tule Desert (to the northeast), Meadow Valley (to the northwest), and Moapa Valley (to the southwest). Based on the high frequency of tortoise records (Fig. 1), this region may be a source population or perhaps a dispersal corridor between tortoises on the Beaver Dam slopes of Arizona and Utah and the Mormon Mesa and Moapa Valley in Nevada. The Moapa Valley has a large population of tortoises at medium to high densities that extends southwest to the Las Vegas Valley, Nevada. Although this area is dissected by Interstate 15 from the Arizona border southwest to Las Vegas, there have been few developments in this region. Thus, extensive areas of tortoise habitats remain on both sides of the highway.

The Meadow Valley Mountains separate tortoises in Meadow Valley to the east from the Coyote Springs Valley to the west. We have found tortoises in the Meadow Valley on lower bajadas and flats, where there are gravelly, sandy loams with low slopes (3–5%). Tortoises have not been reported in adjacent playas (old lake beds) and tall mountain ranges, where no surveys have been conducted.

Northeast of the Mormon Mountains, tortoises seem to have a patchy distribution in the Tule Desert because surveys along many transects revealed no sign (Fig. 2). This pattern may reflect unsuitable local conditions (e.g., impenetrable soils) for tortoises or marginal habitat at the periphery of the species' range.

Coyote Springs and Pahranagat Valleys

The northernmost limit of the range of the desert tortoise is north and northeast of Las Vegas in the Coyote Springs Valley and adjoining valleys (Fig. 1). The valleys are narrow along a north–south axis and are surrounded by high mountains (as high as 2,500 m). Arrow Canyon extends south of the Coyote Springs Valley and into the adjacent Moapa Valley (to the east). Tortoises in the Moapa Valley may be isolated from populations in the Meadow Valley by intervening tall mountains.

Desert tortoises occur in low numbers in the Pahranagat and Kane Springs valleys, which respectively extend north and northeast from the Coyote Springs Valley. Tortoise were recorded at below 1,220 m in the southern ends of these valleys. Tortoises may be present in the northern ends and foothills of both valleys, but these areas have not been searched.

The northernmost record of the desert tortoise is in the southern Pahranagat Valley. Schneider et al. (1985) found some sign adjacent to the Pahranagat National Wildlife Refuge, and S. Sloan (Bureau of Land Management, Las Vegas, Nevada, personal communication) observed two live tortoises 8–10 km northeast of Alamo in the Pahranagat Valley. The valley center is a flat wetland, but some tortoises seem to occur in the upland margins of the valley.

Desert National Wildlife Refuge and Vicinity

Northwest of Las Vegas is the Desert National Wildlife Refuge (NWR; Fig. 2), which is a large region with rugged terrain dominated by the Sheep Mountains, a steep mountain range with peaks as high as 3,000 m. Surveys on the refuge (B. Sharp and B. Zeller, unpublished reports) added several new localities. In March 1990, we found tortoise scats in the Joshua Forest area, a valley east of the refuge headquarters on the south side of the refuge. This record was near the species' upper limit of elevation (Table 1).

Schneider et al. (1985) found tortoise sign on 44 of 60 transects in the Desert NWR, and tortoises seemed to be confined to narrow, less-than-8-km-wide strips along the eastern and western boundaries of the Sheep Range. Several records are from the eastern flanks of the Sheep Range, where the plant community is mostly burrobrush (*Ambrosia dumosa*) and creosotebush. Most of the soil is rocky desert loam. Tortoise sign was found in three areas on the western side: (1) about 5 km north of the headquarters and then east to the Yucca Forest; (2) 13–26 km north of the headquarters; and (3) north of the Sheep Pass, south of Desert Dry Lake and north of Desert Dry Lake. The west side was dominated by shadscale (*Atriplex confertifolia*) and creosotebush.

There are some records of tortoises in Desert Dry Lake west of Coyote Springs Valley. Although the two areas are separated by the intervening Sheep Range, tortoises may have traversed this ridge or invaded from around the northern end of the Sheep Range. Alternatively, tortoises from populations on the western and southwestern sides of the Sheep Range invaded northward to Desert Dry Lake.

Nellis Air Force Base

West of the Desert NWR is Nellis Air Force Base and then the Nevada Test Site. This remote region has a few dirt roads. Access is strictly controlled because of military use. The terrain is rugged mountains and valleys along a north–south orientation and some closed basins.

Few records existed in this region until an extensive survey was conducted over 1,181 km^2 from December 1991 to May 1992 (Revegetation Innovations, unpublished data). Tortoise signs were recorded at 110 of 431 transects, in all major vegetation associations, and from valley bottoms to upper slopes (Table 1). Tortoise sign was only absent in dry playas. Surveys were mostly in winter, which reduced the likelihood of locating tortoise sign. Still, tortoises seem to be widespread and in low density on the Nellis Air Force Base.

We received this report too late for inclusion on our map (Fig. 1). However, the new records from Nellis Air Force Base add significantly to the elimination of a large gap on our map about 60–100 km north-northwest of Las Vegas (e.g., two north–south valleys and adjacent mountains).

Nevada Test Site and Vicinity

The desert tortoise is known from only the southern third of the Nevada Test Site (Fig. 1), including Frenchman Flat, Mercury Valley, Rock Valley, and Jackass Flats (Tanner and Jorgensen 1963; Medica et al. 1980 and unpublished data; EG&G Energy Measurements, unpublished data, available from National Technical Information Services, 5285 Port Royal Road, Springfield, VA 22161; Hunter, unpublished data). Desert tortoises on the Nevada Test Site occur at low numbers and most are in the lowland desert community dominated by creosotebush and burrobrush. Mercury Valley is just north of Highway 95 (a major east–west road) and includes the town of Mercury (about 90 km northwest of Las Vegas). Frenchman Flat is a large dry playa northwest of Mercury, and the Rock Valley and Jackass Flats are to the west. The tortoise has a low density (about 17/km^2) in the CP Hills in the northwestern Frenchman Flat and an even lower density in the Rock Valley and Mercury Valley (EG&G Energy Measurements, available from National Technical Information Services, 5285 Port Royal Road, Springfield, VA 22161; Hunter, unpublished data; Hunter and Medica, unpublished data).

We found scats of desert tortoise along the southern foothills of the Calico Hills, which form the northwestern border of Jackass Flats. Tortoises probably occur in this region, but their abundance is low. Some tortoises are widely distributed and at a low density in the western Jackass Flats, which are bordered by the Yucca Mountain (EG&G Energy Measurements, available from National Technical Information Services, 5285 Port Royal Road, Springfield, VA 22161; Medica et al., unpublished data).

Northeast of the Frenchman Flat along the eastern boundary of the Nevada Test Site, tortoise sign has been found at elevations of 975–1,100 m (Patton et al., unpublished data). In the northern Jackass Flats, desert tortoises occur in creosotebush on flats and on bajadas. Helicopter patrols regularly fly in the Nevada Test Site, and one crew observed an adult tortoise on the top of an isolated hill in the Jackass Flats (Table 1). North of the Jackass Flats and at higher elevations of the rocky slopes and alluvial fans, the vegetation becomes predominantly blackbrush, and tortoises seem to be absent. We found tortoises in and around the Nevada Test Site at elevations of about as high as 1,300 m in washes with steep slopes and caliche outcrops. The vegetation of the upper areas consists primarily of creosotebush and burrobrush that is interspersed with Joshua-trees (*Yucca brevifolia*).

Tortoises also occur on Yucca Mountain (Collins et al. 1986). One tortoise burrow with scats was found on the top of the mountain (Table 1). Other surveys of tortoises around Yucca Mountain (EG&G Energy Measurements, available from National Technical Information Services, 5285 Port Royal Road, Springfield, VA 22161) revealed that the amount of sign per kilometer was the same below and above 1,200 m elevation, and the most frequent sign was in the intermediate range of 1,201–1,300 m.

Desert tortoises are rare or absent in the central portions of the Jackass and Frenchman flats, which are open terrain with alkaline or sandy soil (Medica et al., unpublished data). Vegetation surrounding these flats (playas) is primarily saltbush (*Atriplex* sp.). Low tortoise densities also occur around the periphery of the playa in the Ivanpah Valley, California (Turner et al. 1985). Suitable habitat on playas and surrounding areas may be lacking throughout the range of the desert tortoise in the Mojave Desert (Luckenbach 1982).

Records or sign are of isolated desert tortoises south and west of the Nevada Test Site (Table 2). Collectively, the records from the Nevada Test Site and adjacent areas add appreciably to our knowledge about tortoise distribution in southwestern Nevada (Fig. 1).

Table 2. Isolated records or sign of desert tortoises (*Gopherus agassizii*) south and west of the Nevada Test Site.

Location	Observer or reference
Specter Range, southern bajadas	M. Saethre, University of California, Los Angeles P. A. Medica, BLM[a], Las Vegas, Nevada
Ash Meadows NWR[b], south of Crater	D. Threloff, USFWS[c] in Utah and Arizona
Ash Meadows, Nev. Flats	Karl (1981)
Vicinity of Bare Mountain (elevation of 960–1,158 m)	C. Stevenson, NDOW[d], Las Vegas, Nevada P. A. Medica, BLM[a], Las Vegas, Nevada
North Beatty, between Indian and Crystal springs	L. Grover, BLM[a], Tonopah, Nevada
22–28 km northwest of Springdale (elevation of 1,250–1,300 m)	D. Baepler, University of Nevada, Las Vegas

[a] Bureau of Land Management.
[b] National Wildlife Refuge.
[c] U.S. Fish and Wildlife Service.
[d] Nevada Department of Wildlife.

Discussion

Comparison of Occurrences and Estimated Densities

The chances of finding tortoises or their sign vary by season, time of day, weather, observer experience, and other factors that make estimations of density difficult (Turner et al. 1985; Fritts and Jennings 1994). Thus, we used information collected at transects to indicate the occurrence of tortoises and to estimate the relative abundance of populations.

Generally, transect surveys reliably reveal the presence of tortoises. Most tortoise sign is distinct and relatively long-lasting (e.g., burrows, shells). The observers were well trained and often surveyed along multiple transects in large valleys and adjacent bajadas to increase the probability of locating tortoise sign in major landscapes (e.g., basins, bajadas).

Dixie Valley Tortoises: Native or Introduced?

The occurrence of native tortoises in the Dixie Valley was earlier questioned. Hardy (1945:103) believed that the tortoises were introduced to the Dixie Valley and stated

> The distribution of the desert tortoise (*Gopherus agassizii*) presents a situation similar to that of the Joshua tree as it naturally occurs only west of the Beaver Dam Mountains. Individuals released in the desert regions near Saint George, however, have been able to survive for at least a few years.

Similarly, Woodbury and Hardy (1948:148–149) reported that the Beaver Dam Mountains "...appear to have marked the extreme northeastern limits of the range of the Desert Tortoise until, through the agency of man, the barriers were passed and tortoises were distributed far and wide beyond the mountains."

However, we have not seen a major biogeographic barrier between the Beaver Dam Slope and the Dixie Valley, Utah. For example, the Joshua-tree occurs west and east of the Beaver Dam Mountains. The Joshua-tree occurs in the Motoqua Pass (at an elevation of about 1,400 m and on the other side of the drainage divide northwest of St. George) north of the Beaver Dam Mountains, Utah, and in the Virgin River Gorge (elevation about 1,450 m; southwest of St. George). Furthermore, the desert tortoise occurs in many other habitat types besides Joshua-tree and may occur at an elevation above 1,500 m in the eastern Mojave Desert (Table 1).

Most reptiles in the eastern Mojave Desert, including the banded gecko (*Coleonyx variegatus*), sidewinder (*Crotalus cerastes*), and Gila monster (*Heloderma suspectum*), range eastward into the Dixie Valley (Tanner 1927; Bury et al. 1994). There is no reason to believe that these species were introduced by humans (e.g., the latter two species are venomous reptiles). Rather, the Dixie Valley has a high species richness of almost all plants and vertebrates known to occur in the Mojave Desert in neighboring Nevada (Lindsdale 1940; Rowlands et al. 1982). Based on biogeographic patterns, a widespread species like the desert tortoise is expected to naturally occur in the Dixie Valley.

Captive desert tortoises were released in much of the range of the tortoise, and southwestern Utah is not unique in receiving released animals (Dodd 1986). Earlier, this population was thought to be native tortoises augmented by released captive individuals (Beck and Coombs 1987). However, we suggest that released tortoises are probably not a large proportion of the Dixie Valley population because introduced tortoises from other parts of the range probably cannot survive the cold winters of southwestern Utah.

There is some evidence of failure or low survival of introduced tortoises (Fusari et al. 1987; Dodd and Seigel 1991). In Utah, more than 200 non-native tortoises were marked and released on the Beaver Dam Slope in 1970–82 (Utah Division of Wildlife Resources, unpublished data). Recapture of these released tortoises has been low, and the entire population has declined for several years (Minden and Keller 1981; Coffeen and Welker, unpublished data). This suggests that released tortoises are probably incapable of becoming the founder population in the Dixie Valley, Utah.

Most evidence indicates that the tortoises in the Dixie Valley are native and have a wide distribution and high abundance along the northern parts of the valley. Furthermore, the desert tortoise was listed in 1990 as a federal threatened species in the Mojave Desert and all individuals are now protected under the Endangered Species Act of 1973. Thus, tortoises in the Dixie Valley in the Mojave Desert are protected, regardless of origin.

Surveys for environmental impact statements and other studies of tortoises (Coffeen et al., unpublished data; Esque et al., unpublished data) provided a better understanding of the distribution of the tortoises in the Dixie Valley. Although recent legislation and management (U.S. Fish and Wildlife Service 1993) protect the tortoise, many small and isolated populations in the Dixie Valley may be depleted or lost in the next decade because of increased urban development, roadways, and other human activities.

Beaver Dam Slope of Utah, Arizona, and Nevada

Although often considered distinct, there is no population unique to the Beaver Dam Slopes (i.e., Utah populations). Rather, a genetic exchange of tortoises probably occurs between all populations along the Beaver Dam Slope and adjacent habitat in Utah, Arizona, and Nevada. These tortoises were probably a panmictic population until a recent interstate highway and associated development dissected the area. We suggest that effective protection of the population at the Beaver Dam depends on the maintenance of the metapopulation (interconnected, adjacent local populations).

Limitation of Distribution

There are more than 1,700 locality records of the desert tortoise in the eastern Mojave Desert (Fig.1). The tortoise is widely distributed in a pattern that indicates a panmictic population over much of the region or several metapopulations. Several isolated populations are at the periphery of the range.

Habitat Use

We found that the desert tortoise occupies a broad range of habitats in the eastern Mojave Desert. Apparently, tortoises are absent in few areas in the eastern Mojave Desert: high elevation terrain, near the northern limits of the species' range, restricted-access properties (mostly private), and urbanized or developed lands (Fig. 1).

Most surveys and population censuses were conducted in large valleys and bajadas where tortoises presumably reach their highest densities (Karl 1981; Luckenbach 1982; Berry 1986a). However, this is an assumption that has not been rigorously tested (e.g., with data from randomly selected study sites). The tortoises in other habitats, including cactus gardens, rocky slopes, and steep terrain, are seldom surveyed.

Cover

Cover seems to be an important factor of survival in tortoises, and in the eastern Mojave Desert, the desert tortoises are adapted to a variety of cover such as pallets, burrows, caves, and dens. However, the morphology of the tortoises places constraints on the use of cover types. A rigid shell, boxlike body, and relatively large adult size (compared with other terrestrial reptiles) prevent access to cover that is available to a fusiform, serpentine, or smaller animal.

Most tortoises on the Beaver Dam Slope, Utah, overwinter in deep dens in washes (Woodbury and Hardy 1948). Within 10 km south of the slope, however, we observed that about 50% of the animals overwinter in burrows on uplands between the major washes. Perhaps the gravelly soils at this site are more suitable for burrowing than the rockier soils at the Big Wash (Woodbury–Hardy site).

North of St. George, Utah, overwintering tortoises frequent caves, deep fissures, and rocky overhangs; some burrows are in aeolian sand. One tortoise was in a shallow undercut during winter and in full view for the past 5 years, even during snowfalls that lasted overnight (M. Topham, Utah Technical Advisory Team for the Desert Tortoise, personal communication). Near Las Vegas, in Rock Valley (Nevada Test Site) and in Arrow Canyon, Nevada, we also saw tortoises in shallow, less-than-1-m-long burrows during winter.

In the Sonoran Desert in Arizona, desert tortoises usually occur in rock crevices or under rocky overhangs but rarely construct deep burrows (Auffenberg 1969; Fritts and Jennings 1994). Farther south in Sonora, Mexico, tortoises seem to construct only shallow burrows on Tiburon Island (Reyes Osorio and Bury 1982). Thus, the use of cover and burrowing habits by desert tortoises vary by latitude and inside each major desert or biome (Germano et al. 1994).

Elevational Limits

Most areas above 1,200 m appear as gaps in the mapped distribution of the desert tortoise (Fig. 1), although the species lives in mountainous areas throughout the Mojave Desert (Table 1). In fact, desert tortoises can climb rocky and steep terrains (Woodbury and Hardy 1948) and may reach the tops of rugged outcrops. Shells, scats, and burrows of desert tortoises have been found on mountaintops in the eastern Mojave Desert (Woodbury and Hardy 1948; Tanner and Jorgensen 1963). Although some shells may have been transported there by avian or mammalian predators, live tortoises also have been seen at higher elevations (Luckenbach 1982).

Because surveys are rarely conducted at higher elevations, the habits of the tortoises in montane and upslope habitats and the elevation limits of the species are not well known. These are troublesome gaps of information for the conservation of the tortoises because some tortoise populations may be most abundant on slopes at middle elevations (e.g., near 1,200 m on Yucca Mountain, Nevada; EG&G Energy Measurements, available from National Technical Information Services, 5285 Port Royal Road, Springfield, VA 22161). If the tortoises frequent middle or upper slopes in other areas, the boundaries of known populations extend farther and estimates of population sizes may be larger than currently thought. Furthermore, upper slopes usually are rocky substrata that markedly differ from sandy and gravel soils in typical tortoise habitats on desert valleys and bajadas (lower slopes). There is a need to compare the ecology of tortoises on slopes and flats because these habitats vary in vegetative composition, friable soils (e.g, for construction of tortoise burrows), weather, and other factors.

Threats to Tortoises

In the eastern Mojave Desert, desert tortoises have been extirpated by urbanization, roads, and other developments (e.g., in parts of the Las Vegas Valley; Burge and Bradley 1976). However, desert tortoises may still occur in adjacent undisturbed habitat (Corn 1994).

There have been proposals to move tortoises from areas that are to be developed (e.g., St. George, Utah, and Las Vegas, Nevada) into other habitats with presumed depleted populations. However, such action needs scrutiny because native animals may be displaced to their detriment (Fusari et al.

1987; Berry 1986b; Bury et al. 1994; Dodd and Seigel 1991).

Wildfire may have become a threat to desert tortoise populations in the Pakoon Basin of northwestern Arizona (T. Duck, Bureau of Land Management, Arizona, personal communication). Because of the encroachment of introduced species such as red brome (*Bromus rubens*), the vegetation now carries fires more easily than in the past. These fires can engulf perennial shrubs and Joshua-trees that may provide necessary cover for desert tortoises.

Heavy grazing by feral burros degraded the habitat and available forage for the desert tortoises near Lake Mead, Nevada (R. Haley, National Park Service, personal communication). However, the effects of grazing by burros and livestock on tortoises are not well documented (Oldemeyer 1994) and need assessment in the eastern Mojave Desert.

Protection of Small and Isolated Populations

The eastern Mojave Desert has several areas with moderate to high densities of desert tortoises in extensive habitats (Berry, unpublished data; Spang et al., unpublished data). Many isolated populations of desert tortoises are in the northern Tule Desert in eastern Nevada, Desert Dry Lake in south-central Nevada, and Dixie Valley in southwestern Utah (Fig. 1). Although most of them seem to be small or peripheral populations, they are not extinct and merit protection for several reasons:

- Desert tortoises in small areas may be abundant. For example, desert tortoises north of St. George, Utah, have one of the highest population densities. However, the geographic range of the population covers only a few square kilometers.
- Peripheral populations survive the environmental stresses at the edges of the species' range (e.g., tortoises in northern or high elevation areas probably evolved to remain inactive in deep dens or in caves during cold winter temperatures).
- Small or isolated populations may have a unique genetic composition that is important to the future of this species. Local adaptations add behavioral and evolutionary diversity to tortoises.

Although small populations of vertebrates may face detrimental effects of inbreeding depression, no empirical evidence is available to suggest that this is an immediate threat to the desert tortoise (Bury et al. 1994). Rather, desert tortoises may have a slow rate of inbreeding because of their long generation time (Turner et al. 1987; Germano 1994); they mature late (12–18 years of age) and are relatively long-lived vertebrates. Desert tortoises are also capable of relatively extensive moves (as long as 1 km/day; Berry 1986a) and therefore can interbreed with tortoises in other populations, particularly over their long life spans. Thus, we suggest that individuals in isolated groups can persist intact for extended periods (e.g., perhaps decades).

The largest populations of desert tortoises often attract the most study and, in turn, most funding for habitat protection and other conservation. These major populations have been identified as being in crucial areas that are vital to the continued survival of the species (Berry 1989 and unpublished data; Spang et al., unpublished data). However, it is not clear whether protection is wiser or more prudent for a few large populations or for many smaller populations.

In crucial areas, populations of tortoises are large in relatively continuous habitat and surrounded by other populations, and these probably can endure perturbations more successfully than smaller populations. For example, in the Piute Valley of southern Nevada, part of a large population died in a localized area. However, nearby individuals seemed to move onto the plot from adjacent populations and restored the former abundance (Germano and Joyner 1988). Of course, large-scale losses (e.g., over an entire basin or valley) would negate such a local response.

We suggest that small or isolated populations warrant innovative management because they are more easily lost than larger populations by anthropogenic perturbations and stochastic events (e.g., long-term drought). Furthermore, small populations lend themselves to natural experiments. For example, small populations inhabit the peripheral range of the desert tortoises in the northern Mojave Desert, and studies of these groups could better define the required size of viable populations.

Furthermore, the size of the population as a measure of its worth (i.e., bigger is better) is not the only consideration. The species is now protected by state laws and listed throughout the Mojave Desert as a federal threatened species, whereby all individuals receive equal protection (U.S. Fish and Wildlife Service 1993).

Lastly, we suggest that the protection of populations in the crucial areas and of many small, isolated populations is a prudent option that provides the most effective conservation of the desert tortoise across large geographic areas. A series of habitat reserves (e.g., moderate-to-large patches of protected habitat) and responsible management in the intervening areas may be effective means to ensure the long-term survival of desert tortoises. This approach is an alternative strategy to current conflicts of either no management or total protection of vast tracts of arid land now occupied by the desert tortoise.

Acknowledgments

We thank the Nevada Department of Wildlife, Utah Division of Wildlife Resources, Arizona Fish and Game Department, U.S. Fish and Wildlife Service, U.S. Air Force, and the U.S. Bureau of Land Management for their cooperation in obtaining distribution information. We also thank many people for locality data and other assistance, including R. Bezette, J. Brooks, D. Brown, M. Coffeen, J. Cole, R. Drewes, T. Duck, R. Duncan, P. Greger, R. Haley, B. Hardenbrook, K. Hunter, R. Hunter, D. Lopez, J. Payne, C. Schwalbe, S. Slone, and W. Tanner.

We are also grateful for support to P. A. Medica by the U.S. Department of Energy, through the Basic Environmental Compliance and Monitoring Program, Nevada Test Site. Field studies by T. C. Esque and L. A. DeFalco were funded by the Bureau of Land Management in Utah, Arizona Strip, and Nevada, as well as the U.S. Fish and Wildlife Service. Research was conducted under appropriate state and federal permits. P. S. Corn, D. J. Germano, D. A. Ross, J. Slack, and J. H. Wolfheim provided useful comments and suggestions on the manuscript.

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Adult desert tortoise (*Gopherus agassizii*) inhabiting rocky terrain of southwestern Utah. Photo by *T. C. Esque*.

Range and Habitats of the Desert Tortoise

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Abstract. We determined the current range of the desert tortoise (*Gopherus agassizii*) based on the available latest data from government agencies, the literature, and our experience. We developed the first detailed range map of this species and summarized information about habitat preferences. New records of occurrences were incorporated, and some peripheral localities of questionable authenticity were deleted. The distribution of *G. agassizii* covers the broadest range of latitude, climatic regimes, habitats, and biotic regions of any North American tortoise. The northern portion of its range is in the Mojave

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Desert of southeastern California, southern Nevada, southwestern Utah, and northwestern Arizona. The central portion of the range consists of several subdivisions of the Sonoran Desert in southeastern California, western and southern Arizona, and western Sonora, Mexico. The southern edge of its range is in the semitropical Sinaloan thornscrub and Sinaloan deciduous forest of eastern Sonora and northern Sinaloa, Mexico. This species has marked geographic differences but seems to construct burrows throughout its range.

Key words: Climates, distribution, ecology, *Gopherus agassizii*, Mojave Desert, Sinaloan deciduous woodland, Sinaloan thornscrub, Sonoran Desert, tortoise.

Accurate depiction is important for the description of the range of a species. Details of habitat can provide valuable insights into a species' environmental tolerance and means of survival in various environments. Of the four North American tortoise species, the desert tortoise (*Gopherus agassizii*) has the broadest range of latitude and habitats (Auffenberg and Franz 1978; Bury 1982; Patterson 1982; Stebbins 1985; Lowe 1990; Bury et al. 1994a; Germano 1994). However, the complexity of these habitats has not been well documented.

The earliest comprehensive study of *G. agassizii* was conducted in the northeastern portion of its range (Woodbury and Hardy 1948), and the most recent studies were done in various parts of the Mojave Desert (Luckenbach 1982; Berry 1986; Corn 1994). We believe that this emphasis on only one part of the range biased the understanding of the habitats and general biology of *G. agassizii*. We examined *G. agassizii* across its range and habitats, summarized information about its habitats and its ecology, and constructed the first detailed map of its range.

Methods

We gathered data on range and habitats from the literature, government records, and our many years of field work across the range of the desert tortoise. We constructed the range map from evaluations of published distributions (Smith and Smith 1979; Patterson 1982; Stebbins 1985; Taubert and Johnson 1987; Berry 1989), unpublished maps by state and federal agencies (Arizona Department of Game and Fish; U.S. Bureau of Land Management; U.S. Fish and Wildlife Service), and maps on portions of the range published elsewhere in this volume (Bury et al. 1994b; Fritts and Jennings 1994). We refined the map and summarized habitat use based on our knowledge of the species in various habitats (Medica et al. 1975; Bury 1982; Esque and Duncan 1989; Germano 1989, 1994; Bury et al. 1994a).

Moisture Gradient and Plant Associations in the Range of *Gopherus agassizii*

The following is a composite description of climate in the range of *G. agassizii* (Lowe 1964, 1990; Brown 1982; Turner 1982; Turner and Brown 1982; MacMahon and Wagner 1985; Germano 1989, 1994). Moisture is on a gradient from north to south; rain is least abundant in the north and increases greatly to the south (Table 1). The timing of rainfall also differs along this gradient. Precipitation is limited to winter storms and unpredictable summer thunderstorms in the northwestern portion of the range but increases in summer in the southern portion. Summer rainfall is less than 10% of the total precipitation in the western Mojave Desert but can be as much as 70% of the yearly precipitation in the Sinaloan thornscrub and deciduous forest.

The vegetation types and physiognomy are concordant with the rainfall gradient (Table 2). The northern portion of the range has a relatively sparse cover of low-growing shrubs (MacMahon and Wagner 1985). Plant cover increases to the south, and at the extreme southern portion of the range in Sinaloan deciduous forest, tall shrubs and trees form a dense, closed canopy (Table 2). Summer temperatures are uniformly hot throughout

Table 1. Climatic characteristics of the range of *Gopherus agassizii*. Precipitation and temperature values are 20-year averages (Germano 1989). Each value in a column is from a different weather station.

	Subregion of range and habitat feature				
	Western Mojave Desert	Eastern Mojave Desert	Sonoran Desert	Sinaloan thorn-scrub	Sinaloan deciduous forest
Average precipitation (mm)	102	110	140[a]	278	621
	169	173	183	534	664
	143	101	290		628
	129	209	324		
	105	108	309		
Percent precipitation (June–August)	<10	~30	35–70	~60	67–78[b]
Percent precipitation (November–March)	>75	~50	21–50	~25	~15
Mean high temperatures (° C—July)	39.1	40.4	42.3[a]	30.4[c]	29.1[c]
	36.5	36.7	41.8	32.6[c]	31.5[c]
	37.1	40.8	36.7		32.2[c]
	36.8	39.3			
	39.8	42.7			
Mean low temperatures (° C—January)	–0.4	0.5	0.8[a]	13.6[c]	16.4[c]
	–0.4	1.6	0.7	15.7[c]	17.4[c]
	2.1	1.7	3.3		18.2[c]
	–2.1	3.2			
	–1.9	4.9			

[a] North to south gradient.
[b] July–September.
[c] Average daily temperatures, lows and highs not recorded.

the range of *G. agassizii*, but winter temperatures are mild in the south and increasingly colder toward the north; most of the Mojave Desert portion of the range has subfreezing temperatures during portions of winter (Turner 1982; MacMahon and Wagner 1985; Germano 1989).

Habitats

Mojave Desert

The distribution of *G. agassizii* in the northern part of its range is approximately defined by the boundaries of the Mojave Desert (Fig. 1). The Mojave Desert is a high desert at elevations between 600 and 1,200 m (Luckenbach 1982; MacMahon and Wagner 1985). The most widespread plant is creosotebush (*Larrea tridentata*). Several other sclerophyll shrubs are either codominants or dominants, and cacti of short stature are well represented (Shreve 1942; Turner 1982; MacMahon and Wagner 1985). In many parts of the Mojave Desert, creosotebush and white bursage (*Ambrosia dumosa*) dominate as much as 70% of the landscape (Shreve 1942) and *G. agassizii* often occurs in this habitat type. Where the Joshua-tree (*Yucca brevifolia*) and the Mojave yucca (*Y. schidigera*) are conspicuous in the Mojave Desert, the abundance of *G. agassizii* is usually low to moderate (Luckenbach 1982).

The Mojave Desert is especially rich in ephemeral plants, most of which are winter annuals (Turner 1982). Winter annuals are important foods, but *G. agassizii* also eats perennial grasses (Woodbury and Hardy 1948; Burge and Bradley 1976; Hansen et al. 1976; Berry 1978; Luckenbach 1982).

Table 2. Habitat characteristics of *Gopherus agassizii* in subregions of its range.

Habitat features	Subregion of range and habitat feature				
	Western Mojave Desert	Eastern Mojave Desert	Sonoran Desert	Sinaloan thorn-scrub	Sinaloan deciduous forest
Occupied habitat	Valleys, bajadas hills?	Valleys, bajadas hills	Valleys?, bajadas hills	Hills, mtn. slopes	Hills, mtn. slopes
Substrate	Sandy loam to rocky	Sandy loam to rocky	Rocky	?	?
Vegetation	Low-growing sclerophyll scrub	Low-growing sclerophyll scrub	Low-growing to arborescent sclerophyll scrub	Dense arborescent sclerophyll scrub	Drought-deciduous woodland, closed canopy
Annual plants	Mostly winter germination	Mostly fall germination, some summer germination	Mostly summer germination	Mostly summer germination	Mostly summer germination

Winter annuals include a variety of broad-leaved plants and grasses. Most of the Mojave Desert has been invaded by introduced winter annuals such as *Bromus rubens*, *B. tectorum*, *Schismus barbatus*, and *Erodium cicutarium* that dominate cover and biomass in some years (Hunter 1992; Oldemeyer 1994). Recent studies revealed that *G. agassizii* eats a large variety of plant species, including woody perennials and cacti. Woody perennials and cacti are a minor portion of the diet of *G. agassizii* in spring (Esque, unpublished data) but seem to be important as a late-season food and during drought (Turner et al. 1984).

Gopherus agassizii supplements its herbaceous diet with minerals from either the soil (Marlow and Tollestrup 1982) or weathered bone (Esque and Peters 1994). Based on stomach contents, supplemental mineral ingestion seems to be common in parts of the range in Mexico (Fritts, unpublished data).

Rainfall in the Mojave Desert is low and lower than in other parts of the range of *G. agassizii* (Turner 1982; Germano 1989, 1994). The average yearly precipitation ranged from 102 to 169 mm at five weather stations in the western Mojave Desert and from 101 to 223 mm in the eastern Mojave Desert (Table 1). In the western Mojave Desert, most precipitation is in winter, and less than 10% is in summer (Table 1). Some of this precipitation is in the form of snow, yearly amounts of which are highly variable (Germano 1989).

When the annual precipitation is average or above average, precipitation in fall leads to germination of broad-leaved annuals and annual grasses that cover the ground between shrubs (Beatley 1969; Hunter 1992). In the eastern Mojave Desert, the greatest amount of precipitation is received in fall and winter; summer thunderstorms in the eastern Mojave Desert contribute a greater percentage of the total precipitation than those in the western Mojave (Table 1). The monthly precipitation in the range of *G. agassizii* is least predictable and also most variable among years in the eastern Mojave Desert (Germano 1989, 1994). In the western and eastern Mojave Desert, temperatures are hot in summer and near or below freezing in winter. Throughout the Mojave Desert, *G. agassizii* is often found on valley bottoms and on bajadas (Figs. 2A and 2B), suggesting that this is the preferred habitat (Woodbury and Hardy 1948; Stebbins 1985; Berry 1989). However, tortoises may occur on rocky hillsides and (albeit rarely) at elevations above 1,400 m (Luckenbach 1982). Recently, *G. agassizii* was found on rocky hillsides at an elevation of 1,500–1,600 m in the northern parts of the Mojave Desert in Nevada (Collins et al. 1986). Tortoises occur in

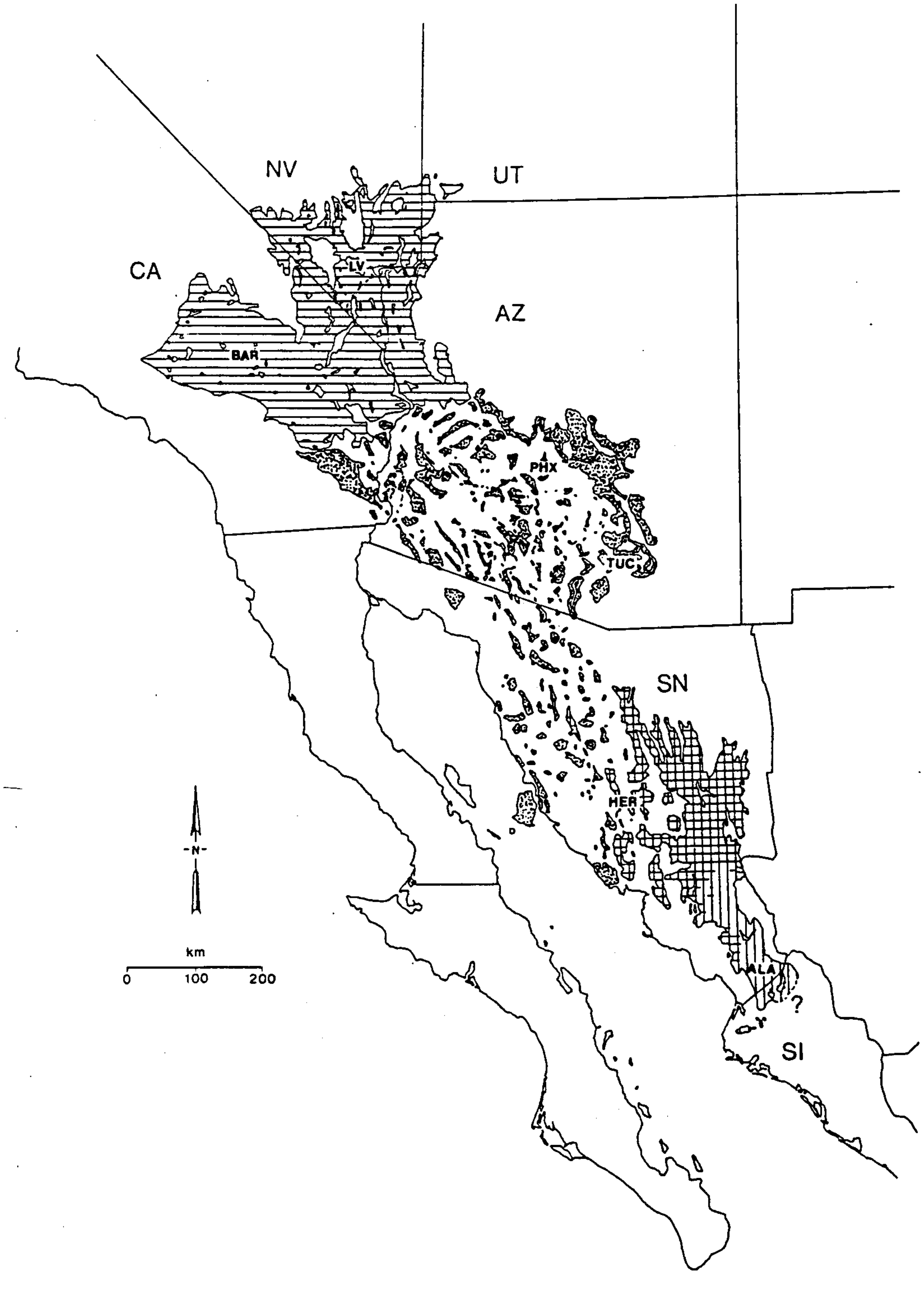

Fig. 1. Distribution of *Gopherus agassizii* in the southwestern United States and northwestern Mexico. This species occurs in three distinct habitat types: Mojave Desert (*horizontal lines*), Sonoran Desert (*shaded*), and Sinaloan deciduous forest (*vertical lines*). Sinaloan thornscrub (*hatching*) is a transitional habitat between the Sonoran Desert and the Sinaloan deciduous forest. States: AZ—Arizona; CA—California; NV—Nevada; SI—Sinaloa; SN—Sonora; UT—Utah. Cities: ALA—Alamos; BAR—Barstow; HER—Hermasillo; LV—Las Vegas; PHX—Phoenix; TUC—Tucson.

sandstone formations (Fig. 2C) in Utah (Bury et al. 1994b; Esque, unpublished data).

The construction and occupancy of burrows seem to be obligatory in *G. agassizii* in the Mojave Desert (Woodbury and Hardy 1948; Luckenbach 1982), perhaps because of frequent freezing temperatures in winter. Burrows can be long and complex. On the Beaver Dam Slope, Utah, the length of dens (long winter burrows) are 2–5 m and can be 10 m (Woodbury and Hardy 1940, 1948). These dens may be occupied by many individuals in winter. On the Nevada test site, some burrows are larger than 7.5 m and under caliche overhangs or in the sides of washes (Fig. 2D; Bury et al. 1994b). In the western Mojave Desert, dens are shallower (usually as long as 2.4 m; Berry 1978) and seem to be less common (Luckenbach 1982). The length of most burrows in the western Mojave is 1–3 m and averages about 1 m (Marlow 1979; Luckenbach 1982). These shorter burrows are at lower elevations or in valleys in the eastern Mojave Desert in southern Nevada (Burge 1978).

The highest densities of *G. agassizii* seem to be in the western Mojave Desert (Luckenbach 1982; Berry 1986, 1989). The estimated densities based on tortoise sign in California range from fewer than 8 tortoises/km^2 to more than 97 tortoises/km^2 and, based on counts of individuals on 2.6 km^2 plots, may be as high as 184 tortoises/km^2 (Berry 1986). The estimated density in one area of the western Mojave Desert was 347–540 tortoises/km^2 (Luckenbach 1982), but the accuracy of this estimate and the area with such a density are not certain. Higher reported estimates (Berry 1989) are questionable (Corn 1994). Densities of more than 150 tortoises/km^2 may occur in parts of the eastern Mojave Desert (Bury et al. 1994b).

The distribution of *G. agassizii* in the eastern Mojave Desert includes populations in the Dixie Valley (St. George area) of Utah (Bury et al.

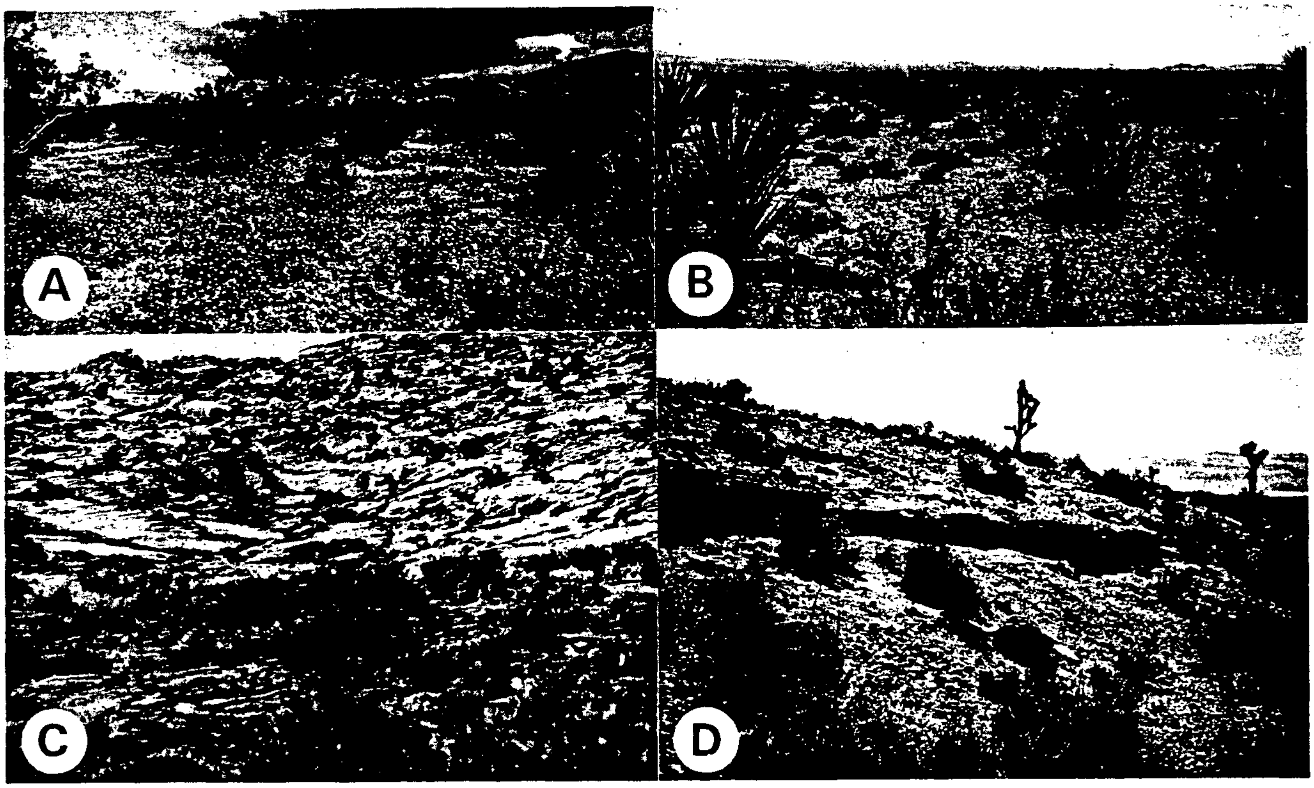

Fig. 2. Representative habitats of *Gopherus agassizii* in the Mojave Desert. *A*: Creosotebush scrub in the western Mojave Desert. Note the covering of herbaceous annuals between shrubs that sometimes occurs (photo by D. J. Germano). *B*: Creosotebush scrub with Mojave yucca (*Yucca schidigera*) in the eastern Mojave Desert (photo by D. J. Germano). *C*: Rocky sandstone habitat at City Creek, Utah, in the extreme northeastern portion of the range of *G. agassizii* (photo by D. J. Germano). *D*: Caliche overhangs and burrows of *G. agassizii* at the Nevada test site (photo by P. A. Medica).

1994b). Previously these populations were either unknown (e.g., a large tortoise population at City Creek north of St. George) or inappropriately considered to be captive releases (e.g., in the Paradise Canyon northwest of St. George; Beck and Coombs 1987; Bury et al. 1994b). We believe that the large population sizes and all age groups in these populations justify the recognition of these populations as important stock. Several passes over the presumed natural barrier of the Beaver Dam Mountains between the Dixie Valley populations and the better known population on the Beaver Dam slope may have been routes of dispersal. Almost all reptiles of the Mojave Desert occur in the Dixie Valley and, based on this biogeographic evidence, desert tortoises also seem to be native there (Bury et al. 1994b).

Sonoran Desert

The Sonoran Desert has been divided into six subunits of recognizable vegetational differences (Shreve 1951; Brown and Lowe 1980), and *G. agassizii* is found in portions of four of them: the lower Colorado River valley, Arizona uplands, plains of Sonora, and central Gulf Coast. *Gopherus agassizii* occurs in the lower Colorado River valley in southeastern California, southwestern Arizona, and western Sonora, but it does not occur in northeastern Baja California (Fig. 1). The mean summer precipitation is less than 20 mm in seven of eight climate stations in the lower Colorado River valley subdivision in Baja California, and the mean summer temperature is greater than 30° C in six of the eight stations (Turner and Brown 1982). This is in marked contrast to other localities in the lower Colorado River valley and other subunits of the Sonoran Desert where the tortoise occurs. *Gopherus agassizii* is also known only from the extreme eastern edge of the Imperial Valley of California (Dimmitt 1977; Luckenbach 1982). It can be found throughout the Arizona uplands and plains of Sonora and on the eastern portion of the central Gulf Coast subdivision in Sonora, Mexico.

The lower Colorado River valley is the driest of the subdivisions of the Sonoran Desert and is vegetated mainly by shrubs in the valleys and bajadas and by various small trees and shrubs in drainageways (Turner and Brown 1982). As in the Mojave Desert, creosotebush is a dominant plant throughout most of the Sonoran Desert, although its importance in the south is reduced. Unlike the Mojave Desert, the Sonoran Desert has a high abundance of tree species (Turner and Brown 1982). In the Lower Colorado River, *G. agassizii* seems to occur mainly on the bajada and rocky slopes of hillsides and in the upper portions of arroyos (Fig. 3A) but not in valleys that constitute most of this subdivision.

In the Sonoran Desert, *G. agassizii* may be most abundant in the Arizona uplands subdivision where tortoises occur on slopes, hills, and multidissected sloping plains (Fig. 3B). The vegetation is scrubland or low woodland of leguminous trees with several layers of shrubs and perennial succulents (Turner and Brown 1982). The central Gulf Coast and plains of Sonora subdivisions are the southernmost portions of the Sonoran Desert on the mainland. Vegetation on the central Gulf Coast is similar to that of the Arizona uplands subdivision. The Sonora plain is predominantly a woodland subdivision and grades into Sinaloan thornscrub on mountains and hillsides and especially at higher elevations (Turner and Brown 1982).

Precipitation is greater in the Sonoran Desert than in the Mojave Desert, and its amount and timing are on a gradient from north to south (Brown 1982; MacMahon and Wagner 1985; Germano 1994). The annual precipitation ranges from 140 mm in the north to 324 mm in the south (Table 1). As the frequency of precipitation increases to the south, the amount in summer also increases (Table 1). Temperatures are hot in summer and cold in winter in the northern part of the Sonoran Desert but more moderate in winter in the southern part (Table 1).

Little information has been gathered on annual plant productivity in the Sonoran Desert, and information on the abundance and season of the production of forage of tortoises is lacking. The Sonoran Desert produces many broad-leaved annual plants in summer (Mulroy and Rundel 1977) that may be the bulk of the diet of *G. agassizii*. The variation in production and the importance of winter annuals to *G. agassizii* in the Sonoran Desert are unknown, but winter annuals are probably less important food there than in the Mojave Desert.

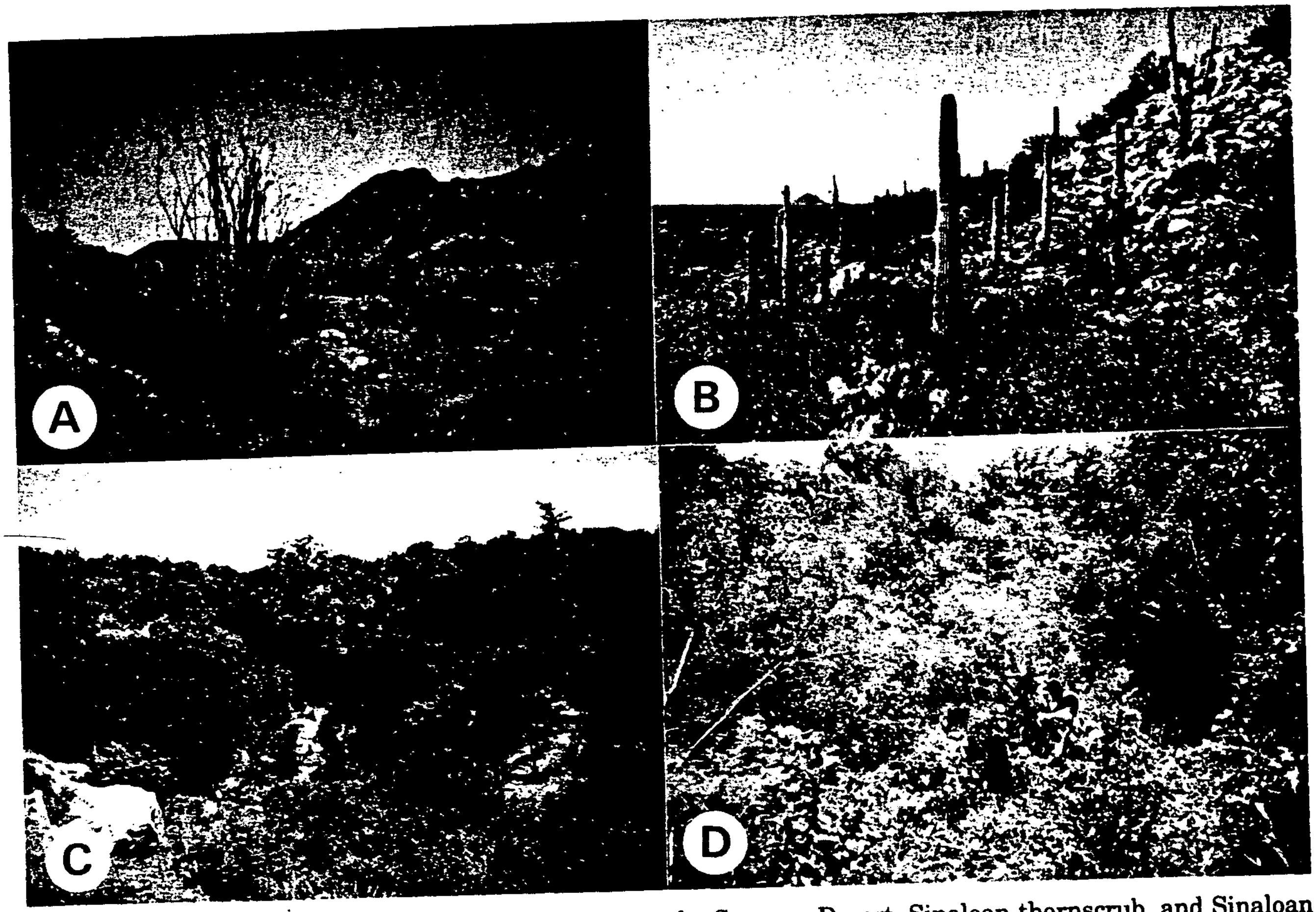

Fig. 3. Representative habitats of *Gopherus agassizii* in the Sonoran Desert, Sinaloan thornscrub, and Sinaloan deciduous forest. *A*: Wash and slope habitat of the lower Colorado River subdivision of the Sonoran Desert (photo by P. A. Medica). *B*: Rocky slopes of the Arizona upland subdivision of the Sonoran Desert (photo by D. J. Germano). *C*: Dense vegetation on hillsides in the Sinaloan thornscrub (photo by D. J. Germano). *D*: Closed canopy of the Sinaloan deciduous forest (photo by D. J. Germano).

Gopherus agassizii seems to be absent from intermountain valley floors in the Sonoran Desert. *Gopherus agassizii* are found on small contiguous tracts of habitat like isolated low hills (Fig. 3). In these areas, rainfall and air circulation are greater and plant cover is markedly different from adjacent valley floors. *Gopherus agassizii* often occurs on steep and rocky terrain. Usually, tortoises construct shallow burrows under boulders and in the banks of washes. Temperatures in winter sometimes dip below freezing but usually not for as long as in the Mojave Desert (Germano 1989). Tortoises on Isla Tiburon in the Sea of Cortez construct burrows that are less than 1.5 m in length in arroyo walls and shallow burrows on flats, and two or more adults (48% of burrows) regularly occupy one burrow (Reyes Osorio and Bury 1982).

The apparent absence or low density of tortoises on valley bottoms in the Sonoran Desert is unexpected because *G. agassizii* occupy similar creosotebush habitat in the Mojave Desert. Past coexistence with *G. flavomarginatus* limited *G. agassizii* to upland habitats because *G. flavomarginatus*, which once may have existed in the Sonoran Desert, seems to be better adapted than *G. agassizii* to valley floor habitat (Morafka 1988). However, few data exist to support or disprove this hypothesis. At present, the habitat limits of *G. agassizii* in the Sonoran Desert do not seem to be due to human influences, but agricultural activity on valley floors may displace or eliminate tortoises (Fritts and Jennings 1994).

In southeastern Arizona, reported locations of *G. agassizii* outside of habitat in the Sonoran

Desert include the Sulfur Spring Valley northeast of Tombstone, Cochise County (Miller 1932); Fort Grant, Graham County (Grant 1946); and several localities near the Arizona–New Mexico border in extreme eastern Cochise County (Hulse and Middendorf 1979). These seem to be in error for the following reasons: These records place *G. agassizii* in transitional desert grassland between Sonoran and Chihuahuan desert habitats. Southeastern Arizona is in the range of the desert box turtle (*Terrapene ornata luteola*), and residents in these areas, including a wildlife manager who regularly searched this habitat, invariably described box turtles (D. J. Germano, unpublished data). The record of tortoises at Fort Grant is secondhand. It was originally from an army officer stationed there (Grant 1946); these animals may have been released captives. Contrary to Hulse and Middendorf (1979), we were told of a resident who released *G. agassizii* regularly in a canyon across the border in New Mexico. We found neither tortoises or signs of tortoises in these areas. Thus, we are unaware of any established populations of tortoises in southeastern Arizona.

Sinaloan Thornscrub

As in the Sonoran Desert, *G. agassizii* has only been found on hillsides in the Sinaloan thornscrub and may be limited to this habitat (Fritts and Jennings 1994). Sinaloan thornscrub is a transitional habitat between the southern Sonoran Desert and the Sinaloan deciduous forest (Fig. 1; Brown 1982; Turner and Brown 1982), and many of the hillsides and mountain slopes in the Sonoran Desert in Mexico are covered by thornscrub vegetation. Vegetation consists of drought-resistant, 2.0–7.5-m-high deciduous trees and shrubs. Many are tropical and subtropical plants with thorns (Brown 1982). The vegetation is often dense but does not form a canopy (Fig. 3C). Precipitation is high, and most rain falls in summer (Table 1).

Although the density of the tortoises in the Sinaloan thornscrub habitat has not been estimated, the greatest relative abundances of *G. agassizii* are between 200- and 500-m elevations; tortoises do not seem to be above 800 m (Fritts and Jennings 1994). In this habitat, tortoises construct burrows that may not be deep and are hard to find because of the dense vegetation. Populations of *G. agassizii* may occur in isolated patches because of the discontinuous distribution of suitable albeit currently undefined habitat and because tortoises in accessible areas are sometimes eaten by humans (Fritts and Jennings 1994). However, human predation on tortoises seems to be opportunistic and may not be a serious threat to tortoises in Mexico because thornscrub is usually impassable to people (Fritts and Jennings 1994).

Sinaloan Deciduous Forest

Sinaloan deciduous forest is similar to thornscrub but distinguished by its greater plant height, larger leafage, a greater proportion of mesomorphic and hydromorphic plants, and the relative infrequency of thorny and succulent plants (Gentry 1982). The Sinaloan deciduous forest (Fig. 3D) is composed of deciduous trees on the slopes and includes evergreen trees on the canyon bottoms and arroyo margins (Gentry 1982). This habitat has the highest yearly rainfall in the range of *G. agassizii*, and most rain falls in summer (Table 1). Freezing temperatures are rare at any time, but spring drought from February to May causes leaves of deciduous plants to drop (Brown 1982). Activity patterns have not been studied; however, tortoises may be active through winter and quiescent during the dry spring. The timing of precipitation in the Sinaloan thornscrub and Sinaloan deciduous forest is essentially a complete reversal of precipitation patterns in tortoise habitat in the western Mojave Desert.

Gopherus agassizii construct burrows in the Sinaloan deciduous forest. However, these burrows are not as conspicuous or as large as those in the Mojave Desert. The dense vegetation conceals many burrows. The apparent lack of deep burrows may be related to the mild winters in these southern habitats.

The southern limit of the range of *G. agassizii* is presently thought to be near El Fuerte and Los Mochis, Sinaloa. However, the Sinaloan deciduous forest extends farther south, where no searches have been conducted (Fritts and Jennings 1994). Tortoises are difficult to find in this wooded habitat, and the southern limit of the range of *G. agassizii* is equivocal.

Rangewide Comparisons of Habitat Use

Several patterns seem to describe the ecology of *G. agassizii* across its range. In the northern part of its range, *G. agassizii* was thought to chiefly occur on bajadas and valley bottoms of the Mojave Desert and in fewer numbers only a short distance up the sides of mountains (Woodbury and Hardy 1948; Berry 1986). However, we now know that at least in certain portions of the Mojave Desert, tortoises frequent cactus–scrub habitat on rocky substrates (Luckenbach 1982) and rocky, hilly terrain (Bury et al. 1994b). The lack of sightings of tortoises on hillsides might be from insufficient searches outside of valleys in the Mojave Desert. In the Sonoran Desert portion of the range, desert tortoises are generally absent in the valleys and instead occupy mostly rocky hillsides (Lowe 1964, 1990; Burge 1980; Walchuk and deVos 1985). This propensity for dwelling on hillsides continues through the Sinaloan thornscrub and deciduous forest (Fritts and Jennings 1994).

The highest known densities of *G. agassizii* are in the Mojave Desert, particularly in the western Mojave Desert, but recent evidence suggests dense populations north of St. George, Utah, and elsewhere in the eastern Mojave Desert (Bury et al. 1994a, 1994b). Populations may reach 65 tortoises/km^2 on Isla Tiburon (Reyes Osorio and Bury 1982), and tortoises may occur in disjunct pockets in rocky habitats at middle elevations on the mainland of northwestern Mexico (Fritts and Jennings 1994). However, published accounts of densities of the desert tortoise on the mainland of Mexico are not available.

The construction and use of burrows also seem to be variable, but burrow construction or the use of caves or dens seem obligatory by tortoises in the Mojave Desert. Some burrows are deep (>2 m long), and large burrows may be used by many individuals in winter. Often, these deep burrows are constructed under caliche overhangs. In many parts of the Mojave Desert, however, shorter burrows are dug into the soft alluvial soil, usually at the base of bushes or in wash banks.

Contrary to earlier statements (Auffenberg 1969), *G. agassizii* constructs burrows throughout its range. We found that *G. agassizii* commonly constructs short burrows throughout the Sonoran Desert, including Isla Tiburon and the Sinaloan thornscrub and Sinaloan deciduous forest. The recognition of the construction of burrows by *G. agassizii* throughout its range is lacking, probably because the southern habitats are either rocky or densely vegetated and make detection of burrows difficult. Tortoises also may use rocky overhangs and caves more often in southern latitudes, perhaps because of the greater occurrence of tortoises on hillsides and rocky substrates.

Acknowledgments

We thank the Arizona Department of Game and Fish, the U.S. Bureau of Land Management, and the U.S. Fish and Wildlife Service for providing us with unpublished maps with information on the distribution of *G. agassizii*. We also thank G. Rhodda and C. Schwalbe for reviews and helpful suggestions.

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Recent Trends of Desert Tortoise Populations in the Mojave Desert

by

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Abstract. The desert tortoise, *Gopherus agassizii* (Cooper), was listed as threatened in the Mojave Desert in 1990. Important factors for the listing were severe recent mortality in tortoise populations and a general decline throughout this century. Recent trends in tortoise populations were examined by plotting total captures of adult and juvenile tortoises from 2.6-km^2 study plots, rather than by mark-and-recapture population estimates. Changes in relative abundance of tortoises were greatest among large tortoises in the western Mojave Desert, which may reflect high levels of human disturbance, and among small tortoises, which may reflect either lower ability of searchers to detect small tortoises or greater mortality of tortoises during drought conditions in 1986–90, or both factors. Further collection of data on population trends is needed, particularly in years with higher-than-average precipitation. Retention of the threatened status of the tortoise is a conservative strategy for the conservation of natural resources but should be reassessed when additional data are available.

Key words: Drought, *Gopherus agassizii*, human disturbance, population analysis, size.

The status of the desert tortoise, *Gopherus agassizii*, has been followed for several years. Woodbury and Hardy (1948) and Carr (1952) expressed concern about overcollection of tortoises for the pet trade. Jaeger (1955) observed that human encroachment was causing the gradual disappearance of *G. agassizii*, and Bury and Marlow (1973) predicted that urbanization would eliminate the tortoise from the northwestern Mojave Desert in California. Luckenbach (1982:1) stated that "a pronounced and steady decline" had been noted in some populations for several years. Besides these long-term trends related mostly to habitat destruction, significant decreases of numbers of tortoises were reported in several populations in the western Mojave Desert during the 1980's, related perhaps to the outbreak of an upper respiratory disease in some locations (Berry 1990). These reported declines in part prompted the U.S. Fish and Wildlife Service to declare Mojave Desert populations of *Gopherus agassizii* as threatened (U.S. Fish and Wildlife Service 1990). This paper evaluates the evidence for short-term declines of populations of *G. agassizii* in the Mojave Desert in Arizona, California, Nevada, and

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[1] Now with the National Biological Survey, same address.

Utah since 1977 with data from the Bureau of Land Management.

The Bureau of Land Management Data Set and Critique of Existing Analyses

Bureau of Land Management personnel collected trend data on populations of *G. agassizii* from 2.6-km^2 study plots (Berry and Nicholson 1984). Standardized surveys usually involved 60 days (fewer calendar days if more than one person was employed). Data from study plots were used to calculate densities of tortoises with the Lincoln–Peterson mark-and-recapture model by dividing the 60-day survey into two approximately equal sampling efforts (Turner and Berry 1984).

There are four assumptions for estimating population size with mark-and-recapture techniques (Otis et al. 1978; White et al. 1982): (1) the population is demographically and geographically closed; (2) marks are persistent; (3) all marks are recorded correctly; and (4) the probability of capture for each animal at each trapping occasion is equal and constant. Data on *G. agassizii* from 2.6-km^2 study plots, however, violate assumptions 1 and 4. Assumption 1 is violated because study plots are not geographically closed but part of larger expanses of suitable tortoise habitat. Tortoises may move freely between the study area and adjacent habitat. Assumption 4 is violated often in two ways: different-sized tortoises have different probabilities of capture (Turner and Berry 1984), and capture probabilities may vary over time. Because tortoises are usually more active during or immediately after rain (Turner and Berry 1984; Nagy and Medica 1986), rainfall during a 60-day survey probably creates unequal capture probabilities. If there is heterogeneity of capture probabilities among animals and across time, a statistically valid population estimate cannot be calculated (Otis et al. 1978; White et al. 1982).

Violation of the assumptions of mark-and-recapture models may lead to density estimates that are biased and that may be too large. One of the strengths of the 60-day survey, however, is that sampling effort is generally equivalent among years. Thus, ignoring recaptures, the total number of tortoises captured (registered) during a 60-day survey may be a more useful index of population trends because the probability of observing adult tortoises is high (Berry and Turner 1986). Lower capture probabilities of smaller tortoises and variation in activity because of weather, however, create greater uncertainty about the total numbers of captured juvenile tortoises. Still, I prefer this technique to estimating numbers based on few recaptures. Here, I analyze recent trends in tortoise populations based on total numbers captured during 60-day surveys.

Methods

I analyzed captures of desert tortoises from 1977 to 1989 at 16 sites in the Mojave Desert (for which multiple years of observations were available) with published data or data in the public domain (Table 1): 2 study plots in Arizona (Duck and Snider 1988; Duck and Schipper 1989), 13 study plots in California (Berry and Nicholson 1984; Turner et al. 1987a; Berry 1990; Berry et al. 1990), and 1 study plot in Nevada (Bureau of Land Management, unpublished data). I did not use data from plots in which sampling was conducted in only one year or in which sampling efforts differed across years. For example, the Fremont Peak plot in California with 15-, 30-, and 60-day sampling efforts and the Sheep Mountain plot in Nevada with 30- and 60-day sampling efforts (Esque and Duncan 1989) were excluded from the analysis. I excluded data from a 30-day sampling effort in the Piute plot in Nevada in 1979 but used data from 60-day efforts in 1983 and 1989 at this site.

To account for size-related differences in capture probabilities, I partitioned my analysis between small (<180-mm maximum carapace length [MCL]) tortoises—immature and juvenile size classes of Turner and Berry (1984), and large (≥180-mm MCL) tortoises—subadult and adult size classes of Turner and Berry (1984). I used the total number of tortoises captured during 60-day surveys; recapture data were not used. I transformed the data to

Table 1. Number of small (<180-mm maximum carapace length) and large (≥180-mm maximum carapace length) desert tortoises (*Gopherus agassizii*) observed at 16 study plots in the Mojave Desert. Data are from Berry (1990, 1994), Berry and Nicholson (1984), Duck and Snider (1988), Duck and Schipper (1989), and Turner et al. (1987a).

Study site	Year	Number observed Large	 Small
Eastern Mojave–Colorado Deserts			
Chemehuevi, California	1979	81	70
Chemehuevi, California	1982	99	108
Chemehuevi, California	1988	112	145
Chuckwalla Bench, California	1979	153	112
Chuckwalla Bench, California	1982	178	84
Chuckwalla Bench, California	1988	86	34
Chuckwalla Valley, California	1980	48	37
Chuckwalla Valley, California	1987	47	31
Goffs, California	1980	188	111
Goffs, California	1983	219	230
Goffs, California	1984	179	100
Goffs, California	1985	175	103
Goffs, California	1986	173	78
Ivanpah Valley, California	1979	94	67
Ivanpah Valley, California	1986	104	64
Littlefield Control, Arizona	1977	24	16
Littlefield Control, Arizona	1981	28	18
Littlefield Control, Arizona	1988	30	19
Littlefield Exclosure, Arizona	1977	13	7
Littlefield Exclosure, Arizona	1981	23	13
Littlefield Exclosure, Arizona	1989	17	3
Piute, Nevada	1983	29	52
Piute, Nevada	1989	30	16
Upper Ward Valley, California	1980	83	57
Upper Ward Valley, California	1987	78	38
Western Mojave Desert (California)			
DTNA[a] Interpretive Center	1979	402	191
DTNA Interpretive Center	1985	388	93
DTNA Interpretive Center	1989	175	42
DTNA Interior	1979	138	51
DTNA Interior	1982	184	50
DTNA Interior	1988	142	20
Fremont Valley	1979	116	87
Fremont Valley	1981	108	99
Fremont Valley	1987	49	27
Johnson Valley	1980	50	29
Johnson Valley	1986	19	7
Kramer Hills	1980	84	62
Kramer Hills	1982	95	90
Kramer Hills	1987	56	30
Lucerne Valley	1980	80	35
Lucerne Valley	1986	69	27
Stoddard Valley	1981	71	26
Stoddard Valley	1987	99	19

[a] Desert Tortoise Natural Area.

relative abundance (RA) of the two age classes with the formula

$$\mathrm{RA} = (N_i + N_0) \times 100,$$

where N_i = number captured in year i and N_0 = number captured in the first survey at each plot. Transforming captures to RA allowed easier comparisons among plots and comparisons among sites where sampling intensities differed. For example, sampling effort in the Interpretive Center plot at the Desert Tortoise Natural Area, California (DTNA) was more intensive (180 days) and over a larger area than in other 60-day plots (Berry 1990). However, the sampling intensity at this site was the same across years, so that transforming to RA allowed a direct comparison of these data with data from plots with standard 60-day surveys.

I analyzed trends in tortoise numbers by plotting relative abundance versus year and used locally weighted regression scatterplot smoothing (LOWESS regression; Cleveland 1979) to produce trend lines. LOWESS regression derives predicted values of Y (RA) for a given X (year) with weighted Y-values associated with neighboring X-values (Trexler and Travis 1993). A tension parameter (f) determines the proportion of data points to predict each Y (f = 1 is equivalent to a standard linear regression). I used LOWESS regression because the RA of tortoises in a given year is probably influenced to a greater degree by recent conditions rather than by conditions throughout the time covered by the data set (Trexler and Travis 1993). I plotted LOWESS regressions with SYSTAT (Wilkinson et al. 1992).

The analysis was split between the western Mojave Desert, including the study plots at the DTNA Interpretive Center, DTNA interior, Fremont Valley, Kramer Hills, Stoddard Valley, Lucerne Valley and Johnson Valley in California, and the eastern Mojave Desert (and the Colorado Desert), including study plots at Ivanpah, Goffs, Upper Ward Valley, Chemehuevi, Chuckwalla Valley, and Chuckwalla Bench in California, and Piute Valley in Nevada and control and exclosure plots at Littlefield, Arizona.

I compiled data on precipitation from seven stations in the eastern Mojave Desert: Beaver Dam and Willow Beach in Arizona; Searchlight and the Desert National Wildlife Range in Nevada; and Blythe, Needles, and Baker in California. I also used data from five stations in the western Mojave Desert in California: Barstow, China Lake, Mojave, Twentynine Palms, and Victorville (Earthinfo, Inc. 1989; National Oceanic and Atmospheric Administration 1989). Precipitation amounts of two 6-month periods each year were summed: winter (October–March) and summer (April–September) because tortoise behavior may be related to seasonal variation in precipitation. The summer period corresponds to the primary activity period of tortoises. Rain during the winter period is necessary for successful germination of annual plants (Beatley 1974), and variation in forage may also affect tortoise behavior (U.S. Fish and Wildlife Service, Portland, Oregon, unpublished data). I did not include precipitation totals from any year at any station with missing data. I used Pearson product–moment correlation to compare the relative abundances of small and large tortoises with winter and summer precipitation and used the data from all surveys (first and revisits) at the 16 sites.

Results

LOWESS trend lines revealed differences between the numbers of large and small tortoises and between study plots in the eastern Mojave Desert and the western Mojave Desert. The f for the LOWESS regression was 0.4. This was the smallest value of f that did not show any relation between the residual of RA minus the LOWESS predicted value and year (Trexler and Travis 1993) and which produced trend lines that could be interpreted. Smaller values of f produced trend lines that responded too strongly to individual data points.

Relative abundance of large tortoises apparently declined in the western Mojave Desert during the latter 1980's, but, during the same time, RA of large tortoises was stable or increased in the eastern Mojave Desert (Fig. 1). The downturn in the trend in the western Mojave Desert was largely influenced by low numbers of large tortoises recorded at the DTNA Interpretive Center plot in 1989 (175 or 44% of the 402 tortoises captured in 1979).

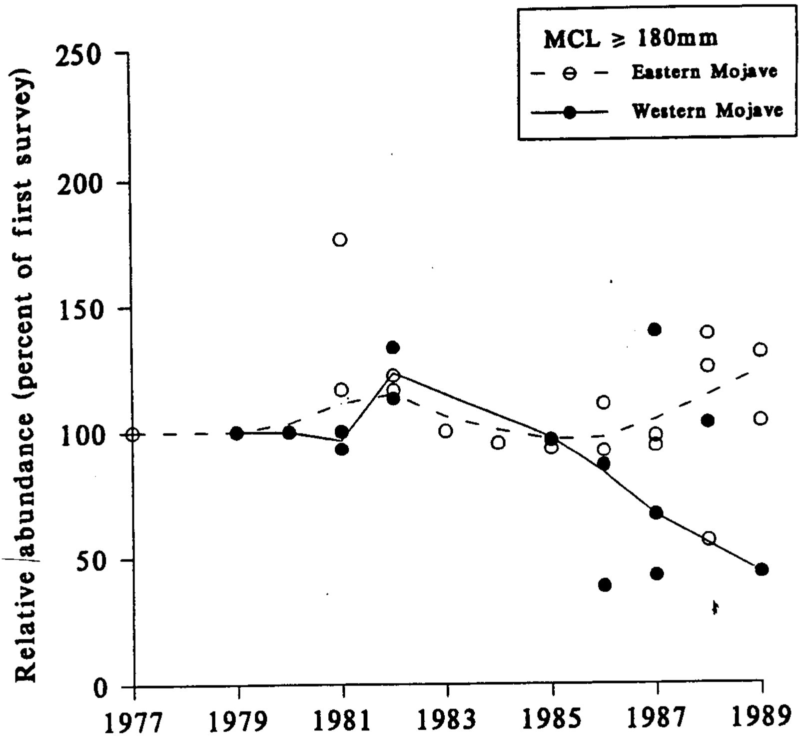

Fig. 1. Relative abundance of large desert tortoises (*G. agassizii*) at seven permanent study plots in the western Mojave Desert (*filled circles*) and nine permanent study plots in the eastern Mojave Desert (*empty circles*), 1977–89. Data were derived from Table 1.

The relative abundances of small tortoises on study plots decreased markedly from the mid-1980's in the western Mojave Desert (Fig. 2). There was also a downturn in RA of small tortoises in the eastern Mojave Desert in 1989. This decrease in RA of small tortoises resulted from data

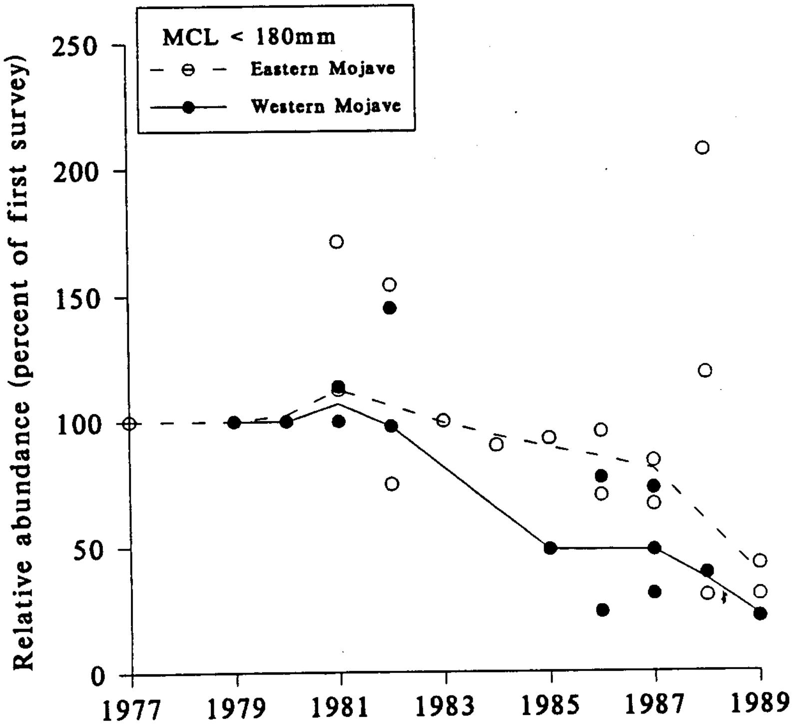

Fig. 2. Relative abundance of small desert tortoises (*G. agassizii*) at seven permanent study plots in the western Mojave Desert (*filled circles*) and nine permanent study plots in the eastern Mojave Desert (*empty circles*), 1977–89. Data were derived from Table 1.

from two plots, the Piute Valley and the Littlefield exclosure.

From 1977 to 1989, when data from trend plots were collected, rainfall varied considerably (Table 2). Whereas 1983 was the wettest year since 1950, 1989 was one of the driest. The relative abundance of neither large nor small tortoises correlated with winter precipitation (in both cases $P > 0.5$). The relative abundance of large tortoises also did not increase with increasing summer precipitation (Fig. 3; $r = 0.353$; $P = 0.07$), but RA of small tortoises increased with summer precipitation (Fig. 3; $r = 0.677$; $P < 0.001$).

Discussion

The decline of large tortoises in the western Mojave Desert may in part be due to increased human disturbance. A slightly different trend analysis in the Draft Desert Tortoise Recovery Plan (U.S. Fish and Wildlife Service, Portland, Oregon, unpublished data) showed a large decline

Table 2. Mean precipitation (cm) in winter (October–March) and summer (April–September) from 1977 to 1989 at seven reporting stations in the eastern Mojave Desert and at five stations in the western Mojave Desert.

	Eastern Mojave		Western Mojave	
Year	Winter	Summer	Winter	Summer
1977	4.5	7.1	6.5	7.7
1978	13.3	7.1	19.6	2.8
1979	19.1	5.8	14.0	4.7
1980	14.2	4.6	15.3	3.4
1981	5.3	5.3	5.7	1.8
1982	7.3	9.8	10.1	4.4
1983	12.9	10.1	24.9	8.2
1984	4.6	10.2	5.7	9.2
1985	12.1	3.8	9.5	2.8
1986	7.6	5.0	10.7	1.8
1987	8.7	4.6	8.8	3.5
1988	10.6	8.5	11.1	4.1
1989	4.8	1.7	3.2	1.6

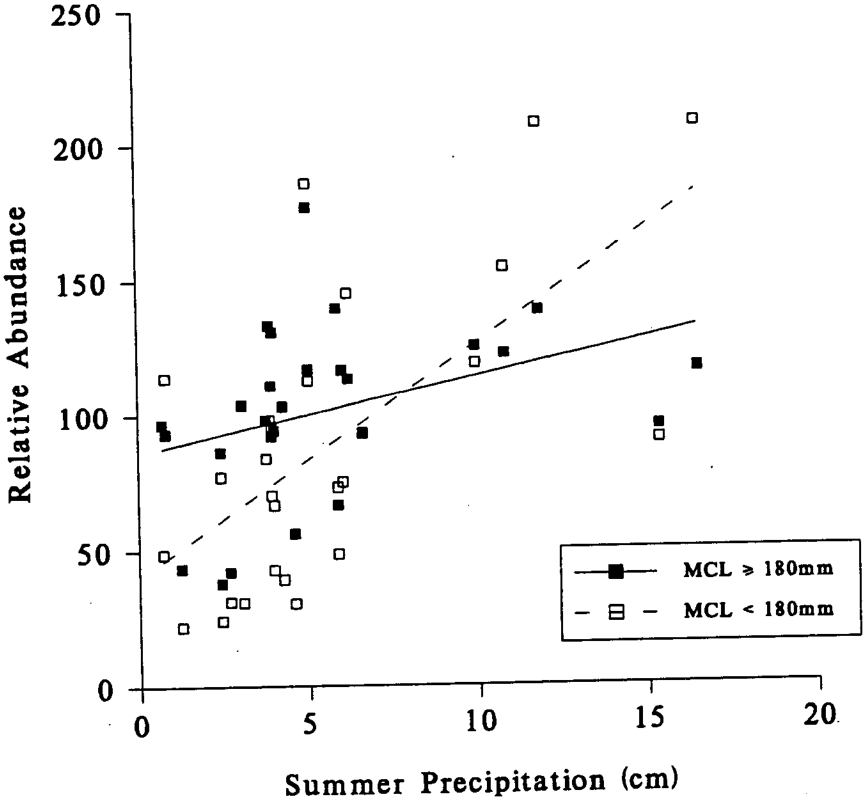

Fig. 3. Relation between relative abundances of large and small desert tortoises (*G. agassizii*; percent of first survey) and summer precipitation (April through September).

in abundances of tortoises at six study plots that have had high levels of human disturbance. The six plots are in the western Mojave Desert. Many of the Bureau of Land Management study plots are near growing human populations, and one plot (Fremont Valley) had a large increase in off-road vehicle use during the 1980's (Berry 1990). Mortality, apparently from the upper respiratory disease, has been more severe at the DTNA than at most other plots (Berry 1990, 1994). The apparent differences in the trends in numbers of small and large tortoises may reflect biases inherent in tortoise surveys. Summer precipitation in the western Mojave Desert averaged 4.93 cm from 1979 to 1985 and 2.73 cm from 1986 to 1989. The decrease in the relative abundance of juvenile tortoises coincided with this reduction in precipitation. Adult *G. agassizii* construct water catchments and drink from these puddles during rainfall (Medica et al. 1980; Turner and Berry 1984), and surface activity of tortoises increases after rains (Camp 1916; Turner and Berry 1984; Nagy and Medica 1986). Differences in activity can be drastic. For example, one biologist observed 40 tortoises while driving along a 6.6-km stretch of dirt road in the Ivanpah Valley, California, during a rainstorm on 28 April 1980. Two days later the ground was still damp, but four people observed only two tortoises during several hours of laying out a study grid (P. A. Medica, REECO/BECAMP, Nevada test site, Mercury, Nevada, personal communication).

Small and large tortoises may have different activities, but, alternatively, small *G. agassizii* may suffer greater mortality in dry years. Decreases in numbers of juveniles captured in recent surveys, therefore, indicate significant decreases in numbers of animals. Juvenile herbivorous reptiles face greater constraints in the desert than adults in acquiring sufficient nutrients for growth and survival (Zimmerman and Tracy 1989). Less food may be available in dry years, and this combined with high temperatures reduces surface activity (Berry and Turner 1986). Data relating mortality of small tortoises to precipitation, however, are scant and contradictory (Turner et al. 1984, 1987b).

Data from 1977 to 1989 do not support a conclusion that *G. agassizii* is now declining throughout the entire Mojave Desert, but declines are apparent in the western Mojave Desert. However, continuing habitat destruction and the possibility of an uncontrolled epidemic (the upper respiratory disease) among tortoises justifies concern about the status of *G. agassizii*. Data presented at the annual meeting of the Desert Tortoise Council in Las Vegas in 1991 indicated continued high mortality of tortoises in the western Mojave Desert (Berry 1994).

Management and recovery of *G. agassizii* require accurate monitoring of population trends. The biases in capture probabilities render the standard 2.6-km^2 study plots unsuitable for this task. The draft Desert Tortoise Recovery Plan advocates short-term sampling in smaller (1-km^2) plots selected in a statistically valid sample from a larger area (U.S. Fish and Wildlife Service, Portland, Oregon, unpublished data). Population size would be estimated with removal techniques. However, this plan calls for sampling in plots during 7 days, and there is a high probability that tortoises will leave and enter the plot during this time. Thus, the bias of the study plot not being geographically closed still applies. Precipitation during the sampling period could also lead to biased capture probabilities. There is still a need to develop reliable techniques to estimate population size and trends of desert tortoises.

Acknowledgments

M. E. Jennings provided valuable assistance with locating literature and weather data. This paper received a policy review by the Office of Research Support. I thank K. H. Berry, R. B. Bury, C. K. Dodd, Jr., T. H. Fritts, D. J. Germano, R. W. McDiarmid, N. J. Scott, Jr., and C. R. Tracy for evaluation and criticism of the arguments set forth in this paper. As is the case with most issues, these scientists did not necessarily agree with all the conclusions. P. H. Niewiarowski and E. L. Rockwell reviewed and commented on the manuscript.

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Female desert tortoise (*Gopherus agassizii*) in the Mojave Desert west of California City, Calif. *Photo by D. J. Germano.*

Livestock Grazing and the Desert Tortoise in the Mojave Desert

by

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Abstract. A large part of the Mojave Desert is not in pristine condition, and some current conditions can be related to past grazing-management practices. No information could be found on densities of the desert tortoise (*Gopherus agassizii*) or on vegetative conditions of areas that had not been grazed to allow managers a comparison of range conditions with data on tortoises. Experimental information to assess the effect of livestock grazing on tortoises is lacking, and researchers have not yet examined whether the forage that remains after grazing is sufficient to meet the nutritional needs of desert tortoises.

Key words: Competition, desert tortoise, domestic livestock, food habits, food requirements, *Gopherus agassizii*, grazing.

Grazing by cattle and sheep has been implicated in the deterioration of habitat of the desert tortoise (*Gopherus agassizii*; Berry 1978; Coombs 1979; Webb and Stielstra 1979; Nicholson and Humphreys 1981). Information from these studies led the U.S. Fish and Wildlife Service (1990) to assert that livestock grazing altered plant species composition, reduced cover of shrubs and perennial grasses, and led to an overall deterioration in the quality of desert tortoise habitat. On the other hand, others (Bostick 1990; Resource Concepts, Inc., Carson City, Nevada, unpublished report; J. Sullins, University of California, Riverside, personal communication) reported that data are not available to assert that domestic livestock harms desert tortoise habitat.

I examined the literature on livestock grazing in the Mojave Desert and evaluated the status of knowledge about the effects of livestock grazing on the desert tortoise. To affect the tortoise, grazing should have some measurable effect on the cover or food supply of the desert tortoise. Grazing may also have an indirect effect by altering the landscape such that factors formerly not important in the Mojave Desert (e.g., wildfires) can now be magnified and affect the tortoise's habitat.

Mojave Desert Vegetation

The Mojave Desert is the smallest of the North American deserts and is generally located north of the Sonoran Desert and south of the Great Basin in extreme southwestern Utah, northwestern Arizona, southern Nevada, and southeastern California. MacMahon (1988) noted that some ecologists describe the Mojave Desert as an ecotone between the Great Basin at a higher elevation and the Sonoran Desert at a lower elevation, but he considers the Mojave Desert sufficiently discrete to warrant

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[1] Now with the National Biological Survey, same address.

individual recognition. Approximately 75% of the Mojave Desert is between 610 and 1,219 m in elevation (Shreve 1942). However, elevations drop to 82 m below sea level in the Death Valley National Monument and rise to above 2,000 m on many of the mountain tops (Rowlands et al. 1982).

Based on low precipitation and high summer temperatures, the Mojave Desert is the most arid of the North American deserts (MacMahon 1988). Most weather stations in the Mojave Desert report an average annual precipitation of less than 13 cm; only the marginal fringe receives higher amounts (Shreve 1942). Winter precipitation (October–March) may provide more than 90% of the annual precipitation in the western Mojave Desert, whereas summer thunderstorms provide more than 30% of the annual precipitation at the eastern and southern (Colorado Desert) edges (Rowlands et al. 1982).

MacMahon (1988) described the soils of the Mojave Desert as generally sandy to gravelly, alkaline in flats and dry lake beds and rocky on higher-elevation slopes and mountains. Furthermore, desert soils are low in organic matter and slightly acidic to alkaline at the surface and have calcium carbonate accumulations in the upper 2 m. These soils have long periods of inactivity because of dry, hot conditions and as a group are termed Aridisols.

Death Valley extends from below sea level to above 1,220 m, which makes the description of the plant ecology of Death Valley (Hunt 1966) a good model for a discussion of general plant occurrence in the Mojave Desert. Salt-tolerant saltbush (*Atriplex hymenelytra* and *A. polycarpa*) occupies sites just above the lowest and essentially bare flats, the soils of which are commonly alkaline (Rowlands et al. 1982). As soils become less alkaline at the foot of alluvial fans, creosotebush (*Larrea tridentata*) becomes common and occurs to about 1220 m in the mountains. With increasing elevation, the total plant density becomes greater, and creosotebush occurs with white bursage (*Ambrosia dumosa*) and white brittlebush (*Encelia farinosa*), which grade into pure stands of blackbrush (*Coleogyne ramosissima*). In the elevational band below the blackbrush, the Joshua-tree (*Yucca brevifolia*) is common and essentially outlines the distribution of the Mojave Desert (MacMahon 1985).

Creosotebush is characteristic of the three hot deserts of North America (MacMahon 1988). In the Mojave Desert, creosotebush is the dominant plant and occurs in pure or mixed stands and in densities of very few to perhaps 1,000/ha on over 70% of the land area (Hunt 1966; Vasek and Barbour 1977). Creosotebush grows where drainage is good and the salt content of soils is low (Hardy 1945), where some organic matter is present (Vasek 1980a), and where the roots can reach soil moisture (Johnson et al. 1975). Individual stems of creosotebush may be more than 100 years old, and clones have been estimated to be 9,400 years old (Vasek 1980b). Because of the long life of the plant, considerable litter accumulates and forms an organic layer that is richer in nutrients than between shrubs and serves as suitable habitat for many herbaceous species.

The diversity and cover of perennial grasses are low in the Mojave Desert (Humphrey 1974), where the dominant perennial grass is big galleta (*Hilaria rigida*). This species occurs in the southern Great Basin, throughout the Mojave Desert, and in the Sonoran Desert. Big galleta grows at elevations below 1,220 m and in the Mojave Desert seems to grow best in nonalkaline and well-drained soils where water is more abundant (Shreve 1942; Schlesinger and Jones 1984). Thus, big galleta often is at the edges of roads and washes in lower elevations (Humphrey 1974) and between and under rocks in upper elevations. Cover of big galleta varies greatly among locations and was less than 1% at a study plot in the Ivanpah Valley in the Mojave Desert (P. A. Medica, C. L. Lyons, and F. B. Turner, University of California, Los Angeles, unpublished report) and over 18% in Canyonlands National Park where precipitation exceeded 25 cm (Kleiner and Harper 1977).

When winter precipitation is sufficient, desert annuals may produce from less than 10 to more than 600 kg/ha of biomass (Turner and Randall 1989), the greatest amount of grass and forb biomass in the Mojave Desert. At the Nevada Test Site, seeds of winter annuals germinated en masse when about 2.5 cm of precipitation fell between September and March (Beatley 1967). Stem elongation does not occur until late March when temperatures are warmer, and flowers develop from April through May. When precipitation is adequate in winter, the period from germination to senescence may last 8 months; however, when precipitation does not occur until late winter, the entire life cycle of winter annuals may be compressed into 6–10 weeks (Beatley 1967).

Survival of seedlings is related to precipitation and ranged from 27 to 77% during a 3-year period at the Nevada test site (Beatley 1967). Turner and Randall (1989) found that the biomass of annuals increases with precipitation, and their model, based on 11 growing seasons, predicts that annuals produce 141 kg/ha of biomass under average conditions (12 cm of winter precipitation).

Exotic annual plants were probably introduced into the Mojave Desert from the Mediterranean region in the late 1800's (Aschmann 1976) and have increased in abundance because they can tolerate heavy grazing. One of the more common and increasingly abundant species is foxtail brome (*Bromus rubens*), which is ecologically similar to native annuals and is frequently the dominant annual under shrubs. It is always in close association with native winter annuals (Beatley 1966), but foxtail brome has a wider moisture tolerance for germination and can better survive periods of high soil moisture tension than native annuals (Beatley 1966). Recent analysis indicates that foxtail brome increased in one of Beatley's plots from 14.0 plants/m^2 in 1969 to 2,034 plants/m^2 in 1988, years of similar precipitation (Hunter 1990).

Because of low precipitation, which results in a scarcity of fine fuels (i.e., grasses), fire apparently has not played an important role in the Mojave Desert plant ecology (Humphrey 1974). Creosotebush and white bursage are too sparse and the creosotebush canopy is too open to carry fire. However, the increased abundance of exotic annual grasses such as foxtail brome (Hunter 1990) could increase the susceptibility of the Mojave Desert to fire.

Range Management in the Mojave Desert

History of Livestock Grazing

Large grazing mammals probably did not evolve west of the Rocky Mountains in recent history (Mack and Thompson 1982). The current ecological condition of the Mojave Desert rangelands has probably been affected by domestic livestock that was first introduced by European settlers. However, documentation about herbaceous plants in the Mojave Desert before the introduction of livestock is scarce, and there are no data for comparison with current conditions.

There is little doubt that livestock grazing has changed the vegetative composition of the Mojave Desert during the past 140 years because numbers of livestock in the western United States were high during the late 1800's (7.6 million cattle in 1886; U.S. Senate 1936) and again during World War I and were unregulated. In 1934, the Congress passed the Taylor Grazing Act, and some semblance of grazing management began.

As more knowledge about range-plant ecology was gained, range management systems became more sophisticated and were incorporated into allotments managed by the Bureau of Land Management (BLM). However, the strict application of grazing systems has not been universally applied because of the increased costs to the individual rancher (Vale 1975). Nonetheless, most ranchers and BLM recognize the importance of managing the range to maximize the production of continual high-quality native forage.

Since 1955, the number of animal unit months (AUMs) allocated to BLM lands in Arizona, California, Nevada, and Utah decreased by 50% (BLM public land statistics, 1961–85). Decreases in AUMs since the early 1940's may be even greater if the 85% cut in AUMs at the Beaver Dam Slope in Utah (Hohman and Ohmart 1978) is typical of the West in general. Despite these cuts in the use of western rangelands by livestock, much public rangeland is still in only fair or poor ecological condition.

A review of 102 BLM environmental impact statements (EIS) revealed little change in condition between 1985 and 1989 (Wald and Alberswerth 1989); however, this is to be expected because the recovery of heavily used arid rangelands probably requires decades. The five EISs that pertain to the Mojave Desert provide the following analysis of condition: 1) in the California Desert Conservation Area Plan, 42% of the area is listed in poor–fair condition, although 93% of the allotments at higher elevations were in fair condition; 2) in the Clark EIS, 85.5% is listed in poor condition; 3) in the Esmeralda–Southern Nye EIS, only 16.9% is listed in fair or poor condition; 4) in the

Hot Desert EIS, 88% is listed in fair or poor condition; and 5) in the Cedar–Beaver–Garfield–Antimony EIS, 62.7% is listed in poor or fair condition. Despite decreased grazing pressure during the past several decades, the ecological condition of the range has not rapidly improved.

An analysis of exclosures and other protected areas revealed that perennial–grass cover in deserts has increased with protection from grazing (Shreve and Hinckley 1937; Gardner 1950; Waser and Price 1981; Durfee 1988). The rate of succession is controlled to a large extent by the moisture conditions of the substrate (Sampson 1919); thus, one expects deserts to improve very slowly after reductions in livestock numbers. However, the ecological condition may never improve as long as exotic annuals are a permanent component of the flora (W. Burkhardt, University of Nevada, personal communication).

Grazing by Livestock in the Mojave Desert

We do not know the status of desert tortoise populations or vegetation before livestock began grazing the Mojave Desert, and only few studies have been conducted on the effects of grazing on Mojave Desert vegetation. Most of the literature addresses the Great Basin, the Sonoran Desert, and the Great Plains.

Cattle and sheep are the dominant domestic livestock in the Mojave Desert. Domestic sheep grazed on the Beaver Dam Slope in Utah until the 1950's (Hohman and Ohmart 1978), but only cattle graze the area now. Much of the Mojave Desert in Nevada is grazed by only cattle. Cattle generally are not herded, and their distribution on an allotment is restricted by fences, availability of water, and rugged terrain. Development of watering locations by BLM and ranchers have probably changed the distribution of cattle during the past several decades. The California Desert Conservation Area Plan (U.S. Bureau of Land Management, California Desert District, Riverside, California, unpublished data) designated use of the desert for cattle and sheep. Sheep are generally herded daily in the direction of food, water, and bedding areas (Nicholson and Humphreys 1981).

Grazing allotment plans generally allow livestock use in tortoise habitat during winter and spring (U.S. Bureau of Land Management, California Desert District, Riverside, California, unpublished data; U.S. Bureau of Land Management, Stateline Resource Area, Las Vegas, Nevada, unpublished data; U.S. Bureau of Land Management, Dixie Resource Area, Cedar City, Utah, unpublished data; U.S. Bureau of Land Management, Las Vegas District, Las Vegas, Nevada, unpublished data; U.S. Bureau of Land Management, Las Vegas District, Las Vegas, Nevada, unpublished data), when plants can usually tolerate more grazing pressure. These habitats are usually at lower elevations in what is termed ephemeral or sometimes ephemeral–perennial range (U.S. Bureau of Land Management, California Desert District, Riverside, California, unpublished data). After the use of these ranges, livestock is moved to higher perennial ranges where grasses are more abundant and diverse. When annual vegetation on ephemeral ranges exceeds defined amounts (224 or 293 kg/ha), extensions to the grazing permit may allow livestock to graze those ranges longer into spring. However, the proper use of ephemeral ranges is still judged by levels of use of perennial plants. These levels of use are generally 45–55%, depending on the key species. The Bureau of Land Management assumes that the general condition of the range improves under these levels of use.

Cook (1977) found that defoliation (by sheep) was less harmful in fall, winter, and early spring than in late spring and summer on Great Basin ranges that contained several perennial species common to the Mojave Desert: winterfat (*Eurotia lanata*), Indian ricegrass (*Oryzopsis hymenoides*), and bottlebrush squirreltail (*Sitanion hystrix*). Vigor of these plants depended on the season and intensity of use; 50% defoliation of plants during late spring and summer was too severe, and 50% defoliation in winter would sustain optimum vigor (Cook 1977). On the Beaver Dam Slope pasture of the Beaver Dam Slope allotment, levels of use of perennials did not seem to be related to the percentage of the remaining annual vegetation after cattle were removed from the allotment (U.S. Bureau of Land Management, Dixie Resource Area, Cedar City, Utah, unpublished data).

Food Habits of Livestock

Few detailed analyses of food habits of cattle have been made in the Mojave Desert. Grasses characteristically dominate cattle diets; however, in a study in the Piute Valley, Nevada, diets of cattle consisted largely of shrubs during the dormant season and herbaceous annuals during the spring growing season (Burkhardt et al., unpublished manuscript). Specifically, fecal samples collected during the dormant season were dominated by white bursage (30%), littleleaf krameria (*Krameria parvifolia*; 14%), big galleta (12%), blackbrush (11%) and Nevada ephedra (*Ephedra nevadensis*; 7%). During the growing season, fecal samples were dominated by redstem filaree (*Erodium cicutarium*; 27%), six-weeks annual fescue (*Vulpia octoflora*; 23%), wooly plantain (*Plantago patagonica*; 11%), foxtail brome (9%), desert globemallow (*Sphaeralcea ambigua*; 7%), and sixweeks grama (*Bouteloua barbata*; 6%). As the ephemeral plants disappeared during summer, the cattle resumed a diet of perennial shrubs and grasses.

Forage plants of sheep consist more of forbs and shrubs and less of grasses (Hansen et al. 1976; Nicholson and Humphreys 1981). An examination of feeding sites at the Kramer study plot in California showed that sheep made heavy use of perennial and annual forbs *Machaeranthera*, *Eriogonum*, *Dalea*, white bursage, *Astragalus*, *Grayia*, western fiddleneck (*Amsinckia tessellata*), desert dandelion (*Malacothrix glabrata*), redstem filaree, and *Chaenactis* (Nicholson and Humphreys 1981). Ninety-two percent of the white bursage plants were browsed in a light-use study site, but little use was made of Indian ricegrass, winterfat, or split grass (*Schismus arabicus*).

Desert Tortoise

Desert Tortoise Food Habits

Probably more research (Burge and Bradley 1976; Coombs 1979; Nicholson and Humphreys 1981; Luckenbach 1982; Turner et al. 1984) in the Mojave Desert has been conducted on food habits of desert tortoises than on food habits of sheep and cattle combined. Studies of food habits at seven locations in the Mojave Desert revealed considerable variation in the dominant plant species eaten by tortoises: *Plantago* in southern Nevada (Burge and Bradley 1976), *Cryptantha* spp. in southern Nevada (P. A. Medica et al., University of California at Los Angeles, unpublished report), foxtail brome in Utah (T. C. Esque et al., U.S. Fish and Wildlife Service, Fort Collins, Colorado, FY91 unpublished report) and in northwestern Arizona (Hansen et al. 1976), split grass in southern California (Nicholson and Humphreys 1981), *Aristida* spp. in northwestern Arizona (Hansen et al. 1976), and slim tridens (*Tridens muticus*) in Utah (Hansen et al. 1976). The intake of individual plant species in one site may vary by availability from year to year. In the Ivanpah Valley, for example, grasses comprised 3.6–33.0% and annual forbs comprised 5.0–18.6% of the diet during a 2-year study (Turner et al. 1984). The second year was a drought year and forbs and grasses produced less than 10 kg/ha (almost 100% forbs) in contrast to 87 kg/ha (97.7% forbs) in the previous year, and the consumption of grasses and forbs by tortoises was low. As an alternative food source, cacti (especially *Opuntia* spp.) comprised 86.9% of the diet during May and June.

Food Requirements of Desert Tortoises

The forage needs of a large population of desert tortoises is relatively small and may be met during years with lower than average precipitation. If tortoises eat from 201 g/kg body weight/year (Marlow 1979) to 4.52 g/kg body weight/day (Nagy and Medica 1986), then 96.5 tortoises/km^2 (density of desert tortoises at the Desert Tortoise Natural Area in the western Mojave Desert) require from 0.39 to 1.59 kg/ha forage per year (Resource Concepts, Inc., Carson City, Nevada, unpublished report; J. Sullins, University of California, Riverside, personal communication). Even during 1981, a year of very little rainfall, forage production was 0.7 kg/ha (Turner et al. 1984). Tortoises ate cacti, but females still reproduced, laying an average of 1.1 clutches (in contrast to 1.6 clutches during 1980 when rainfall was about twice that of 1981). However, the mortality of radio-tagged adults was significantly higher than during the year of average precipitation.

Forage quality is probably of greater importance than forage quantity, but requirements by the desert tortoise for energy and other nutrients have not been determined. The quality and abundance of curing or senescent forage may be the critical determinant in the nutrition of the tortoise. Nagy and Medica (1986) found that during spring when they were eating succulent, high-quality vegetation, desert tortoises were in a negative energy balance. Presumably this was due to the high water content of plants that satiated the tortoises before they had ingested enough nutrients to meet energy requirements. A prolonged decline in nutrient availability may have been responsible for osteologic lesions and higher than normal mortality in tortoises from the Beaver Dam Slope (J. L. Jarchow and C. J. May, Arizona Game and Fish Department, Phoenix, unpublished report). Studies of the nutrition of tortoises, however, have not been published, and deficiency levels of protein have not been established.

Effects of Grazing by Livestock on the Desert Tortoise

Grazing by livestock has been implicated as a factor in decreasing populations of desert tortoises (Berry 1978; Coombs 1979). Some argued that, because livestock has been detrimental to the range, it has had a similar detriment on desert tortoises (Berry 1978). The effects of grazing on desert tortoises, however, have not been studied in a quantitative or scientifically rigorous manner. References have been made to the early research on desert tortoises on the Beaver Dam Slope (Woodbury and Hardy 1948), but these researchers did not investigate the effects of grazing on tortoise populations and only offer the opinion that livestock grazing may cause range deterioration. The primary evidence that grazing by livestock harms desert tortoises relates to an overlap in food habits of livestock and tortoises. One study—on the Beaver Dam Slope, Utah—revealed an overlap in food habits of cattle and desert tortoises when forage was grouped by class (grasses, forbs, and shrubs; Coombs 1979). In that study, foxtail brome was heavily used by cattle and tortoises. Other important plant species for the desert tortoise (tridens and redstem filaree) comprised little of the diet of cattle (Coombs 1979). A later study on the Beaver Dam Slope, Arizona, revealed the greatest degree of dietary overlap in April 1977 when both cattle and tortoises ate plantain (*Plantago* sp.) and foxtail brome and in April 1978 when both ate plantain, redstem filaree, and split grass (*Schismus* sp.; J. Hohman and R. D. Ohmart, Center for Environmental Studies, Arizona State University, Tempe, unpublished report). During other months when cattle were still on the range, dietary overlap was not as great. Researchers did not measure the amount of forage available to tortoises after cattle were removed from the range to determine whether forage was in short supply for tortoises. In the Piute Valley, Nevada, the abundance of desert tortoise sign was qualitatively related to grazing pressure (C. Mortimore and P. Schneider, Nevada Department of Wildlife, Reno, unpublished report).

A recent analysis of soils in the Piute Valley, however, revealed that the abundance of tortoises was more closely related to soil conditions than forage production (R. W. Wilson and R. D. Stager, Bureau of Land Management, Las Vegas, Nevada, unpublished report). The investigators categorized soils on perceived needs for burrow construction and found that the three soil types categorized as best contained higher densities of tortoises and burrows than soil types of poorer quality for burrow construction but of higher forage production.

Alternatively, in a 2-year study designed for evaluating the effects of grazing in the Ivanpah Valley, plant biomass, tortoise weights, and tortoise reproduction did not differ between a grazed site and a recently constructed cattle exclosure (Turner et al. 1981; P. A. Medica, C. L. Lyons, and F. B. Turner, University of California, Los Angeles, unpublished report). In view of the long recovery time of desert sites, differences after only 2 years of protection from grazing are unlikely.

One analysis of the effects of grazing by cattle on desert tortoises (Bostick 1990) suggests that cattle may have a beneficial effect on desert tortoises. This analysis suggests that the numbers of desert tortoises declined as cattle AUMs decreased during the past 50 years and that tortoises are more adapted to ranges that are in poor condition than ranges in good condition. This analysis, like previously cited reports suggesting that cattle negatively affect desert tortoise habitat, lacks experimental evidence.

An analysis of the effects of grazing by sheep on desert tortoises suggests that the decline of tortoises roughly parallels reductions in grazing pressure by sheep and that tortoises continue to decline in areas that have not been recently grazed (Resource Concepts, Inc., unpublished letter). Grazing by sheep has been evaluated in California (Webb and Stielstra 1979; Nicholson and Humphreys 1981). Webb and Stielstra (1979) reported that after sheep passed through the site, 100 g/cm^2 [probably m^2] of forage remained, whereas 260 g/cm^2 [probably m^2] was available in an adjacent (<1 km away) site. Perennial vegetation was more abundant in the ungrazed than in the grazed plot before sheep grazed the site, and the cover of individual perennial shrubs was decreased by 16–19%. A reduction of biomass by 61.5% probably indicates a real decrease in biomass, but this decrease may not have been totally accurate because of the inherent differences in the perennial vegetation of the grazed and ungrazed plots and the lack of measurements before and after grazing. After sheep made a second pass through the grazed plot, an estimated 10–25% of the annual plant biomass remained. If 10% remained and the plots were identical, approximately 260 kg/ha remained after sheep had grazed the area twice.

At a study plot in California, the cover of live annual plants decreased from 24 April to 22 May by 40.8% in a site not grazed by sheep, by 49.6% in a light-use site, and by 69.2% in a heavy-use site (Nicholson and Humphreys 1981). The decrease in the no-use site represented the normal maturing of annual plants, whereas the 69.2% decrease in the heavy-use site probably reflected maturing as well as removal by sheep. Many of the annual forbs eaten by tortoises were also eaten by sheep; western fiddleneck, redstem filaree, and desert dandelion were the species with greatest overlap. Sheep also damaged tortoise burrows in the same study plot: 4% were totally destroyed and 10% were damaged (86% of these were in the areas with moderate-to-heavy use by sheep). Burrows that had more shrub and soil cover seemed to have been unaffected by sheep (Nicholson and Humphreys 1981).

Research Needs

The purpose of this review was to examine known factors of the plant ecology in the Mojave Desert and the effects of livestock on the plant ecology and the desert tortoises. Considerable research has been conducted on the distribution of plants in the Mojave Desert, on the life history of the creosotebush, and on the relation between desert annuals and annual precipitation. Essentially no researcher has yet evaluated the effects of livestock grazing on the productivity or availability of perennial grasses in the Mojave Desert, but research revealed that the activities by livestock (primarily sheep) reduced the cover of shrubs and annual forbs. Desert tortoises seem to prefer grasses and forbs, and the overlap between the diets of livestock and the desert tortoises has been documented. However, researchers have not yet investigated whether desert tortoises alter food habits to compensate for livestock grazing or if desert tortoises are nutritionally limited by livestock grazing.

For the scientific management of desert tortoise habitat, the effect of livestock on desert tortoises must be rigorously evaluated. The following questions have to be addressed: (1) What in situ nutrients (when and how much) are required for the growth, reproduction, and long-term survival of desert tortoises? (2) How many tortoises can exist on a given piece of habitat that is in excellent ecological condition (what is the carrying capacity)? (3) Does the use of the range by livestock change the availability of critical nutrients that affect tortoises? (4) Does currently accepted proper use of the range by livestock change the plant composition in such a way as to either lower the ecological condition of the range or reduce the availability of nutrients for desert tortoises? Too many scientifically unsupported statements have been made about the effects of livestock grazing on desert tortoises. Answers to the stated questions will improve our ability to manage desert tortoise habitat.

Acknowledgments

M. Jennings provided considerable assistance with locating the literature for this manuscript. W. Burkhardt, D. Germano, R. Hunter, and P. Medica provided helpful suggestions for improving the manuscript.

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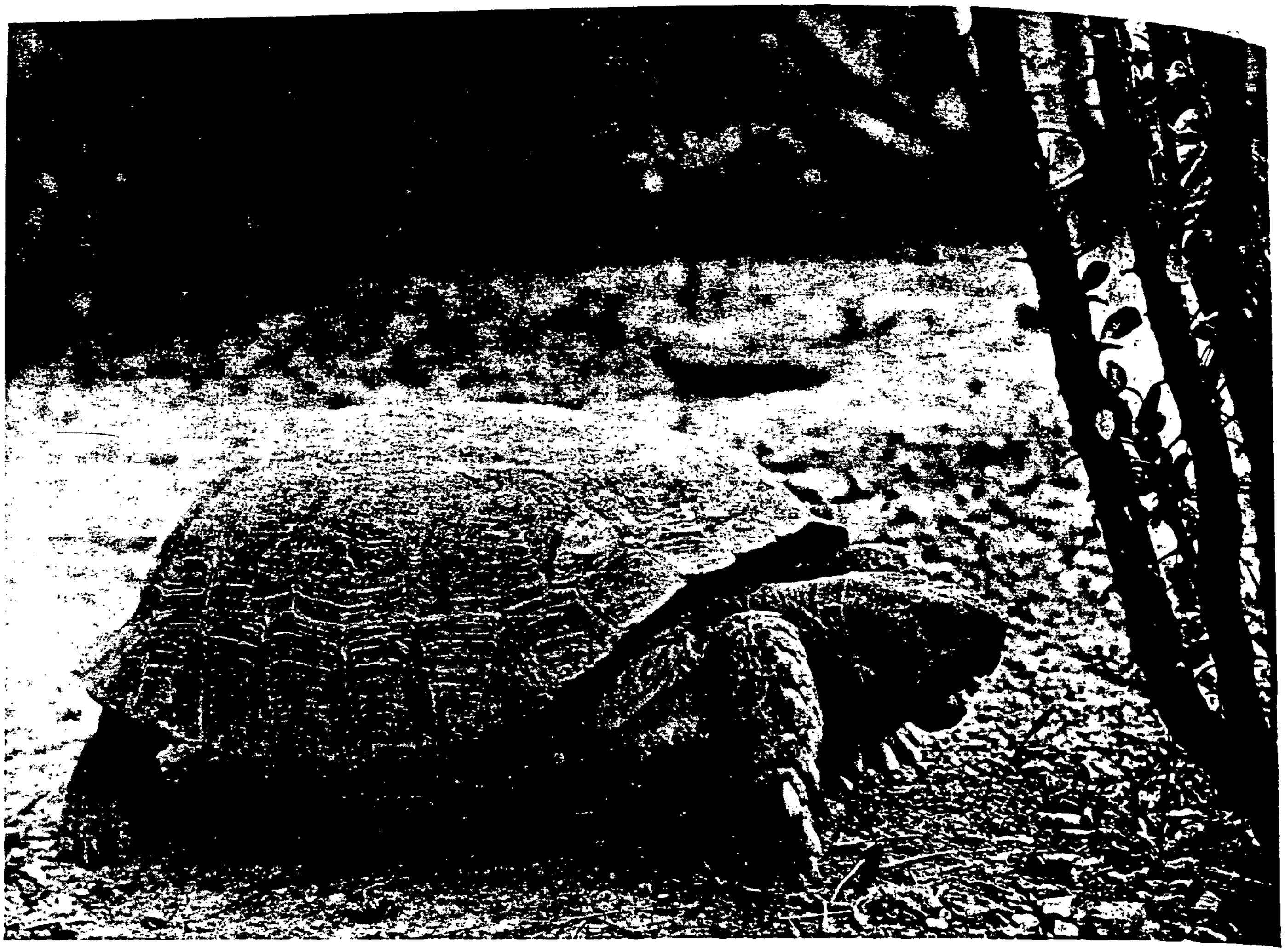

Adult Bolson tortoise (*Gopherus flavomarginatos*) at Mapimi MAB Reserve, Durango, Mexico. *Photo by D. E. Biggins.*

Ingestion of Bones, Stones, and Soil by Desert Tortoises

by

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Abstract. We used field observations and radiographs to document that desert tortoises (*Gopherus agassizii*) ingest soil and stones. The ingestion of soil and stones can be a common albeit rarely observed behavior of desert tortoises. We also describe the ingestion of bones by wild tortoises. Desert tortoises readily eat weathered bones, and some individuals persist in eating bone even when they are disturbed. Eating soil, stones, and bones could be important in supplementing the herbivorous diet of tortoises, and thus the relative use of these behaviors in different localities could serve as indicators of nutritive stress. Other possible benefits from the ingestion of soil, stones, and bones include the maintenance of gut pH, nullification of plant secondary compounds, control of intestinal parasites, or maintenance of beak shape (in a fashion analogous to the behavior of birds). Bones and other mineral resources seem to be important to tortoises. However, the mechanistic explanations for eating soil, stones, and bones are currently unknown. Research into the mineral physiology of tortoises is necessary to determine the causes of the ingestion of soil, bones, and stones and to provide guidance for management.

Key words: Bone eating, *Gopherus agassizii*, nutrition, soil ingestion, stones in diet, Utah.

The ingestion of bone, stones, and soil has been observed in a variety of domestic and wild vertebrates (Robbins 1983). These behaviors may be caused by dietary deficiencies of macronutrients such as calcium, phosphorus, and sodium and of micronutrients such as iron, copper, and selenium (Robbins 1983). Mineral deficiencies in vertebrate diets may be caused by a low mineral content of soils where plants grow, low availability of required minerals in plants, use of specific minerals for the detoxification of secondary compounds, imbalances in dietary ratios of essential nutrients, and physiological demand for minerals during certain life stages.

Vertebrates obtain most essential dietary elements from food. Where sufficient amounts of criti-

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cal nutrients are lacking, however, vertebrates may supplement forage. The intake of supplemental minerals is known in ungulates (Sutcliffe 1973; Brothwell 1976; Langman 1978; Barrette 1985), primates (Hyslop 1977; Davies and Baillie 1988), and rodents (Duthie and Skinner 1986; Hansson 1990). Supplementation of nutrients may be more common in herbivores than in carnivores because wild carnivores probably acquire a more diverse selection of minerals in their normal diet (e.g., through the ingestion of bone in prey).

Although supplementation of nutrients seems to be common, it is infrequently observed. During field studies, osteophagia was noted in only 3 of 1,000 observations of mule deer (*Odocoileus hemionus*; Krausman and Bissonette 1977) and in 7 of 2,500 observations of desert bighorn sheep (*Ovis canadensis*; Warrick and Krausman 1986). When osteophagia and related behaviors are observed, they can be an all-encompassing activity for the animal (Warrick and Krausman 1986) and may result in agonistic behaviors toward conspecifics over these resources (Bowyer 1983; Keating 1990).

Birds are also known to supplement their diet with minerals by ingesting, for example, snail shells (Krapu and Swanson 1975; Beasom and Pattee 1978) and lemming bones (MacLean 1974). Developing young and egg-laying females are most likely to supplement calcium in the diet for bone and eggshell formation (Robbins 1983).

Captive herbivorous reptiles are especially prone to nutritional deficiencies when their food lacks minerals (Jacobson 1989), and captive reptiles consume material with minerals. For example, box turtles (*Terrapene ornata*) in captivity ingest stones and soil (Kramer 1973).

The ingestion of stones by desert tortoises (*Gopherus agassizii*) is known in the Mojave Desert of California (Luckenbach 1982; Marlow and Tollestrup 1982) and Nevada (T. C. Esque, field data), but there are few data. Fecal pellets of *G. polyphemus* from Florida contained stones (MacDonald and Mushinsky 1988). In the wild and in captivity, tortoises may consume calcareous stones to supplement dietary elements and to macerate a herbivorous diet (Sokol 1971).

Desert tortoises may mine minerals by scraping away the top soil to reach calcium-rich deposits in the underlying caliche (calcium carbonate) strata (Marlow and Tollestrup 1982). Moreover, tortoises apparently alter their normal patterns of moves to visit these sites, which may be at some distance from the normal home range (Marlow and Tollestrup 1982).

To our knowledge, osteophagy has been observed in captive tortoises and rarely in wild tortoises. We observed captive desert tortoises consuming small bones, stones, and bone meal. Bally (1946) observed a captive leopard tortoise (*Testudo pardalis*) eating bone. Bones were also found in the fecal pellets of wild leopard tortoises (Milton 1992). In Brazil, Moskovits (1985) observed two species of tortoises (*Geochelone denticulata* and *G. carbonaria*) eating carrion containing bones. Another North American tortoise, the gopher tortoise (*G. polyphemus*), was observed eating animal matter (MacDonald and Mushinsky 1988). The giant tortoise (*G. elephantopus*) eats bones and other animal materials on the Galapagos Islands (Cayot 1987).

Here, we describe the occurrence and frequency of phagous behavior in wild desert tortoises, discuss the possible need for mineral supplementation in tortoises, and offer alternative hypotheses for the ingestion or chewing of soil, stones, and bones in tortoises.

Materials and Methods

We recorded 991 observations of 52 desert tortoises in the northeastern Mojave Desert near St. George, Utah, during April–June 1989, May–June 1990, and June–July 1991; on the Beaver Dam Slope, Utah, in June 1989; and near Littlefield, Arizona, in May 1990. We also followed tortoise tracks near St. George, Utah, where sandy soils often revealed the daily routes of tortoises for long stretches (>100 m).

We conducted field trials to observe eating of bone by wild tortoises. We gently tossed weathered pieces of bones in front of tortoises in the wild. We presented samples of cow bones to 11 tortoises near St. George, Utah, during 7–27 June 1990 (Table). For each trial, a bone was placed <10 cm in front of the tortoise. A different piece of bone was used for each trial to reduce the possible attraction or avoidance of it because of lingering scent of conspecifics from previous trials. The bone samples were too large (>10 cm long and >3 cm thick) to be grasped and broken by the animals.

Furthermore, we examined 185 radiographs (provided by colleagues) of 31 adult tortoises for stones or other material in the intestines. These radiographs were earlier used to denote the number of eggs in female tortoises and, in a few cases, to examine the digestive tract in male tortoises.

Results

Ingestion of Stones and Soil

During 991 observations of foraging behavior of desert tortoises, we recorded 12 cases of ingestion of soil and stones near St. George and on the Beaver Dam Slope, Utah, and near Littlefield, Arizona. Phagous behavior mostly lasted only a few minutes, but one lasted as long as 20 min. Most ingestion of stones and soil was by adult female tortoises in spring.

Although most stones in the St. George study area were brown, grey, or another dull color, tortoises consumed only white stones. White stones in the Mojave Desert are primarily composed of caliche (calcite), which is mostly calcium carbonate (Marlow and Tollestrup 1982). When encountering such stones, some tortoises nudged them with their snouts, took them into their beaks, and manipulated them with the tongue. Some of these stones were large (>1 cm diameter) in relation to the size of the mouth. The behavior was deliberate. Plant material was not present in the immediate area, and the ingestion of stones was not incidental to foraging.

During a study of growth and reproduction in Nevada tortoises (Turner et al. 1987), radiographs (Figs. 1 and 2) revealed many stones in the alimentary canal (R. B. Bury, National Ecology Research Center, Fort Collins, Colorado, personal observation). Similarly, M. Coffeen (Utah Division of Wildlife Resources, personal communication), who studied reproduction in tortoises in southwestern Utah, collected radiographs from 29 adult female tortoises during April–July 1987–89. Radiographs revealed stones and soil in 122 of 183 tortoises from Utah: 9 tortoises had rocks and soil in >90% of the alimentary canal; 18 had aggregations of 30–160-mm-long stones in their guts; 21 had <20 large stones (i.e., >5-mm diameter); and 74 tortoises had scattered small stones (i.e., <5-mm diameter) in their guts.

We observed fewer than 1% of tortoises eating soil and stones. Furthermore, this consumption was brief during surface activity. We could not observe tortoises while they were in their burrows or dens.

Table. Trials in which weathered cow bones were offered to 11 wild desert tortoises (*G. agassizii*) near St. George, Utah, in 1990–1991.

Maximum carapace length (mm)[a]	Accepted[b] bones	Rejected bones
<100	1	1
100–140	2	0
>140–180	3	1
>180	2	1

[a] Tortoises >180 mm were females.

[b] Defined here as grasping bones with the beak and chewing them.

Ingestion of Bones

At St. George, Utah, our first indications of osteophagia were tortoise tracks around weathered cattle bones and the skeletons of a fox, a rabbit, and a tortoise. Concentrated tracks in small areas around the bones resembled patterns of tracks by tortoises who fed on low-growing desert annuals and not track patterns (generally in one direction) by traveling tortoises.

On the morning of 6 June 1989 on the Beaver Dam Slope, Utah, an adult female took several white stones into her mouth without swallowing them. Then, at 1030 h, this tortoise encountered three weathered limb bones of a black-tailed jackrabbit (*Lepus californicus*). The diameters of two of the bones were smaller than the third. The tortoise nudged the bones with her snout, consumed the two smaller bones, and grasped the third bone without breaking it with her beak. This behavior occurred in 4 minutes, and then the tortoise foraged on vegetation. On 4 June 1991, we observed a wild desert tortoise attempting to eat fox bones (Fig. 3).

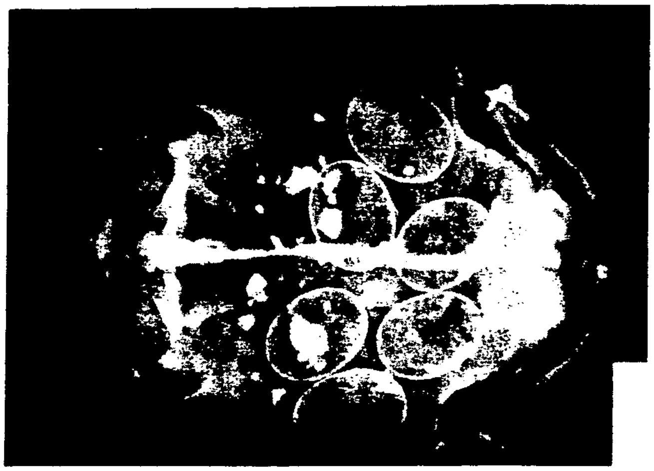

Fig. 1. Radiograph of the intestines of an adult female desert tortoise (*G. agassizii*) from the Nevada test site. Shelled eggs and stones are visible.

On 16 June 1990, we located a female tortoise with a radio transmitter and tossed a weathered cow vertebra (2-cm diameter) about 1 m in front of her. After about 5 minutes, the tortoise nudged the bone with her snout and then began chewing the bone between her mandibles. The bone sample was large and the tortoise could not break it. However, the tortoise scraped off and consumed chips of the bone. As we moved to within about 3 m to photograph the animal, the tortoise became disturbed and turned away from the bone. When we were out of sight at a distance of 15 m, the tortoise quickly resumed chewing the bone.

Tortoises grasped bones in their mandibles and chewed them during 8 of 11 trials (Table). On 1 May 1991, we observed one tortoise remove and eat 28 chips from a large cow bone (about 10-cm diameter). The tortoises usually used their forefeet to hold down the bone, and they were sometimes persistent in these behaviors. If we approached them to within 5 m, the tortoises ceased eating and moved away from the bones, but when the observer retreated, the tortoises sometimes returned to consume the bones (3 of 11 observations).

Osteophagy contrasted with the general feeding behavior. When we inadvertently interrupted tortoises feeding on plants, they abandoned the food and rarely returned to it.

Discussion

Although the ingestion of bones, stones, and soil is known of a wide variety of vertebrate taxa, its importance to the health of herbivores is not well documented. We concur with Sokol (1971), Marlow and Tollestrup (1982), Moskovits (1985), Cayot (1987), and MacDonald and Mushinsky (1988) that eating bones, stones, and soil may be important for mineral supplementation. Calcium can be obtained from the ingestion of all three items and may well be the mineral that tortoises seek. However, we do not know whether the diet of tortoises or the

Fig. 2. Radiograph of the intestines of an adult female desert tortoise (*G. agassizzii*) from the Nevada test site. Note the presence of many ingested stones.

Fig. 3. Osteophagy by an adult female desert tortoise (*G. agassizii*) near St. George, Utah, in the spring of 1991. *Photo by T. Schaffer.*

environments are deficient in nutrients and minerals. Tortoises may simply ingest minerals opportunistically or alternatively be able to locate and use mineral-rich deposits (e.g., by mining caliche; Marlow and Tollestrup 1982). However, the deficiency of a mineral other than calcium or a ratio of minerals may be responsible for the ingestion of bones, stones, and soils by tortoises.

Concentrated tracks around plants and bones indicate that tortoises consumed them. In most of these cases, the plants were missing flowers and leaves, and the bones had bite or scrap marks. We found that tortoises who feed on bones usually leave no evidence other than feces or tracks. Furthermore, tortoises may consume bones rapidly (e.g., 2 rabbit leg bones in 4 minutes). Observations of the ingestion of bones are seemingly uncommon but not less frequent than observations of copulation and agonistic behaviors that are also seldom observed in wild tortoises.

The ingestion of stones is seldom noted in the field. However, radiographs of wild tortoises show a high frequency of ingested soil and stones. About 60% of a large sample of tortoises (n = 185) had stones in the intestines; most stones were small (<5-mm diameter), but a few were larger (>5 mm). Thus, the ingestion of stones, soil, and bones seems to be more common in tortoises than was previously known.

The need to supplement the diet of tortoises with minerals may depend on several factors. The regional flora may be diverse or depauperate in mineral-rich plant species, which may affect mineral availability in the forage of tortoises. The physiological condition of tortoises probably affects mineral requirements. For example, juveniles, which grow rapidly, and gravid females are expected to have a large demand for minerals. The availability of different chemical and crystalline forms of mineral species may also affect the assimilation efficiency of the required mineral. Furthermore, tortoises may require additional minerals to nullify the toxic effects of secondary compounds in food plants (Reese 1979).

Alternatively, the ingestion of stones, bones, and soil may be important to the physical well-being of the animals or other functions not directly related to nutrition. Many gallinaceous birds require small stones in their gizzards to grind hard-shelled foods (Welty 1975). Similarly, eating of stones and soil by wild and captive reptiles may be for grinding foods (Cott 1961; Johnson 1966; Sokol 1971).

Furthermore, tortoises may consume quantities of soils or stones as a vermifuge (to expel parasites). Captive and wild tortoises may harbor high densities of parasitic worms in their intestines (personal observation). Stones or soils that are rich in calcium carbonate may rid tortoises of parasites by dislodging parasites or changing the chemical environment of the gut. Herbivorous reptiles may eat soil to acquire cellulytic intestinal flora (Sokol 1971), and tortoises, like birds, may chew hard objects to maintain the quality of their beaks.

Because the ingestion of bones, stones, and soil seems important to the nutrition or other functions in the desert tortoise, management could enhance habitats for tortoises. If tortoises require supplemental minerals, we suggest that weathered bones from carcasses of tortoises and other vertebrate species (i.e., jackrabbits, cattle) are valuable to live tortoises.

Currently, some study protocols (unpublished reports) call for the removal of all tortoise skeletons from study areas during population surveys. As a result, tortoise skeletons may become rare and those that accumulate between surveys may not have become weathered, which is the advanced stage of decomposition necessary for their ingestion by live tortoises. We think that the collection of bones and tortoise shells may deplete supplies of nutrients in the wild and possibly prevent cycling of necessary mineral sources.

There are alternatives to removing all tortoise skeletons from study plots or transect lines. Tortoises and their skeletons (with scutes) can be aged in the field by counting growth rings (Germano 1988). In most cases, only a single skeletal element from each carcass has to be collected or a sample (subset) of the total number of skeletons retained. Thus, we suggest that investigators collect minimal samples or record measurements from tortoise bones and shells in the field.

Acknowledgments

We thank R. Bezette, R. Bransfield, P. Budkovich, D. Holt, W. Kohn, A. McLuckie, S. Ribarich, J. Roberts, E. Rominger, J. Rotolo,

J. Rourke, T. Schaffer, C. Shershanovich, J. Snider, L. Thomas, M. Topham, S. Topham, and others for field assistance. R. Fridell, J. P. Hohman, H. Martin, C. Pregler, and especially R. B. Bury and C. R. Tracy provided helpful comments and reviews of the manuscript. R. Benton, T. A. Duck, D. Pietrzak, and R. Radant provided workspace, logistical support, or advice. M. Coffeen generously provided unpublished data from radiographs. R. B. Bury, P. A. Medica, and F. B. Turner gave us permission to use their radiographs. T. Schaffer allowed us to print his photograph of a desert tortoise eating a bone. We are especially gratefully to J. Payne for securing the support of many cooperating agencies and to L. A. DeFalco for managing the field crew and providing expert field assistance. Field research was funded by the U.S. Bureau of Land Management (Cedar City–Utah and Arizona Strip districts), U.S. Fish and Wildlife Service, and Utah Department of Wildlife Resources.

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Uncovered nest of a gopher tortoise (*Gopherus polyphemus*), showing position of eggs in front of the burrow mouth. *Photo by J. E. Diemer.*

Organic Composition and Energy Content of Eggs and Hatchlings of the Gopher Tortoise

by

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Abstract. In the gopher tortoise, *Gopherus polyphemus*, we determined the percentage (% of dry mass) of ash and percentages (% ash-free dry mass; AFDM) of lipid, NaOH-soluble protein, carbohydrate, and insoluble protein in eggs (eggshell and egg contents) and in seven components of hatchlings. The egg contents contained 33.6% lipid and 62.3% insoluble protein. Whole eggs had 346.7 kilojoules (kJ) of energy and egg contents had 246.4 kJ. The egg dry mass (g), energy in the egg content, and total kJ in the egg increased with egg wet mass. The mean egg wet mass of a clutch increased with the mean egg diameter measured directly on eggs or in radiographs but not with clutch size or with the mass, carapace length, or plastron length of the female tortoise. Insoluble protein was the major constituent of all hatchling components except the liver and reserve yolk. Lipid comprised 76.9% of the liver. Reserve yolk contained 38.6% lipid in day-0 and 49.1% lipid in day-2 hatchlings. Hatchlings contained 209.1 kJ of energy. The hatchling wet mass, hatchling dry mass, and energy content (kJ) in the hatchling increased with the wet mass of the egg from which a hatchling emerged. The conversion of energy from egg to hatchling averaged 76.2% (range 66.9–93.6%). The eggs of gopher tortoises and several other reptiles contained lower lipid levels than the eggs of most species of birds and thus contained less energy per gram AFDM. The moisture content of the environment in which an egg is incubated may affect energy conversion. Hatchlings with lower-percent conversion may be smaller and more vulnerable to predation or less capable of obtaining food than hatchlings with higher-percent conversion. This study facilitates estimation of the amount of energy (kJ) invested by a female in a clutch, hatchling biomass (g), and energy content (kJ) of hatchling biomass without destroying the eggs or hatchlings.

Key words: Conversion efficiency, eggs, energy, Florida, *Gopherus polyphemus*, hatchlings, organic composition.

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The gopher tortoise (*Gopherus polyphemus*) is distributed in numerous, disjunct populations along the southeastern coastal plain between South Carolina and Louisiana. It inhabits xerophytic plant associations such as longleaf pine–oak uplands, xeric hammocks, sand pine–oak ridges, and ruderal communities (Auffenberg and Franz 1982). Populations are declining throughout the species' range as a result of habitat destruction (McRae et al. 1981; Auffenberg and Franz 1982; Lohoefener 1982) and human predation (Hallinan 1923; Hutt 1967; Lohoefener 1982; Taylor 1982).

Knowledge of the reproduction biology of the gopher tortoise is important to better protect this species. Several aspects of the reproduction biology of the gopher tortoise have been studied: the minimum age and minimum size at sexual maturity (Douglass 1976; Iverson 1980; Landers et al. 1982), cycles of vitellogenesis and spermatogenesis (Taylor 1982), timing of mating (Kenefick 1954; Ernst and Barbour 1972; Landers et al. 1980; Wright 1982) and oviposition (Ernst and Barbour 1972; Landers et al. 1980; Taylor 1982; Wright 1982), and clutch size (Hallinan 1923; Arata 1958; Brode 1959; Iverson 1980; Landers et al. 1980; Taylor 1982; Wright 1982). However, little is known about the energetics of egg production.

For a single annual clutch of eggs (Iverson 1980; Landers et al. 1980; Taylor 1982; Wright 1982), a female must consume sufficient amounts of essential amino acids, vitamins, and minerals to produce the eggs and to supply to the eggs all of the nutrients needed by the embryos throughout the incubation period. A female also must provide sufficient nutrient reserves in the spare yolk (yolk not converted into hatchling biomass) to ensure the optimum survival and growth of the hatchling (Scott 1972). The amounts of nutrients and energy in the egg are important costs of reproduction by a female for egg production and embryonic development.

Only one study has been done on the energy content and organic composition of eggs of the gopher tortoise (Congdon and Gibbons 1985), and no data are available on the energy content of hatchlings. In this paper, we report on the organic composition of eggs and hatchlings of gopher tortoises, the total energy in eggs and hatchlings, and the conversion efficiency of the egg. We also wished to determine whether this information may be obtained through nondestructive measurements of animals in the field.

Materials and Methods

From spring 1983 through summer 1985, we studied a population of tortoises in the University of South Florida Ecology Research Area in Tampa, Florida. We weighed (nearest g), measured (nearest mm) the carapace length (CL) and the plastron length (PL; McRae et al. 1981), and marked (Cagle 1939) each captured tortoise. During May and June, we palpated adult females for the presence of shelled (i.e., calcified) eggs. Gopher tortoise eggs are hard-shelled and nearly round. We used radiographs of gravid tortoises to establish the number of eggs in the oviducts (Gibbons and Greene 1979). We assumed eggs were mature as soon as their shells appeared completely calcified (Ewert 1979). In 1984, the clutches of 9 of the 10 tortoises appeared completely calcified and the remaining clutch appeared lightly calcified. We induced oviposition in the 10 tortoises by injecting oxytocin (3 units of oxytocin/100 g body mass; Ewert 1979) into the gastrocnemius muscle. We found another freshly laid clutch in the field and presumed it was completely calcified.

The tortoises deposited eggs in an outdoor enclosure, and eggs were numbered as they were laid. We weighed (nearest 0.1 g) and measured (nearest 0.1 mm) the eggs for the greatest (length) and least (breadth) diameter. We froze approximately half of each clutch for analyses of organic composition. The other half of each clutch was placed in moistened vermiculite in a 18.5- × 15.0- × 8.0-cm plastic container and incubated at 30° C while the tops of the eggs were exposed. We misted the eggs with water about every 4–10 days. Thirteen of the 46 eggs hatched after 91 to 105 days of incubation. The remaining 33 eggs never hatched. We weighed each hatchling (nearest 0.1 g) and measured (nearest 0.1 mm) CL and PL. At hatching (pipping), all tortoises had an external yolk sac that was large enough to prevent the animals from walking. Within 2 days of hatching, the yolk sac was fully resorbed into the body cavity, and the hatchlings could walk. Even though the external yolk sac is not present 2 days after hatching, a large internal yolk reserve still exists in the body cavity.

We froze all hatchlings and later analyzed them for proximate organic composition. We ascertained differences in the proximate organic composition and energy content of the yolk sac and its contents (defined as the reserve yolk component) of hatchlings immediately after hatching and after the yolk sac had been resorbed into the body cavity. We froze six hatchlings on the day of hatching (day 0) and froze the remaining seven 2 days after hatching (day 2).

We separated eggs into eggshell (ES) and egg contents (yolk and albumin combined; YA). We separated hatchlings into seven components by dissection: eggshell, carapace, plastron, reserve yolk (RY), liver (LI), forelimb muscle (FM), and gut and all remaining tissue (GM). We placed the components in aluminum pans and weighed them to the nearest 0.01 g. We placed the pans in vacuum desiccators over concentrated sulfuric acid to dry their contents. We weighed dried components to the nearest 0.01 g and calculated the percentage of water. We ground each component into a homogenous mixture with a Wiley mill or mortar and pestle and analyzed subsamples for ash, lipid, NaOH-soluble protein, and carbohydrate content. We expressed the content of all organic constituents as a percentage of ash-free mass. The insoluble protein content is the sum of percentages of all other organic constituents subtracted from 100. We determined ash content by burning a 20–60-mg subsample from each component in a muffle furnace for 4 h at 500° C.

We treated eggshells of hatchlings and newly laid eggs differently than the other components. The eggs of one female may not have been fully calcified at induction. Therefore, we averaged one to four ash determinations of each eggshell component. We made one ash determination for all other tissue components. We analyzed one subsample from each component for lipid, NaOH-soluble protein, and carbohydrate content.

We determined total lipid content by analyzing a 48–177-mg subsample with the chloroform–methanol extraction method (Freeman et al. 1957). We determined the NaOH-soluble protein content of a 10–117-mg subsample by the colorimetric method (Lowry et al. 1951) with bovine serum albumen as the standard. We determined the carbohydrate content of a 9–63-mg subsample by the colorimetric method (Dubois et al. 1956) with glycogen as the standard.

We calculated the kilojoules (kJ) of energy of the eggs and hatchlings on an ash-free dry mass (AFDM) basis contained as specific organic constituents in each component with the following equation:

$$\begin{aligned}\text{Energy in kJ (ash-free)} &= (\text{dry mass of the component in g}) \\ &\times (\text{ash-free \% of organic constituent} \div 100) \\ &\times (\text{energy in kJ/g of organic constituent}).\end{aligned} \qquad (1)$$

On an AFDM basis, lipid contains about 9.45 kcal/g, protein 5.65 kcal/g, and carbohydrate 4.10 kcal/g (Paine 1971). By the energetic equivalent of 1 kcal for each 4.184 kJ, the equivalent energy content is 39.54 kJ/g of lipid, 23.64 kJ/g of protein, and 17.15 kJ/g of carbohydrate (Weast 1974). We obtained the total energy of a component by summing the energy content of each organic constituent.

We calculated the percentage of the conversion (AFDM) of energy (E) from egg to hatchling with the equation:

$$\%\ \text{conversion (AFDM)} = 100\ ([E_t - E_r] \div [E_c - E_r]) \qquad (2)$$

where E_t = total energy in hatchling,
E_r = energy in the reserve yolk, and
E_c = energy in the egg contents.

We used an arcsine transformation of the percentage values (arcsine of the square root of the percentage; Sokal and Rohlf 1981) to normalize the data. We used ANOVAs to detect differences in the proximate organic composition (AFDM) of the components (eggs and hatchlings) between four female tortoises and between groups of hatchlings frozen on either the day of hatching or 2 days after hatching. To ascertain differences between hatchlings of different females, we averaged the percentages of the individual organic constituents (AFDM) of day-0 and day-2 hatchlings (from a single female) and analyzed the percentages by one-way ANOVAs. It was impossible from these ANOVAs to determine if significant differences existed in the organic composition of components between day-0 and day-2 hatchlings; therefore, we performed one-way ANOVAs grouping hatchlings by age, regardless of female, for all body components and all four organic constituents (AFDM). Unless otherwise stated, we accepted levels of significance at $P = 0.05$.

Results

Egg Characteristics

Whole eggs, including YA and ES, averaged 38.1 g in wet mass (SE = 0.9, $n = 37$) and differed by females ($F_{10,26} = 57.40$, $P < 0.001$). Clutch size was not related to mean egg wet mass. Water comprised an average of 66.1% (SE = 0.5, $n = 37$) of the whole egg and 73.7% (SE = 0.6, $n = 37$) of the egg contents (YA). The percentage of water in the eggs did not differ by females. Eggshells averaged 33.1% (SE = 1.0, $n = 37$) of the total dry mass (TDM) of eggs, and the ES percentage differed by females ($F_{10,26} = 12.75$, $P < 0.001$). The dry mass of an egg increased with the wet mass of the egg ($t = 7.24$, $df = 35$, $P < 0.001$; Fig. 1).

The mean percentages (±SE) of four organic constituents (AFDM) in the YA and ES components of eggs did not differ by females (Table 1). The ash levels of the ES components of 2 eggs from one female ($F_{10,26} = 7.11$, $P < 0.001$) were greater than the ash levels of the ES components of the remaining 35 eggs (including the freshly laid clutch found in the field) and revealed that only 2 eggs from one female were not completely calcified when oviposition was induced.

The mean ($n = 37$) total energy (kJ) in the eggs was 346.7 ± 7.3 SE. The total energy in the egg increased with egg wet mass ($t = 6.93$, $df = 35$, $P < 0.001$; Fig. 2). We could not demonstrate a linear relation between total energy in the egg and clutch size. In each of eight clutches (Fig. 3), the mean egg mass of the clutch increased with either the actual mean egg diameter of the clutch ($t = 6.70$, $df = 6$, $P < 0.001$) or the mean egg diameter of the clutch determined from radiographs ($t = 3.84$, $df = 6$, $P < 0.01$).

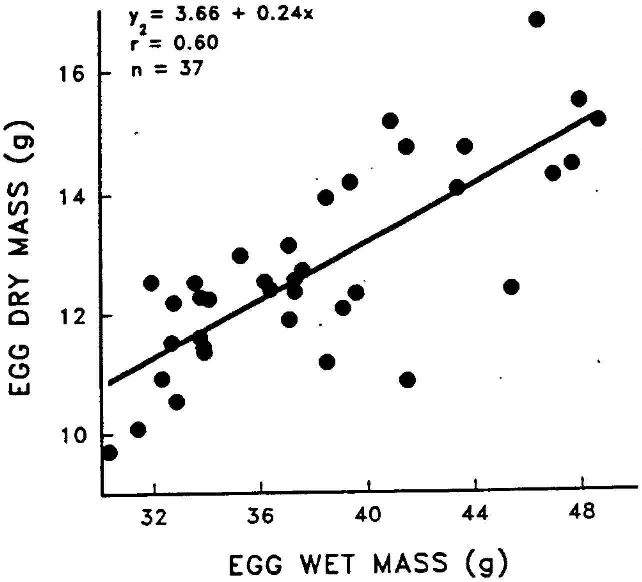

Fig. 1. Regression of egg dry mass on egg wet mass of *Gopherus polyphemus*.

Furthermore, the mean total energy in the egg contents (YA) of 10 clutches increased with the mean egg diameter of the clutch determined from radiographs ($y = -304.98 + 123.57x$; $r^2 = 0.76$, $t = 5.07$, $df = 8$, $P < 0.001$). The mean egg diameter is the average of the mean greatest diameters and the mean least diameters of all eggs in the clutch.

Table 1. Organic composition (in percentage ash-free dry mass) and percentage of ash (in percentage of dry mass) of the egg contents (YA) and eggshells (ES) of eggs of the gopher tortoise (*Gopherus polyphemus*). Values are means ± SE, $n = 37$. Eggs were obtained from one freshly laid clutch and by induction in May and June 1984 from 10 wild gopher tortoises in Tampa, Florida.

Component	Lipid(%)	NaOH-soluble protein(%)	Carbohydrate (%)	Insoluble protein(%)	Ash(%)
YA	33.61	3.00	1.10	62.29	5.36
	±0.53	±0.10	±0.03	±0.52	±0.15
ES	1.03	1.32	0.77	96.88	76.81
	±0.12	±0.10	±0.09	±0.21	±1.33

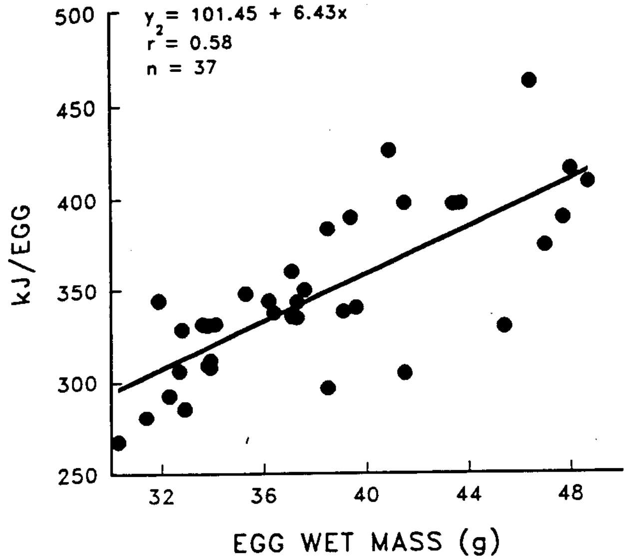

Fig. 2. Regression of kilojoules (kJ) in the egg on egg wet mass of *Gopherus polyphemus*.

Hatchling Characteristics

We analyzed 13 hatchlings. Unless otherwise noted, data of day-0 and day-2 hatchlings are combined. Excluding ES, hatchlings averaged 27.0 g in wet mass (SE = 0.9, n = 13) and 71.8% in water (SE = 1.2, n = 13). The wet mass ($F_{3,9}$ = 18.22, $P < 0.001$) and water content ($F_{3,9}$ = 29.86, $P < 0.001$) of hatchlings differed among females. The eggshell averaged 37.6% of TDM of the hatchling (SE = 0.7, n = 13) and differed among the hatchlings of different females ($F_{3,9}$ = 9.06, $P < 0.01$). The mean percentages (±SE) of TDM (excluding ES) of six components, but not of forelimb muscle, differed among hatchlings of different females (Table 2).

The mean percentages (±SE) of ash and four organic constituents (AFDM) in all components differed among the hatchlings of different females in the mean percentage of lipid and insoluble protein in the liver (% lipid: $F_{3,9}$ = 9.05, $P < 0.01$; % insoluble protein: $F_{3,9}$ = 8.53, $P < 0.05$) and reserve yolk (% lipid: $F_{3,9}$ = 9.71, $P < 0.01$; % insoluble protein: $F_{3,9}$ = 9.36, $P < 0.01$).

Only the mean percentages (AFDM) of lipid ($F_{1,11}$ = 8.57, $P < 0.05$) and insoluble protein ($F_{1,11}$ = 8.33, $P < 0.05$) in RY differed (Table 3). Day-2 hatchlings contained a significantly higher percentage of lipid (AFDM; $F_{1,11}$ = 8.57, $P < 0.05$) and a significantly lower percentage of insoluble protein (AFDM; $F_{1,11}$ = 8.33, $P < 0.05$) in RY than day-0 hatchlings.

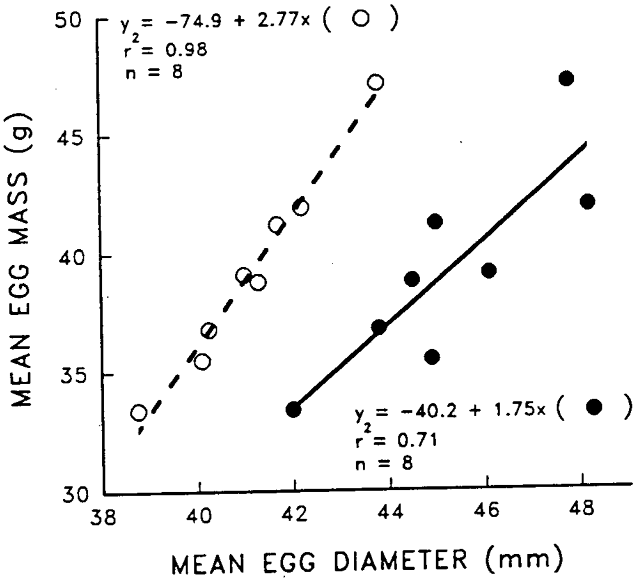

Fig. 3. Regression of actual mean egg mass on actual mean egg diameter (○) and mean egg diameter measured from radiographs (●) of *Gopherus polyphemus*.

Table 2. Mean percentages (± SE) of the total dry mass of the hatchling (without eggshell) in six components (n = 13). Day-0 and day-2 hatchlings are combined. F-values, df, and significance levels are from one-way ANOVAs comparing hatchlings from different female gopher tortoises (*Gopherus polyphemus*). Eggs were obtained in the wild (see Table 1).

Component of hatchling	Percentage of total dry mass (TDM)	$F_{3,9}$	P
Liver	11.92 ± 0.70	7.22	<0.05
Forelimb muscle	2.20 ± 0.23	2.85	NS
Gut and remainder	31.61 ± 2.20	14.47	<0.01
Carapace	17.01 ± 1.32	17.98	<0.01
Reserve yolk	27.00 ± 4.96	13.80	<0.01
Plastron	10.26 ± 0.87	18.47	<0.01
Total	100		

Table 3. Organic composition (in percentage ash-free dry mass) and percentage of ash (in percentage of dry mass) of the eggshell (ES), carapace (CA), plastron (PL), reserve yolk (RY), liver (LI), forelimb muscle (FM), and gut and remaining tissue (GM) of hatchlings of the gopher tortoise (*Gopherus polyphemus*). Values are means ± SE ($n = 13$). Data of day-0 and day-2 hatchlings are combined for all components except the reserve yolk; values of the reserve yolks of day-0 ($n = 6$) and day-2 ($n = 7$) hatchlings are presented separately. Eggs were obtained in the wild (see Table 1).

Component	Lipid (%)	NaOH-soluble protein (%)	Carbohydrate (%)	Insoluble protein (%)	Ash (%)
ES	1.16	1.25	0.77	96.82	81.61
	±0.09	±0.06	±0.08	±0.15	±0.63
CA	5.69	2.78	1.24	90.30	7.34
	±0.53	±0.05	±0.08	±0.55	±0.29
PL	4.19	2.63	1.26	91.92	10.66
	±0.24	±0.10	±0.05	±0.28	±0.49
RY day 0	38.58	2.14	0.87	58.41	5.06
	±0.99	±0.15	±0.04	±0.94	±0.26
RY day 2	49.09	1.87	0.81	48.23	3.84
	±3.20	±0.08	±0.09	±3.15	±0.39
LI	76.89	0.88	3.46	18.78	1.53
	±1.13	±0.06	±0.44	±1.10	±0.09
FM	8.61	2.95	2.37	86.07	5.78
	±0.74	±0.12	±0.16	±0.80	±0.34
GM	12.33	2.57	1.73	83.38	14.25
	±0.51	±0.08	±0.14	±0.54	±0.50

The hatchlings contained an average of 209.1 ± 9.7, $n = 13$) of energy. Excluding ES, the total energy in a hatchling increased with the wet mass of the egg from which it emerged ($t = 3.21$, $df = 11$, $P < 0.01$; Fig. 4) and with the hatchling dry mass ($y = -18.05 + 30.10x$; $r^2 = 0.99$, $t = 48.53$, $df = 11$, $P < 0.001$). Excluding ES, the hatchling wet mass ($t = 5.71$, $df = 11$, $P < 0.001$) and hatchling dry mass ($t = 3.47$, $df = 11$, $P < 0.01$) increased with the wet mass of the egg from which a hatchling emerged (Fig. 5). Excluding ES, the hatchling wet mass was not related to the dry mass or total energy of a hatchling.

Conversion Efficiency

Conversion efficiency is the efficiency (%) with which energy in the egg contents (YA) is converted into hatchling energy. In our study, the mean ($n = 37$) total energy (kJ) in the YA component was 246.4 ± 6.3. The total energy in the YA component increased with the egg wet mass ($t = 3.71$, $df = 35$, $P < 0.001$; Fig. 6). Furthermore, the total energy in the YA increased with the dry mass of YA ($y = -4.64 + 29.47x$; $r^2 = 0.99$, $t = 52.73$, $df = 35$, $P < 0.001$) and with the egg dry mass ($y = 4.80 + 18.96x$; $r^2 = 0.64$, $t = 7.86$, $df = 35$, $P < 0.001$). The percent conversion for hatchlings ranged from 66.9 to 93.6% (mean = 76.2 ± 2.6%). The conversion efficiency of day-0 and day-2 hatchlings did not differ.

Discussion

Egg Characteristics

The eggs of different females differed by wet mass and the percentage of TDM, which is composed of the eggshell. The genetic variation between females may account for some of the variation in egg wet mass, but the amount and quality of the food eaten by the females during vitellogenesis may be the most important effects on egg

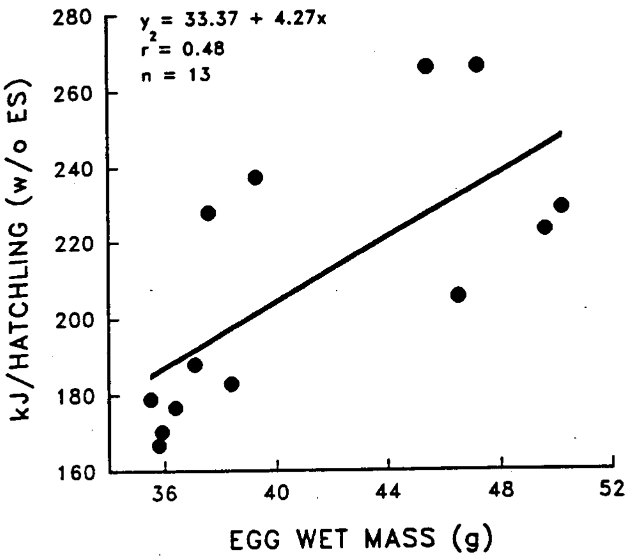

Fig. 4. Regression of kilojoules in the hatchling (without eggshell [ES]) on egg wet mass of *Gopherus polyphemus*. Day-0 and day-2 hatchlings are combined in the analysis.

wet mass. Egg wet mass did not correlate with the mass, carapace length, or plastron length of the female or with clutch size. Some differences in the percentage of TDM of the ES may have been caused by the variation in the calcification of the eggshells when oviposition was induced.

The proximate organic composition and energy level of the eggs of gopher tortoises, other reptiles, and birds are similar (Table 4). The total energy level of the eggs of most reptilian species, including the gopher tortoise, is between 6 and 7 kcal/g (25.1–29.3 kJ/g) AFDM. The mean energy level of the eggs (yolk and albumin only, uncorrected for ash) of 10 lizard species (6 genera) is 6.2 kcal/g (25.8 kJ/g) and ranges from 6.0 to 6.4 kcal/g (25.1–26.6 kJ/g; Ballinger and Clark 1973). The mean energy level of the whole eggs of 10 lizard species (6 genera) is 6.4 kcal/g (26.7 kJ/g) AFDM and ranges from 5.9 to 7.2 kcal/g or 24.6–30.1 kJ/g AFDM (Tinkle and Hadley 1975).

The variation in the organic composition of the egg within and among reptile species is considerable. The nonpolar lipid level (on a dry mass basis and uncorrected for ash content) of each of four eggs (without the eggshell but including the yolk and albumin) from a single clutch of the gopher tortoise was 25.6% (Congdon and Gibbons 1985). This lipid content is similar to the 28.2% lipid content of the painted turtle (*Chrysemys picta*) egg (Congdon and Tinkle 1982) and the 32% lipid content of the loggerhead sea turtle (*Caretta caretta*) egg (Needham 1963) but much lower than the 65% lipid in the yolk of the chicken (*Gallus gallus*) egg (Romanoff 1967). The nonlipid (protein, polar lipids, and carbohydrate) fractions of eggs of gopher tortoises was an estimated 74.4% (Congdon and Gibbons 1985).

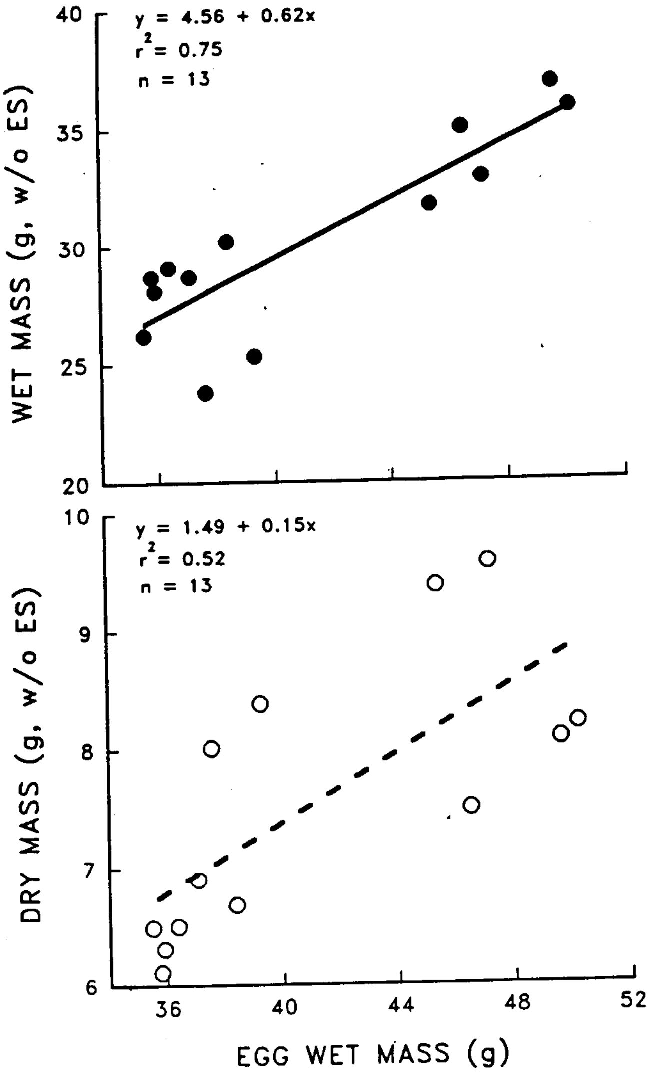

Fig. 5. Regression of hatchling wet mass (without eggshell, ES [*solid circles and line*]) and hatchling dry mass (without eggshell [ES; *open circles and dashed line*]) on egg wet mass of *Gopherus polyphemus*. Day-0 and day-2 hatchlings are combined.

The variation in the egg lipid content between studies may be caused in part by differences in

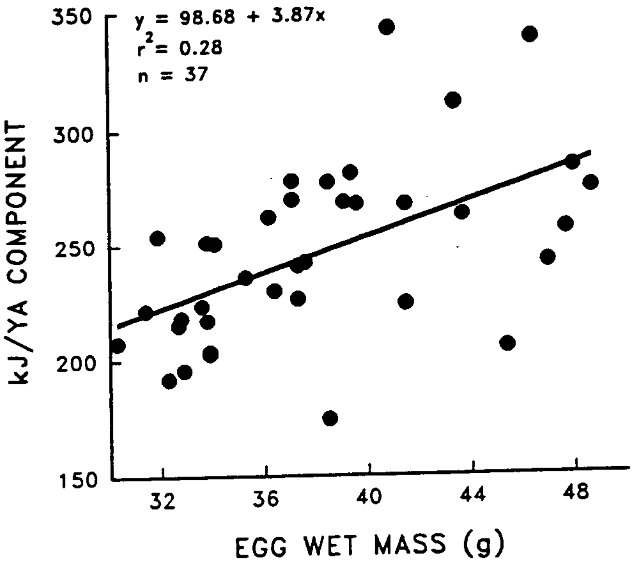

Fig. 6. Regression of kJ in the yolk and albumin (YA) component of the egg on egg wet mass of *Gopherus polyphemus*.

technique related to questions addressed. For example, one study (Congdon and Gibbons 1985) found the lipid level of eggs of *G. polyphemus* to be 25.6% by a neutral (nonpolar) lipid-extraction method (a petroleum ether extraction), whereas we obtained a lipid level of 33.6% by a total (polar and nonpolar) lipid-extraction method (a chloroform–methanol extraction). About 24% of the lipids (polar phospholipids) were not extracted with the ether-extraction method. Congdon and Gibbons (1985) were interested in lipid reserves (nonpolar lipids), whereas we were interested in the conversion of all organic constituents (including polar and nonpolar lipids) from egg to hatchling (conversion efficiency).

Species with high percentages of lipid in their egg contents usually have high total energy values (Table 4). The young of these species may require an energy-rich nutrient reserve to hatch during a time of environmental stress (e.g., drought) or to complete energetically expensive activities

Table 4. Organic composition and energy level of eggs of selected reptile and bird species. Mean values are reported, and the number of eggs, if known, is in parentheses. Unless otherwise noted, (1) values of only the egg contents are reported; (2) determinations are uncorrected for ash content; and (3) values are on a dry-mass basis. The total energy in kcal/g was estimated from the percentages of lipid and nonlipid fractions with the calorific equivalents of 9.45 kcal/g lipid and 5.65 kcal/g protein. It is assumed that the nonlipid fraction is protein (P); where the carbohydrate (C) level is known, a calorific equivalent of 4.10 kcal/g is used. The actual total energy is given by some sources. The approximate total energy in kJ/g was calculated with 4.184 kJ/kcal as the energetic equivalent.

Class:Order Family Species (locality)	Organic composition: Lipid fraction(%)	Organic composition: Nonlipid fraction(%)	Total energy (kcal/g) kJ/g	Source
Reptilia:Testudines				
Testudinidae				
Gopherus polyphemus (Moultrie, GA)	25.56(4)	74.44(4)	(6.62) 27.70	Congdon and Gibbons (1985)[b]
(Tampa, FL)	33.61(37)	65.29(P;37) 1.10(C;37)	(6.91) 28.91	Present study[c]
Kinosternidae				
Kinosternon subrubrum (South Carolina)	31.57(25)	68.43(25)	(6.85) 28.66	Congdon and Gibbons (1985)[b]
Sternotherus odoratus (South Carolina)	25.84(17)	74.16(17)	(6.63) 27.74	Congdon and Gibbons (1985)[b]
(Michigan)	11.85(2)	88.15(2)	(6.10) 25.52	Congdon et al. (1983a)[b]
Trionychidae				
Trionyx ferox (Moultrie, GA)	27.99(10)	72.01(10)	(6.71) 28.07	Congdon and Gibbons (1985)[b]
Emydidae				
Chrysemys picta (SE Michigan)	28.20(22)	70.40(22)	(6.64) 27.78	Congdon and Tinkle (1982)

Table 4. *Continued.*

Class:Order Family Species (locality)	Organic composition		Total energy (kcal/g) kJ/g	Source
	Lipid fraction(%)	Nonlipid fraction(%)		
(SE Michigan)	22.68(51)	77.32(51)	(6.51) 27.24	Congdon et al. (1983a)[b]
(Cherry Co., NE)	37.10(13)	62.90(13)	(7.06) 29.54	Gutzke et al. (1987)
(Wisconsin)	22.75(17)	77.25(17)	(6.51) 27.24	Congdon et al. (1983a)[b]
C. p. bellii	14.80(13)			Chaikoff and Entenman (1946)[d]
C. p. dorsalis (Athens, GA)	32.99(5)	67.01(5)	(6.90) 28.87	Congdon and Gibbons (1985)[b]
Clemmys marmorata (San Luis Obispo, CA)	26.87(6)	73.13(6)	(6.67) 27.91	Congdon and Gibbons (1985)[b]
Deirochelys reticularia (South Carolina)	32.42(50)	67.58(50)	(6.88) 28.79	Congdon and Gibbons (1985)[b]
(South Carolina)	32.40(43)	67.60(43)	(6.88) 28.79	Congdon et al. (1983b)[b]
Emydoidea blandingi (Michigan)	15.56(13)	84.44(13)	(6.24) 26.11	Congdon et al. (1983a)[b]
Graptemys geographica (Michigan)	15.90(4)	84.10(4)	(6.25) 26.15	Congdon et al. (1983a)[b]
Graptemys ouachitensis (Wisconsin)	24.36(53)	75.64(53)	(6.58) 27.53	Congdon et al. (1983a)[b]
Malaclemys terrapin (New Jersey)	26.40(21)	73.60(21)	(6.88) 28.79	Ricklefs and Burger (1977)
Pseudemys concinna (South Carolina)	27.71(15)	72.29(15)	(6.70) 28.03	Congdon and Gibbons (1985)[b]
Pseudemys floridana (South Carolina)	29.03(33)	70.97(33)	(6.75) 28.24	Congdon and Gibbons (1985)[b]
Pseudemys scripta (South Carolina)	30.45(33)	69.55(33)	(6.81) 28.49	Congdon and Gibbons (1985)[b]
(South Carolina)	29.52(11)	70.48(11)	(6.77) 28.33	Congdon et al. (1983a)[b]
(Locality unknown)			(6.70) 28.03	Slobodkin (1962)[c]
Terrapene carolina (South Carolina)	25.76(19)	74.24(19)	(6.63) 27.74	Congdon and Gibbons (1985)[b]
Chelydridae				
Chelydra serpentina (Winston-Salem, NC)	23.54(31)	76.46(31)	(6.54) 27.36	Congdon and Gibbons (1985)[b]
(Michigan)	14.63(30)	85.37(30)	(6.21) 25.98	Congdon et al. (1983a)[b]
(Wisconsin)	14.29(20)	85.71(20)	(6.19) 25.90	Lynn and von Brand (1945)[a]
(Locality unknown)			(6.60) 27.61	Slobodkin (1962)[c]
Reptilia:Squamata				
Anguidae				
Gerrhonotus coeruleus			(6.40) 26.78 (whole egg)	Vitt (1974)[c]

Table 4. *Continued.*

Class:Order Family Species (locality)	Organic composition Lipid fraction(%)	 Nonlipid fraction(%)	Total energy (kcal/g) kJ/g	Source
Iguanidae				
Iguana iguana			(6.13) 25.65	Ricklefs and Cullen (1973)
Sceloporus jarrovi	35.60	64.40	(7.00) 29.29 (whole egg)	Hadley and Christie (1974)[b]
Sceloporus undulatus			(6.70) 28.03	Slobodkin (1962)[c]
Urosaurus ornatus			(6.90) 28.87	Slobodkin (1962)[c]
Aves:Pelecaniformes				
Pelecanidae				
Pelecanus occidentalis	28.80(6)	70.10(P;6) 1.10(C;6)	(6.73) 28.16	Lawrence and Schreiber (1974)[a,c]
Sulidae				
Morus bassanus	25.80(10)	74.20(10)	(6.63) 27.74	Ricklefs and Montevecchi (1979)
Aves:Anseriformes				
Anatidae				
Anas platyrhynchos	41.10(3)	58.90(3)	(7.21) 30.17	Ricklefs (1977)[b]
Aves:Galliformes				
Phasianidae				
Coturnix coturnix	39.00(15)	61.00(15)	(7.13) 29.83	Ricklefs (1977)[b]
Gallus gallus	29.74(5)			Chaikoff and Entenman (1946)[d]
	64.99	33.52(P) 1.49(C)	(8.10) 33.89	Romanoff (1967)[c,e]
Aves:Charadriiformes				
Laridae				
Larus atricilla	43.20(9)	56.80(9)	(7.29) 30.50	Ricklefs (1977)[b]
Aves:Columbiformes				
Columbidae				
Zenaida macroura	36.50(4)	63.50(4)	(7.04) 29.46	Ricklefs (1977)[b]
Aves:Passeriformes				
Icteridae				
Quiscalus major	33.92 (19–23)	63.84(P;19–23) 2.25(C;19–23)	(6.90) 28.87	Bancroft(1985)[a,c,f]
Sturnidae				
Sturnus vulgaris	35.10(12)	64.90(12)	(6.98) 29.20	Ricklefs (1977)[b]

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[a] We calculated values from referenced data.

[b] Mean % nonlipid fraction is obtained by subtracting the mean % lipid fraction from 100.

[c] Values are on an ash-free basis.

[d] Values are on a wet-mass basis.

[e] Only values of the yolk are reported.

[f] Carbohydrate content (%) of the yolk equals the sum of the percentages of lipid and protein contents (ash-free) minus 100. The nonprotein fraction of the albumin was assumed to be 40% lipid and 60% carbohydrate (after Lawrence and Schreiber 1974).

immediately after hatching. Significantly higher levels of lipid have been found in species of turtles, the hatchlings of which overwinter in the nest (Congdon et al. 1983b).

The eggs of tortoises in our study contained less energy per gram AFDM than most bird eggs (Table 4). The difference is attributable to the high lipid levels of bird eggs. The eggs of 40 bird species had lipid levels of between 17.0% and 50.0%, and the eggs of most species ($n = 29$) had at least 33% lipid (Carey et al. 1980). The energy level ranged from 6.4 to 7.5 kcal/g (26.7–31.5 kJ/g) dry mass (uncorrected for ash content), and the eggs of 25 species had at least 7.0 kcal/g (29.3 kJ/g). The energy level of the egg yolks in 10 bird species averaged 8.0 kcal/g (33.5 kJ/g) AFDM (Slobodkin 1962).

Precocial birds are homeothermic at hatching and must maintain a high body temperature; altricial birds are ectothermic at hatching (Welty 1979). Precocial birds, therefore, require more energy than reptiles to maintain body temperature at hatching. Hatchlings of altricial and semiprecocial species may have to compete with one or more siblings for food and need an energy-rich nutrient reserve. The food reserves in the yolks of chicks of the herring gull (*Larus argentatus*) may be important to the survival and activity of the chicks while the parent–chick bond develops (Parsons 1970).

Hatchling Characteristics

We found significant differences in the wet mass of a hatchling (excluding ES) of different females. The wet mass of a hatchling increased with the wet mass of the egg from which it emerged and therefore is tied to the genetic and nutritional constraints that determine egg wet mass. The percentage of water of hatchlings (excluding ES) also varied between hatchlings of different females. This difference probably was responsible for the absence of linearity between the wet masses and dry masses of hatchlings.

The variation in the percentages of the organic constituents was considerable among hatchlings of gopher tortoises and of other reptile and one bird species (Table 5). The total energy levels varied little among species, except in the alligator lizard (*Gerrhonotus coeruleus*), which contained only 5.6 kcal/g (23.5 kJ/g) AFDM (Vitt 1974). Young of this species are born live and may appear during times of abundant food; thus, they may not require nutrient-rich reserves. Alternatively, much of the yolk lipid (52%) is metabolized during development in *G. coeruleus* (Stewart and Castillo 1984). Energy in the reserve yolk (RY) component of the hatchlings is included in the total energy level (Table 5) and may account for some of the variation in the percentages of the organic constituents. The total energy level between species varies greatly if the energy in the RY component is subtracted.

We found a large portion of the energy level of a hatchling is in the RY component, comprising about 27% of TDM of hatchlings (excluding ES) of the gopher tortoise (Table 2). The sizes of the yolk sacs of tortoise hatchlings averaged 10 × 10 × 5 mm 24 h after pipping, and resorption of the yolk sac into the body requires an additional 18–24 h (Arata 1958). All newly emerged hatchlings of the Aldabra giant tortoise (*Geochelone gigantea*) had external yolk sacs with a diameter of approximately 17.5 mm and were resorbed into the body within 5–7 days after hatching (Swingland and Coe 1978). The posthatching (reserve) yolk in loggerhead sea turtles probably functions as an energy source to support the metabolic demands of hatching, activity in and emergence from the egg chamber, and initial swimming from the nesting beach (Kraemer and Bennett 1981). The reserve yolk supplies a store of nutrients that enables the developing chick to survive for a limited time without additional food (Romanoff 1944).

The proximate organic composition of the reserve yolk changes over time in the chicken and in the gopher tortoise. Protein levels (%) are higher and lipid levels (%) lower in the reserve yolks of chicks at 2 days of age than on the day of hatching (Romanoff 1967). We found the reverse in tortoise hatchlings. Hatchling gopher tortoises seem to use reserves of protein before the lipid reserves in the RY component. However, we did not detect significant changes in the size of the RY component between day 0 and day 2 and, therefore, could not determine changes in the amounts of energy.

Table 6. Mean conversion efficiency (% conversion) of energy from egg to hatchling for selected species of reptiles and one bird. Unless otherwise noted, (1) the reserve yolk was not separated from the body of the hatchling; (2) determinations are uncorrected for ash content; (3) values are on a dry-mass basis; and (4) hatchlings were killed on the day of hatching (day 0). The number of hatchlings, if known, is in parentheses after values.

Class:Order Family Species (locality)	Lipids (% conversion)	Total energy (% conversion)	Source
Reptilia:Testudines			
Testudinidae			
Gopherus polyphemus (Tampa, FL)	53.6(13) (range 40.6–72.6)	76.2(13) (range 66.9–93.6)	Present study[b,c,d]
Emydidae			
Chrysemys picta (SE Michigan)	62.0(9)		Congdon and Tinkle (1982)
Deirochelys reticularia (South Carolina)	61.0(15)		Congdon et al. (1983b)
Chelydridae			
Chelydra serpentina (Wisconsin)	77.7(17)		Lynn and von Brand (1945)[a]
Reptilia:Squamata			
Anguidae			
Gerrhonotus coeruleus		59.0(3)	Vitt (1974)[b]
Iguanidae			
Iguana iguana		85.3(6)	Ricklefs and Cullen (1973)[a,c]
Aves:Galliformes			
Phasianidae			
Gallus gallus		60.4	Romanoff (1967)[a,b,c]

[a] Values are calculated by the authors from referenced data.

[b] Values are on an ash-free basis.

[c] Reserve yolk was separated from the body of the hatchling.

[d] Hatchlings killed on day 0 and day 2 are combined.

3 and equation 1. Where hatchling dry mass (without eggshell) is available by direct measurement, the total energy in the hatchling (without eggshell) may be determined with the regression $y = -18.05 + 30.10x$ ($r^2 = 0.99$, $t = 48.53$, $df = 11$, $P < 0.001$).

5. The hatchling wet mass (without eggshell; Fig. 5) from which the hatchling biomass on a study site may be determined when all female tortoises in the site are radiographed or freshly deposited clutches are located.
6. The energy in the yolk and albumin component (Fig. 6) from which the energy available for conversion to hatchling biomass may be determined.

Sometimes the mass of the eggs in a clutch is not available. In eight clutches in our study, the actual mean egg wet mass of a clutch did not correlate with the mass, carapace length, or plastron length of the female tortoise or with clutch size. If the mean egg diameter of a clutch is available from direct measurement or from a radiograph, the actual mean egg mass of a clutch may be determined (Fig. 3). The mean egg mass derived from the regression (Fig. 3) then may be substituted into regressions (Figs. 1–2, 4–6) to estimate other variables of reproduction. One must be cautious with application of data from one regression into another regression because the error is compounded. However, direct analysis of tortoise eggs and hatchlings disturbs nests and sacrifices individuals. Because of the diminishing populations of the gopher tortoise, we feel some error in estimation is a more acceptable alternative than direct analysis of eggs and hatchlings.

Acknowledgments

We thank J. Lawrence for the use of his laboratory and his advice on laboratory methods and J. Congdon and G. Woolfenden for comments on the manuscript. We received assistance in the field and laboratory from S. Boyer, C. Bromley, K. Hagood, P. Heeschen, B. Kaiser, and P. Martin. J. R. Linley helped with the data analysis.

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Reproduction of Gopher Tortoises in North-central Florida

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Abstract. We obtained data on the reproduction of the gopher tortoise (*Gopherus polyphemus*) in north-central Florida from 1981 to 1987. The smallest radiographed female tortoise with shelled eggs had a 232-mm carapace length. The overall mean clutch size was 5.80 (range 3–10) and did not vary significantly from those of tortoise populations on a sandhill site (5.73), a planted pine site (5.83), and a pasture site (6.50). Most mature females radiographed during mid-May to mid-June had shelled eggs. The mean egg diameter and clutch size increased with mean carapace length. Nests were in burrow mounds, sandy roads, or roadsides, and one each was found in a clear-cutting and in a scrub-oak thicket. Evidence of egg and hatchling depredation was observed.

Key words: Age of reproduction, clutch size, Florida, *Gopherus polyphemus*, nesting, predation, radiography.

Gopher tortoise (*Gopherus polyphemus*) populations in Florida declined despite a 1988 statewide prohibition on taking tortoises. Although the decline may in part be attributed to agriculture, mining, illegal harvest, and certain forestry practices, urbanization poses the greatest threat to this fossorial reptile (Auffenberg and Franz 1982; Diemer 1987a). In recent years, numerous gopher tortoise populations were relocated as mitigation for the loss of xeric habitats on development sites (Diemer 1987b, 1989). One criterion for evaluating the success of relocating tortoises is a population's postrelocation reproductive status. The usefulness of this criterion depends on an understanding of reproduction in indigenous tortoise populations. We present data about the reproduction of gopher tortoises in north-central Florida and synthesize pertinent findings from other researchers.

Materials and Methods

Study Sites

Data were gathered during 1981–87 in conjunction with studies of population dynamics on three sites in north-central Florida. We marked and recaptured tortoises during 1982–86 on the Roberts Ranch in Putnam County, during 1981–87 in the Lochloosa Wildlife Management Area in Alachua County, and during 1985–86 on Wolfe's Pasture, 0.6 km southeast of the Lochloosa Wildlife Management Area study site.

The Roberts Ranch study site was a 10.8-ha portion of a larger (160-ha) sandhill, approximately 15 km west of Palatka. The excessively drained sand supported an overstory of scattered longleaf pines (*Pinus palustris*) and mature turkey oaks (*Quercus laevis*); a midstory of smaller turkey oaks, sand-live oaks (*Q. geminata*), and sand-post oaks (*Q. margaretta*); and a diverse ground cover dominated by wiregrass (*Aristida stricta*), various composites (Asteraceae), and legumes (Fabaceae). The site remained unburned for more than 7 years before a hot burn in 1983.

The Lochloosa Wildlife Management Area study site was a 1.1-km grassy roadside strip with a surrounding mature slash pine (*P. elliottii*) plantation, approximately 20 km southeast of Gainesville. The major soil type was a moderately well-drained sand. The dense canopy of tall slash pines and scattered live oaks (*Q. virginiana*) and water oaks (*Q. nigra*) had reduced the herbaceous ground cover of the plantation. The most recent prescribed burn was in 1982. The roadsides were mowed annually, and cattle grazed in the area. In 1984, the landowner cleared timber and replanted slash-pine seedlings in a small section of the southwestern portion of the study site and in larger sections immediately southwest and approximately 0.5 km northwest of the main study site.

We included Wolfe's Pasture as a study site in 1985 when a radio-instrumented tortoise moved there from the Lochloosa Wildlife Management Area. The soil was a moderately well-drained sand. Vegetation included scattered large live oaks, seedling slash pines, bahia grass (*Paspalum notatum*), and hairy indigo (*Indigofera hirsuta*).

Data Collection and Analysis

Tortoises were snared, manually captured, removed from their burrows with a pulling hook (Taylor 1982a), or captured in pitfall traps (19-L buckets sunk directly in front of the burrow opening). We measured the carapace length (CL) and drilled small holes in the marginal scutes (Cagle 1939) to permanently mark tortoises. Adult tortoises were sexed by morphology (McRae et al. 1981). We aged tortoises by counting plastral growth rings, assuming a 1:1 correspondence between age and ring count (Germano 1988; Landers et al. 1982). We radiographed all confirmed female tortoises to determine clutch size (S; Gibbons and Greene 1979). We recorded egg diameter (D) as the average of the maximum and minimum diameters (mm) of the egg radiograph image. The egg diameters were averaged by clutch, then averaged again by all clutches ($\overline{D}$). We also averaged S and CL over multiple captures of each female ($\overline{S}$,$\overline{CL}$).

With data available only in years 1982–86, we compared S among the three study sites in a completely randomized analysis of variance. We weighted $\overline{S}$ by number of clutches to stabilize variability in $\overline{S}$, and we separated means with Tukey's test. The productivity trend of each female was estimated by the regression coefficient of S on year (1982–86 only). We compared productivity trends between individuals from the Lochloosa Wildlife Management Area and individuals from the Roberts Ranch in a two-sample *t*-test, weighted by the corrected sum of squares of year to control trend–variance heterogeneity. We used linear regression to test the relations of $\overline{S}$ and $\overline{D}$ with $\overline{CL}$. Differences in regression equations (either $\overline{S}$ vs. $\overline{CL}$ or $\overline{D}$ vs. $\overline{CL}$) among the animals of the three study sites were assessed with analysis of covariance. Tukey's test was used to separate estimated regression coefficients by study area.

The estimated minimum production of hatchlings was defined as the ratio of all hatchlings captured in a particular year or of all juveniles from that year class captured in subsequent years to the number of shelled eggs produced that year. We assumed that each female laid her eggs in the study sites, that no eggs were laid by females not caught, and that no juveniles immigrated into the study sites.

Results

Size at Maturity

The smallest female tortoise with detected shelled eggs had a 232-mm CL (Table 1). Approximately 16 annuli were counted on her worn plastron. Three other small gravid females captured at the Roberts Ranch had 233-mm (approximately 15–16 annuli), 233-mm (annuli illegible), and 238-mm (annuli illegible) CL. All other gravid females had a ≥240-mm CL. A female on the Roberts Ranch reached maturity during the study: we did not detect eggs in 1983 (209-mm CL, 12 plastral rings) or 1985 (228-mm CL, 14 rings) but in 1986 (242-mm CL, 15 rings). Three immature females on the Roberts Ranch had 194-mm (*n* = 2) and 215-mm CL (11–14 plastral rings). Radiographs of three small females in the Lochloosa Wildlife Management Area coupled to thermistors (222-, 227-, 233-mm CL) also revealed no eggs, although the largest female and a mature male were trapped in early May, and she may have produced eggs later. The smallest gravid female in the Lochloosa Wildlife Management Area had a ≥242-mm CL. Plastral abrasion made tortoises in the Lochloosa Wildlife Management Area especially difficult to age. One immature female grew 1 mm (221–222-mm CL) and 0 plastral annuli (12 rings, both years) between 1982 and 1984. By legible plastral annuli, female tortoises in north-central Florida seemed to reach sexual maturity at 14–18 years of age (Table 1).

The smallest apparently mature male tortoises had 177-mm CL (Table 1) on the Roberts Ranch and 182-mm CL in the Lochloosa Wildlife Management Area. Maturity was indicated by an elongated gular and a well-defined plastral concavity (McRae et al. 1981) in the smaller male and observation of the larger male visiting females. Two young tortoises on the Roberts Ranch first showed male morphological characteristics at 196-mm and 203-mm CL. Other young males on the Roberts Ranch had 188–196-mm CL and showed 9–12 plastral rings. A male in the Lochloosa Wildlife Management Area (204-mm CL, 13 plastral annuli) was first observed visiting females in 1985. By legible plastral annuli, male tortoises in north-central Florida seemed to reach sexual maturity at 9–13 years of age (Table 1).

Table 1. Size, age at maturity, and mean clutch size of the gopher tortoise (*Gopherus polyphemus*) by region.

Region	Size[a] at maturity		Age[b] at maturity		Mean clutch size	Source
	Males	Females	Males	Females		
North Florida	177	232	9–13	14–18	5.8	This study
	230	238				Auffenberg and Iverson (1979)
	187	210			6.7	Taylor (1982b)
		226–236		10–15	5.2	Iverson (1980)
Central Florida		238				Linley (personal communication)
				13	7.8	Linley (1986)
		255			7.6	Godley (1989)
South Florida	222					Douglass (1990)
	225	282	9–13	12	6.9	McLaughlin (1990)
					8.9	Burke (1987)
Southwest Georgia	230–240	250–265	16–18	19–21	7.0	Landers et al. (1980, 1982)
Southwest Alabama					5.3	Marshall (1987)
South Carolina	153		12		3.8	Wright (1982)

[a] Carapace length in mm.
[b] Years.

Clutch Size

The weighted $\bar{S}$ of 62 radiographed female tortoises on the Roberts Ranch ($\bar{S} = 5.73$, $n = 30$), in the Lochloosa Wildlife Management Area ($\bar{S} = 5.83$, $n = 26$), and in the Wolfe's Pasture study sites ($\bar{S} = 6.50$, $n = 6$) was similar (2, 59 df; $P = 0.598$). Tukey's test could not distinguish any pair of means at the $P = 0.05$ level. The overall weighted $\bar{S}$ (Table 1) was 5.80 ($n = 62$, range 3–10, SE = 0.156) with a 95% confidence interval of (5.49, 6.11).

The trends in weighted mean productivity of individuals in the Lochloosa Wildlife Management Area (–0.0702 eggs/year) and on the Roberts Ranch (–0.1301 eggs/year) were not different (26 df, $P = 0.790$). The mean of the overall trend in weighted productivity was not different from 0 (–0.1195 eggs/year, df = 27, $P = 0.562$). Eighteen tortoises on the Roberts Ranch had shelled eggs in 2 or more consecutive years, and five of these tortoises produced shelled eggs in all 5 years. Nine tortoises in the Lochloosa Wildlife Management Area had shelled eggs in 2 or more consecutive years, and one tortoise produced shelled eggs for 6 consecutive years. The other 29 gravid tortoises on both sites were captured only once or in alternate years.

The mean annual proportion of gravid females was 0.73 (range = 0.40–0.89). We detected shelled eggs 138 times and failed to detect eggs 46 times. Of the failed detections, 12 were of immature females, 16 were of mature females before 12 May or after 10 June (Table 2), and 18 (only 10% of all radiographs) of the mature females during 12 May–10 June. One female without eggs on 10 May had four eggs on 3 June, and another without eggs on 12 May had seven eggs by 19 May and nested on 18 June. We saw no indication of more than 1 clutch/year.

The rate of increase of clutch size with CL was consistent among study sites ($F = 0.90$; 2, 55 df; $P = 0.414$). The mean clutch sizes of tortoises of equal CL also did not vary by area ($F = 1.15$; 2, 57 df; $P = 0.323$). Ignoring area, clutch size increased with CL ($t = 4.10$, 59 df, $P < 0.001$, $R^2 = 0.222$) in the estimated regression model

$$S = -4.744 + 0.04035 \text{ CL}.$$

Thus, a 25-mm increase in CL produced a one-egg average increase in clutch size.

The rate of increase of mean egg diameter with clutch size did not vary among study sites ($F = 1.00$; 2, 54 df; $P = 0.375$). In any area, an expected 1-mm increase in mean egg diameter occurred with every 13-mm increase in CL. However, at any tortoise size, the mean egg diameter varied by area ($F = 7.50$; 2, 56 df; $P < 0.001$). Tortoises in the Lochloosa Wildlife Management Area produced eggs approximately 1.75 mm smaller than similar-sized tortoises from other areas. Thus, mean egg diameter was positively related to CL ($t = 5.68$, 56 df, $P < 0.001$, $R^2 = 0.413$) in a regression model allowing mean egg diameters to depend on area: Wolfe's pasture $D = 21.96 + 0.07585$ CL; Roberts Ranch $D = 21.82 + 0.07585$ CL; and Lochloosa Wildlife Management Area $D = 20.14 + 0.07585$ CL.

Table 2. Total radiographs (*n*) and proportion with shelled eggs (%) of mature female gopher tortoises (*Gopherus polyphemus*) by time interval in north-central Florida, 1981–1987. Most females were radiographed only once per year. Twenty-eight observations were multiple X-rays taken in a single year.

Date	*n*	%
Before 12 May	4	25
12–21 May	75	89
22–31 May	42	88
1–10 June	33	85
11–20 June	10	50
After 20 June	8	0

Nesting

Female tortoises nested on 8 June 1982 and 18 June 1986; another female was near an uncovered egg on 15 June 1986. Seven nests were in burrow mounds. The mean depth of five measured nests was 13 cm (range 10–18 cm), and their mean distance from the burrow mouth was 41 cm (range 25–53 cm).

Eggs in each of two nests in the Lochloosa Wildlife Management Area, one in a clear-cutting and one along a road, were uncovered within 1–4 weeks of deposition and subsequently removed by an unidentified predator. On the Roberts Ranch, fox tracks were at a destroyed nest in a sand road. An intact but uncovered nest was in a thick sand–live oak stand on the Roberts Ranch; the eggs were broken or removed within 3 days. Numerous eggshell pieces were in or near burrow mounds on both sites.

Hatchling Production

Hatchlings were in nest cavities on 3 October 1983 (Lochloosa Wildlife Management Area) and on 6 October 1983 (Roberts Ranch). On the earlier date, one hatchling was partially in the shell and another was resting at the burrow entrance. The hatchling in the nest and the remaining eggs were destroyed the following day by an unknown predator.

The estimated minimum production of hatchlings in the Lochloosa Wildlife Management Area, where the number of females and eggs was half of that on the Roberts Ranch, was nearly 3 times as great as on the Roberts Ranch (Table 3). The minimum number of offspring per mature female per year was greater in the Lochloosa Wildlife Management Area ($\bar{x}$ = 1.1 tortoises/female/year) than on the Roberts Ranch ($\bar{x}$ = 0.37 tortoises/female/year).

Discussion

The sizes and ages at sexual maturity of gopher tortoises were within expected geographic and individual variations of previous findings (Table 1). However, tortoises on a southwestern Florida barrier island apparently reached maturity at comparable ages but at larger sizes than tortoises from northern Florida (McLaughlin 1990). Size may not be the sole determinant of sexual maturity in *G. polyphemus* (McLaughlin 1990).

The overall clutch size (5.80) of gopher tortoises was also comparable to charted size in other recent findings (Table 1). Earlier literature references to clutch size in the gopher tortoise were reviewed by Iverson (1980) and included some unsubstantiated high estimates. However, a large female (356-mm CL) on a central Florida site produced an apparent record clutch of 25 eggs (Godley 1989). In a comparison of clutch sizes within and among the four species of *Gopherus* (Judd and Rose 1989), mean clutch size was highest in *G. polyphemus*.

The high annual percentage of gravid females ($\bar{x}$ = 73%) in our study sites may have been site-specific. Of 47 female tortoises radiographed in May and June 1985 in central Florida, 66% were gravid (Godley 1989). No evidence of egg laying during 1 or more years was reported in some

Table 3. Estimated minimum hatchling production in gopher tortoises (*Gopherus polyphemus*) on two north-central Florida study sites.

		Radiographed females		Captures			
Site	Year	No. gravid	No. eggs	Hatchlings	Production estimate (%)[a]	All young of year class[b]	Production estimate (%)[a]
Lochloosa	1982	9	53	4	8	13	25
Wildlife	1983	9	56	1	2	4	7
Management	1984	7	37	4	11	11	30
Area	1985	9	47	7	15	8	17
	$\bar{x}$	8.5	48.3	4.0	9.0	9.0	19.8
Roberts	1982	18	110	3	3	8	7
Ranch	1983	14	76	5	7	7	9
	1984	18	112	0	0	0	0
	1985	13	70	8	11	8	11
	$\bar{x}$	15.8	92.0	4.0	5.3	5.8	6.8

[a] (Number of tortoises captured)/(number of shelled eggs produced).

[b] Year class estimated from plastral annuli.

gopher tortoise colonies where females were not radiographed (Auffenberg and Iverson 1979; Landers et al. 1980). Observations in the field revealed that most (56%) wild female Bolson tortoises (*G. flavomarginatus*) may not lay eggs each year (Adest et al. 1989). Less than half of the female Texas tortoises (*G. berlandieri*) radiographed in 1986 (37.5%) and 1987 (35.7%) did not have eggs (Judd and Rose 1989). In contrast, all but one routinely radiographed female desert tortoise (*G. agassizii*) laid 1 or more clutches in each of 3 consecutive years (Turner et al. 1986).

Our findings and those of previous researchers (Iverson 1980; Landers et al. 1980; Taylor 1982b; Wright 1982) indicate a single annual clutch in *G. polyphemus*. Similarly, no evidence exists to indicate 2 or more annual clutches in *G. berlandieri* (Judd and Rose 1989). However, multiple clutches were reported in *G. agassizii* (Turner et al. 1984, 1986) and *G. flavomarginatus* (Adest et al. 1989).

The clutch size in the gopher tortoise increased with carapace length. In another study in northern Florida, clutch size of the gopher tortoise very nearly significantly ($r = 0.43$, $n = 16$, $P > 0.05$) increased with plastron length—that is, by one egg with each 27-mm increase in length (Iverson 1980). Clutch size also increased with plastron length ($r = 0.68$, $P < 0.01$) in the gopher tortoise in southern Georgia (Landers et al. 1980). At a California site, the sizes of first clutches in 1983 and 1984 but not the sizes of second clutches in 1985 increased with carapace lengths in all desert tortoises (Turner et al. 1986). Clutch size did not increase with carapace length in *G. berlandieri* in southern Texas (Judd and Rose 1989).

We did not specifically address the length of the breeding season but observed burrow cohabitation by a female and 1 or more males from mid-May to mid-November in the Lochloosa Wildlife Management Area. Male courtship behavior was observed in early September and late October (Diemer, unpublished data) and coincided with fall spermatogenesis (Taylor 1982b). Males visited burrows of females from 2 March to 1 November on a southern Florida study site (Douglass 1990). In southwestern Georgia, females were receptive to males only during spring, but males remained sexually active through fall (Landers et al. 1980). If successful copulation does occur in some parts of the species' range in fall, the reasons are unclear. Sperm were in the endometrial glands of tortoise oviducts throughout the reproductive cycle (Palmer and Guillette 1988). Sperm could possibly be carried over winter until the spring nesting season, but whether these sperm are used for fertilization is not known (Palmer and Guillette 1988).

Mid-May to mid-June is the prime nesting period in gopher tortoises (Iverson 1980; Landers et al. 1980). Nesting occurred from late May through late June in South Carolina (Wright 1982). However, the discovery in northern Florida of several females with oviductal eggs in April and one female with well-calcified oviductal eggs on 26 March suggested an earlier start of the main portion of the nesting season (Taylor 1982b). April through May was the primary nesting season of tortoises on a southwestern Florida barrier island (McLaughlin 1990). Ovarian regression follows nesting in the summer months, and vitellogenesis resumes in fall (Iverson 1980; Landers et al. 1980; Taylor 1982b).

Nests were also located away from gopher tortoise burrows in southwestern Georgia (Landers et al. 1980). However, most (85% of 110 nests) were in or near burrow mounds, and the eggs were 15–25 cm below the soil surface. The mean distance from the burrow entrance was 18 cm ($n = 93$). Two clutches in north-central Florida were in burrow mounds approximately 15 cm below the surface (Arata 1958). Seventy-four percent of the nests in a South Carolina study were in the female's burrow mound close ($\bar{x} = 16$ cm) to the entrance (Wright 1982). Nine percent were in abandoned burrow mounds, but the other 17% were in sand near ($\bar{x} = 11$ m) a burrow mound. Eggs were at depths of about 10 cm, estimated from several observations of nesting females. Eggs in a nest in Louisiana were 12-cm deep in a burrow mound and 25 cm from the burrow entrance (Martin 1989).

Nest-depredation rates were 89% ($n = 38$) in southwestern Georgia (Landers et al. 1980) and 74% ($n = 23$) in South Carolina (Wright 1982). Seventy-one percent ($n = 7$) of the nests were depredated on one southwestern Alabama site, but none ($n = 4$) was destroyed on another site (Marshall 1987). Raccoons (*Procyon lotor*) destroyed most nests in southwestern Georgia (Landers et al. 1980), whereas armadillos (*Dasypus novemcinctus*) were the primary predators of eggs in southwestern Alabama (Marshall 1987) and south-central Florida (Douglass and Winegarner 1977). Nests were depredated by raccoons and opossums (*Didelphis virginianus*) in South Carolina, but dog (*Canis familiaris*) prints were also around one freshly destroyed nest (Wright 1982). Striped skunks (*Mephitis mephitis*) and gray foxes (*Urocyon cinereoargenteus*) are also predators of eggs (Hallinan 1923; Douglass and Winegarner 1977; Landers et al. 1980).

On several occasions, eggs of gopher tortoises were uncovered but not immediately destroyed or carried away. Predators infrequently (8% of depredated nests) destroyed only part of a clutch in southwestern Georgia (Landers et al. 1980). All eggs were usually destroyed when a nest was uncovered on a South Carolina study site (Wright 1982).

The destruction of nests precluded our determination of incubation periods. The incubation period of gopher tortoises is 80–90 days in northern Florida (Iverson 1980), 102 days in southwestern Georgia (Landers et al. 1980), and 110 days in South Carolina (Wright 1982). Clutches from captive tortoises in northern Florida hatched from mid-August through September (Iverson 1980).

Hatching occurred from 29 August to 9 October in southwestern Georgia (Landers et al. 1980). The hatching process was described by Arata (1958).

Partially or entirely unhatched clutches were occasionally found by others (Arata 1958; Iverson 1980; Wright 1982; Marshall 1987). Only 14% of 179 protected and closely monitored eggs in southwestern Georgia failed to hatch (Landers et al. 1980). In Mississippi, most of the five or six eggs in each nest ($n = 40$) hatched (Brode 1959). However, 50% of the hatchlings were unable to escape the characteristic hard-packed overburden of the Mississippi clay hills and subsequently died in the nest.

Hatchling gopher tortoises may immediately excavate burrows, enlarge insect or rodent holes, or temporarily use larger tortoise burrows or shelter under vegetation or litter (Douglass 1978; Wright 1982; Diemer, unpublished data). A hatchling gopher tortoise in Alabama used an egg chamber for a burrow (Marshall 1987).

Hatchling and juvenile gopher tortoises are extremely vulnerable to depredation by a variety of mammalian, avian, and reptilian predators (Douglass and Winegarner 1977; Fitzpatrick and Woolfenden 1978; Maehr and DeFazio 1985; Diemer 1987a; Layne 1989). Hatchlings have also been injured or killed from fire ant (*Solenopsis saevissima*) bites (Landers et al. 1980).

The estimated minimum production of hatchlings was probably biased by female and juvenile moves on or off the study sites. Undoubtedly, not all juveniles were captured. The estimated lower mean minimum hatchling production on the Roberts Ranch could be attributed either to difficulty in detecting small burrows in the thick ground cover or to higher depredation rates in the area. Factors of underestimated productivity are the emigration of ovipositing females and the cryptic appearance of juveniles. Conversely, overestimation would result from juvenile immigration and eggs laid by females that were not captured.

Depredation rates of eggs and hatchlings vary among sites and years but are generally high and severely depress recruitment. The depredation of gopher tortoise hatchlings was 70% during the first year and 41% during the second year of a study in South Carolina (Wright 1982).

In northern Florida, the recruitment potential, measured by burrow counts, may be reduced by about 94% from the time of egg laying through the first year (Alford 1980). The estimated minimum hatchling production in southwestern Georgia was about 0.58 hatchlings/female/year (Landers et al. 1980). In all four species of North American tortoises, apparent low recruitment is confounded by the cryptic appearances, small sizes, and possibly reduced surface activities of the juveniles (Douglass 1978; Schneider 1980; Shields 1980; Judd and Rose 1983; Turner et al. 1985; Adest et al. 1989; Corn 1994; Diemer, unpublished data). Yet, high hatchling mortality of Bolson tortoises was indicated in a study isolating problems from cryptic appearance (Adest et al. 1989).

We found that most variables of reproduction in gopher tortoises were quite similar among three north-central Florida sites with dissimilar habitats. Our findings were also comparable to those of previous researchers. However, we emphasize the substantial geographic and individual variation in this species. A data base should be constructed by gathering information on reproduction during several years at other Florida sites—for instance, information on tortoise reproduction on Florida's southern coasts is minimal. Future investigation topics should include annual and geographic variations in nest depredation rates and hatchling survival, viable sperm storage, and multiple clutch frequency. The intervals between copulation, fertilization, and egg shelling remain unclear. Information is also needed on the reproductive status of seemingly isolated females in extremely low-density or fragmented habitats; past intensive human depredation in the Florida panhandle and ongoing rampant urbanization in the peninsula left no shortage of appropriate study sites.

Acknowledgments

Appreciation is extended to the Nekoosa Packaging Corporation, Owens-Illinois, I. Roberts, and J. Wolfe on whose lands this study was conducted. R. Burke, C. Nelms, R. Stratton, and K. Williams provided field assistance. C. Abercrombie and J. Hamblen assisted in data analysis. The manuscript was reviewed by P. Moler and typed by T. Steele. Funding for this study was provided by the Florida Game and Fresh Water Fish Commission.

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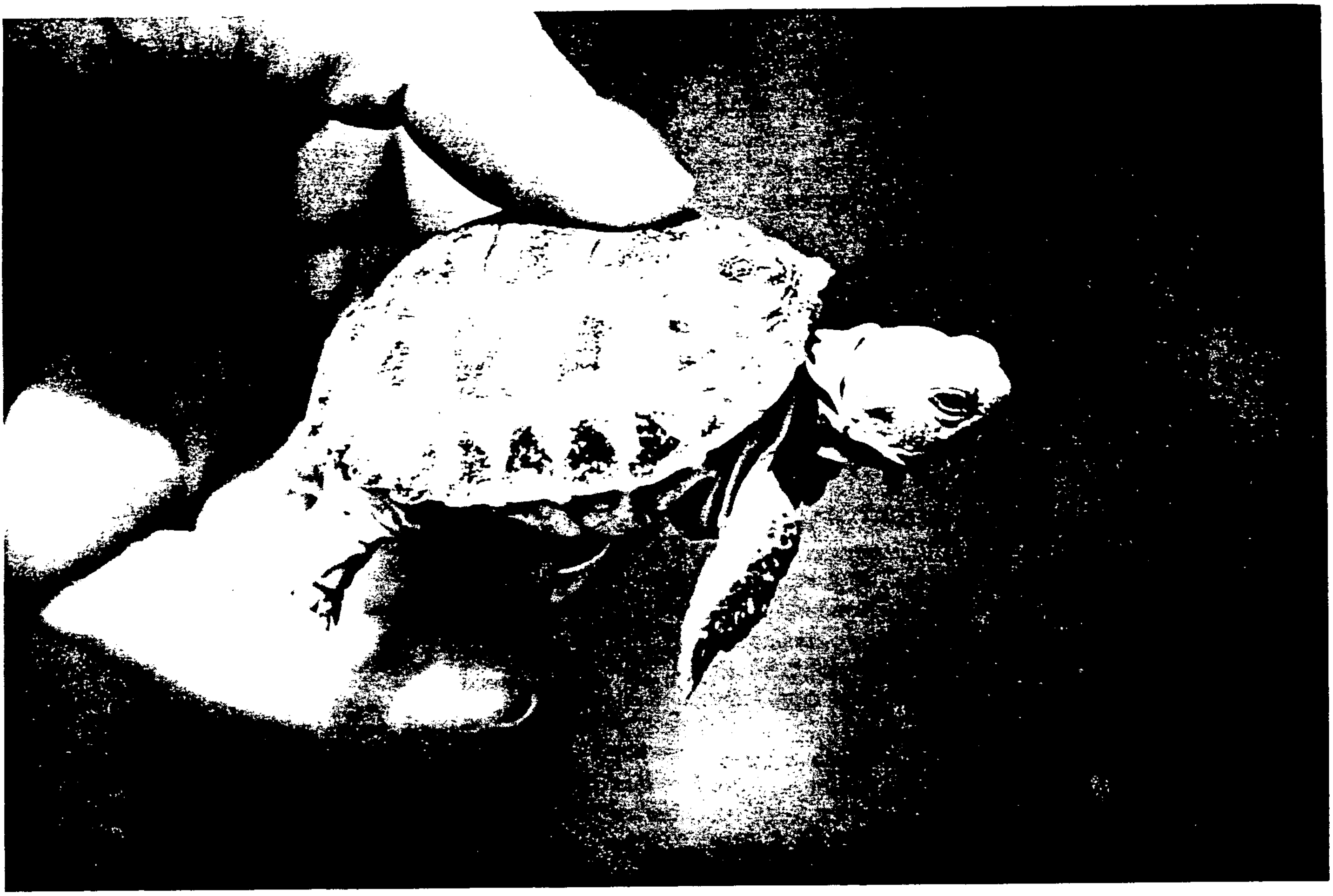

Hatchling Bolson tortoise (*Gopherus flavomarginatus*) that has been raised at an outdoor facility of the Mapimi Field Station, Mexico.

Microhabitats and Use of Burrows of Bolson Tortoise Hatchlings

by

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Abstract. The use of microhabitat and burrows of 10 free-ranging Bolson tortoise (*Gopherus flavomarginatus*) hatchlings was studied by radiotelemetry during the hot rainy season of 1986 and the warm dry season of 1987. Tortoises were under vegetation most of the time in each season (rainy season 85.3%; dry season 97.9%). Each tortoise excavated multiple burrow and pallet sites during the rainy season and moved between sites rather quickly. In contrast, each tortoise occupied only one burrow throughout the dry season. Regardless of season, tortoises preferred to excavate or opportunistically inhabit burrows under prickly pear cactus (*Opuntia rastrera*).

Key words: Burrow use, Chihuahuan Desert, *Gopherus flavomarginatus*, hatchlings, seasonal behavior, vegetation as cover.

Gopherus and other chelonians of different age and sex may differ in their physical size and strength (McRae et al. 1981; Pluto and Bellis 1986), thermal biology (Boyer 1965; Hutchinson et al. 1966; Rose and Judd 1982), water balance (Ernst 1972; Nagy and Medica 1986), and diet (Gibson and Hamilton 1983; Appleton 1986; Bury 1986; Macdonald and Mushinsky 1988). Consequently, conspecifics sometimes differ ecologically and behaviorally. For example, Bolson tortoise (*Gopherus flavomarginatus)* hatchlings have higher mortality rates and eat a higher protein diet than older conspecifics and prefer forbs over grass (Janulaw 1978; Appleton 1986; Adest et al. 1989a; Morafka 1994). The activity patterns, home range sizes, and preferred microhabitats of chelonians may vary with age and sex (Rose and Judd 1975; Douglass and Layne 1978; McRae et al. 1981; Aguirre et al. 1984; Stubbs and Swingland 1985; Berry and Turner 1986; Ernst 1986).

These findings suggest that management to prevent the extinction of *G. flavomarginatus* should address the ecological requirements of each age class. However, most information on hatchlings is based on captive individuals. Our understanding of the natural behavior and ecology of *G. flavomarginatus* and other *Gopherus* hatchlings is minimal because hatchlings are rarely encountered in the field (Aguirre et al. 1979; Alford 1980; Morafka 1982; Reyes Osorio and Bury 1982; Judd and Rose 1983; Berry and Turner 1986; Adest et al. 1989b).

I examined the microhabitat and burrow use of free-ranging *G. flavomarginatus* hatchlings in their native environment. Information on these two aspects may clarify why few hatchlings are observed in the field.

Methods and Materials

The study site was in the Mapimi Biosphere Reserve (26° 29′–26° 52′ N latitude and 103° 32′–103° 58′ W longitude) about 1 km northeast of the

Laboratorio del Desierto field station in Durango, Mexico. The vegetation is a patchy distribution of thornscrub grassland on a 2–3% grade. Dominant and important plant species were creosotebush (*Larrea tridentata*), prickly pear cactus (*Opuntia* sp.), mesquite (*Prosopis* sp.), tarbush (*Flourensia cernua*), tobosa grass (*Hilaria mutica*), mallow (*Sphaeralcea angustifolia*), and grama grass (*Bouteloua* sp.; Martinez and Morello 1977; Morafka et al. 1981).

I obtained 10 *Gopherus flavomarginatus* hatchlings from eggs incubated in a passive solar incubator at the field station (Adest et al. 1989a). The eggs had been collected from wild females brought to the field station. I randomly selected the hatchlings from six different clutches and assigned them individual codes by clutch. The codes were either written on or tagged onto the plastron and coated with a thin layer of epoxy for protection.

I fitted each tortoise with a transmitter of a distinct frequency (model SM1, AVM Instrument Co.) for radiotelemetric observation in the field. I used epoxy to affix the transmitter to the posterior surface of the carapace to minimize its extension beyond the tortoise's natural outline and shortened the transmitter's antenna so that it did not extend beyond the carapace. The mean transmitter package weight was 3.9 g (range 3.6–4.3 g) and the mean weight of the package was 9% (range 7–11%) of the tortoises' body weights. The transmitter's battery was changed about every 4–6 weeks or at the first sign of failure. I tracked the tortoises with a Telonics TR-2 receiver and RA-1A bidirectional antenna by the peak–null method (Cochran and Lord 1963). The maximum tracking range was about 30 m.

I released the tortoises in the study site 9–25 days after hatching ($\bar{x}$ = 17 days) during the hot rainy season of 1986 when the animals would have naturally hatched in the wild. The exact point of release was determined by two random numbers assigned to each tortoise. The random numbers represented imaginary X- and Y-coordinates in reference to one of four poles placed in a 85.9- × 154.3-m rectangular configuration on the study site. The poles delineated only the area in which the tortoises were released; the area of observation varied with the moves of individual tortoises.

I observed the tortoises during a portion of each of the hot rainy season of 1986 (26 August–15 October) and the warm dry season of 1987 (9 May–30 June). I randomly selected three to five tortoises for sampling each day. I observed each animal in this subgroup for about 5 min/h for 4–10 consecutive hours on 3 to 4 consecutive days before changing the individuals in the subgroup. The remaining tortoises were located at least once each day. I made daytime radiotelemetric and visual observations of the tortoises primarily between 0800 and 1700 h and placed toothpicks or sticks at burrow and pallet entrances to detect nighttime activity. I followed 10 tortoises in the rainy season for 5,196 min and 4 tortoises in the dry season for 7,193 min. The number of tortoises I observed during each season and between seasons varied because some tortoises died or could not be relocated. The study periods of individual tortoises ranged from 12 to 51 days ($\bar{x}$ = 38.8 days, SD = 16.2) in the rainy season and from 40 to 53 days ($\bar{x}$ = 49.7 days, SD = 6.5) in the dry season.

I recorded the amount of time (min) the tortoises inhabited each microhabitat and plant species. Microhabitats were defined as open (i.e., relatively unvegetated substrate except for scattered annuals or perennial shoots), grass, cactus, shrub, and miscellaneous (i.e., *Agave* spp. and *Jatropha* spp.). I used the Wilcoxon paired-sample test ($P < 0.05$) to determine if the tortoises spent equal amounts of time in open and vegetated areas during and between seasons. I used Friedman's test and a multiple range test to determine if there were significant differences ($P < 0.05$) between the percentages of time the tortoises inhabited each microhabitat and plant species within each season.

I classified shelters of the tortoises as burrows (i.e., the tortoise was completely covered by soil) or pallets (i.e., the tortoise was not completely covered) and as excavated or preexisting. I also recorded the location of each shelter by microhabitat and plant species. I calculated the mean and standard deviation of the number of burrows and pallets per tortoise, burrow length, the number of days before tortoises occupied their first shelter, the duration (days) burrows and pallets were occupied, and the transition time (days) between shelters. I used the Wilcoxon paired-sample test to determine if the tortoises occupied burrows and pallets for an equal number of days ($P < 0.05$) and Friedman's test, a multiple range test, and chi-square to determine if shelters were equally or preferentially distributed among the different microhabitats or plant species ($P < 0.05$). For the chi-square analysis, I only included shelters in cactus and shrub species because expected values were derived from the relative frequencies reported of sclerophyll vegetation sampled 6.5 km northwest of the Laboratorio del Desierto (Morafka et al. 1981).

Results

Use of Microhabitats

The hatchlings of *Gopherus flavomarginatus* were under vegetation significantly more often than in open areas during the rainy season of 1986 (85.3 vs. 14.7%) and during the dry season of 1987 (97.9 vs. 2.1%) and spent similar amounts of time under vegetation in both seasons. Although the tortoises spent about twice as much time under cactus than the next most-occupied microhabitat (shrub) during the rainy season and about one-sixth less time in the next most-occupied microhabitat (open) during the dry season (Table 1), there was no significant difference between the percentage of time the tortoises inhabited the cactus microhabitat and the next most-occupied microhabitat (Q = 1.1 in 1986, 1.94 in 1987; $P > 0.05$).

Significant differences were only between the miscellaneous microhabitat and other microhabitat types during the rainy season (Q = 4.3–5.7, $P < 0.05$) and between cactus and the shrub (Q = 3.29, $P < 0.05$) and grass (Q = 4.07, $P < 0.05$) microhabitats during the dry season.

The tortoises inhabited 10 different plant species among the four vegetated microhabitats during the rainy season and six different plant species among the three vegetated microhabitats during the dry season (Table 1). Only four of the 12 plant species were used in common during both periods. Although the tortoises were present under *Opuntia rastrera* about twice as much than under *Prosopis glandulosa* and about 6 times more than under *Hilaria mutica* during the rainy season, differences were not significant between the percentages of time spent in these three most inhabited plant species of the season (Q = 0.67 and 2.05, $P > 0.05$). However, tortoises were significantly more often under *O. rastrera* than under the other seven plant species during the rainy season (Q = 3.57–5.91, $P < 0.05$) and all other plants species in the dry season (Q = 2.78–4.17, $P < 0.05$).

Table 1. Microhabitat use by Bolson tortoises (*Gopherus flavomarginatus*) during the rainy season of 1986 and during the dry season of 1987 at the Mapimi Biosphere Reserve, Durango, Mexico. Numbers represent the percentage of observations that tortoise hatchlings were associated with a given microhabitat or plant species.

Microhabitat/ species	Study period 1986	1987	1986–87
Cactus			
Opuntia rastrera	51.1	77.5	66.0
Ferrocactus sp.	0.0	0.3	0.2
Subtotal	51.1	77.8	66.2
Shrub			
Prosopis glandulosa	19.0	0.3	8.4
Larrea sp.	2.2	0.4	1.2
Ziziphus obtusifolia	0.7	0.0	0.3
Lycium berlandieri	0.4	0.0	0.2
Flourensia cernua	0.4	0.0	0.2
Unidentified shrub	0.6	0.0	0.2
Subtotal	23.3	0.7	10.5
Grass			
Hilaria mutica	9.7	7.9	8.7
Unidentified grass	0.0	1.5	0.9
Subtotal	9.7	9.4	9.6
Miscellaneous			
Agave sp.	0.8	0.0	0.4
Jatropha dioica	0.3	0.0	0.1
Subtotal	1.1	0.0	0.5
Open	14.7	12.1	13.2

Use of Burrows

Soon after their release onto the study site, most of the tortoises regularly occupied burrows or pallets ($\bar{x}$ = 2.3 days, SD = 1.3, range 1–5 days). Four tortoises used burrows and five tortoises used pallets as their initial underground shelters. One tortoise used neither a burrow nor a pallet but remained aboveground under vegetation during 13 nights and in the open for 1 night.

In the rainy season of 1986, 10 tortoises occupied a total of 21 burrows and 14 pallets (Table 2). Twelve burrows were excavated, 8 were preexisting, and 1 was of unknown origin; 9 pallets were

Table 2. Comparison of the number of burrows and pallets occupied by Bolson tortoises (*Gopherus flavomarginatus*) at the Mapimi Biosphere Reserve, Durango, Mexico. Observations were in the rainy-season study period of 1986.

Tortoise	Burrows	Pallets
Complete observations[a]		
149-8	2	2
152-7	2	3
152-8	1	1
204-4	1	5
A-1	4	0
X-3	3	1
Subtotal	13	12
Partial observations[b]		
152-12	2	1
154-5	5	0
204-1	1	1
X-1	0	0
Subtotal	8	2
Total	21	14

[a] Tortoises observed throughout the study period.

[b] Tortoises that died or disappeared during the study period.

excavated, 2 were preexisting, and 3 were of unknown origin. Excavated burrows were either established by one bout of burrowing behavior (e.g., about 2–3 h) or were modified pallets. Opportunistic use of four small rodent burrows as preexisting shelters also was observed. Two of these were abandoned woodrat (*Neotoma* sp.) burrows. The remaining six preexisting shelters were hollows or depressions formed by irregularities in the substrate or where the vegetation entered the ground. Burrow lengths ranged from 6.0 to 19.0 cm ($\bar{x}$ = 14.2 cm, SD= 6.9, n = 11).

A significantly greater number of shelters (burrows and pallets) were in the cactus and shrub microhabitats than in the grass microhabitat. Hatchlings did not use any shelters in the open or miscellaneous microhabitats. Among the plant species of each microhabitat, most shelters were under *O. rastrera* and *P. glandulosa* (Table 3). However, the tortoises preferred to excavate burrows significantly more often under *O. rastrera* (83.3% of self-excavated burrows) than under *P. glandulosa* (16.7% of self-excavated burrows). Irrespective of origin, the tortoises preferred to inhabit burrows that were under *O. rastrera* (66.6% of burrows; $P < 0.0001$) and pallets that were under *P. glandulosa* (42.9% of pallets; Table 3).

The tortoises typically used more than one shelter during the study (Table 2). The six tortoises observed throughout the 1986 study period occupied 13 burrows and 12 pallets ($\bar{x}$ = 2.2 burrows and 2.0 pallets/tortoise). The tortoises changed burrows and pallets 19 times during the rainy season. The time between occupying shelters was relatively short, averaging 4.1 days (SD = 2.5; Table 4).

In general, the tortoises occupied burrows significantly longer than pallets (Table 5). The six tortoises observed throughout the rainy season were in burrows for an average of 14.4 days (SD = 14.1) and in pallets an average of 2.3 days (SD = 2.4). The tortoises were in 11 of the 12 pallets

Table 3. The microhabitat distribution of burrows and pallets of all Bolson tortoises (*Gopherus flavomarginatus*) at the Mapimi Biosphere Reserve, Durango, Mexico. Observations were in the rainy-season study period of 1986.

	Burrows		Pallets		Burrows and pallets	
Location	*n*	%	*n*	%	*n*	%
Opuntia	14	66.6	3	21.4	17	48.6
Prosopis	3	14.3	6	42.9	9	25.7
Hilaria	1	4.8	2	14.3	3	8.6
Ziziphus	0	0.0	2	14.3	2	5.7
Larrea	1	4.8	1	7.1	2	5.7
Open	2	9.5	0	0.0	2	5.7
Total	21	100.0	14	100.0	35	100.0

Table 4. The number of relocations to different burrow or pallet sites within a specific time span (days) by Bolson tortoises (*Gopherus flavomarginatus*) observed throughout the rainy-season study period of 1986 at the Mapimi Biosphere Reserve, Durango, Mexico.

Number of days to effect change	Relocations		Cumulative percent of relocations
	n	%	
1	1	5.3	5.3
2	7	36.8	42.1
3	1	5.3	47.4
4	3	15.8	63.2
5	3	15.8	79.0
6	0	0.0	79.0
7	1	5.3	84.3
8	1	5.3	89.6
9	2	10.4	100.0

Table 5. The duration (days) of burrow and pallet occupancy by tortoises (*Gopherus flavomarginatus*) observed throughout the 1986 rainy-season study period at the Mapimi Biosphere Reserve, Durango, Mexico.

Days of occupancy	Number occupied	
	Burrows	Pallets
1	2	7
2	2	2
3	0	1
5	1	1
7	1	0
8	1	0
9	0	1
12	1	0
17	1	0
24	1	0
34	2	0
40	1	0

for 5 or fewer days (range 1–9 days) and in 8 of the 13 burrows for longer than 5 days (range 1–40 days).

In the dry season, 4 tortoises did not change burrow or pallet sites. The tortoises remained in the same burrow in which they were found on the first day of the dry season ($\bar{x} = 49.7$ days, SD = 6.5). Only one tortoise was in a burrow it previously had occupied in the rainy season of 1986. All four burrows were under *O. rastrera*.

Discussion

Microhabitat use by *Gopherus flavomarginatus* hatchlings is primarily determined by the location of burrow sites. Secondary factors are foraging sites and areas traversed while changing burrows. Differences in microhabitat use between the hot rainy season and warm dry season may be due to ontogenetic changes or seasonal variation. Seasonal differences may be behavioral, physiological, or resource-driven (Gourley 1972; Rose and Judd 1975; Burge 1977; Douglas and Layne 1978; McRae et al. 1981; Gibson and Hamilton 1983; Nagy and Medica 1986; Adest et al. 1989a).

Like adult conspecifics (Morafka et al. 1981; Morafka 1982; Aguirre et al. 1984), hatchlings are more active during the hot rainy season (Tom 1988). Therefore, seasonal differences in microhabitat use may simply be caused by the greater activity and mobility of the tortoises during the rainy season. Hatchlings and adults are away from burrow sites longer and travel across more terrain in the rainy season.

Hatchlings that just emerged from the nest may be more nomadic because they search for a suitable burrow site. I found that hatchlings changed burrows frequently during the rainy season but did not change burrows during the second, drier period. Therefore, site fidelity may increase with age. However, *G. flavomarginatus* hatchlings have not been followed in subsequent years of life, and I do not know to what extent age or seasonal variation affects microhabitat or burrow use.

The burrows of most *G. flavomarginatus* adults and hatchlings are under vegetation (Aguirre et al. 1979). Most burrows of adults, however, are at the base of *Prosopis* and *Larrea*, whereas burrows of hatchlings are primarily at the base of *Opuntia*. This difference may reflect differences in the thermal biology, water balance, physical strength, and susceptibility to predation between *G. flavomarginatus* adults and hatchlings.

Smaller chelonians heat and cool more rapidly and have a higher rate of cutaneous water loss relative to their body mass than larger chelonians

(Boyer 1965; Ernst 1972; Rose and Judd 1982; Morafka 1994). Smaller chelonians are also physically weaker and morphologically more susceptible to predation. The shells of young *Gopherus* remain relatively soft for 5–10 years, which renders them more vulnerable to predation than hard-shelled adults (Luckenbach 1982; Appleton 1986; Adest et al. 1989b).

Microhabitat differences between juvenile and subadult–adult sizes of map turtles (*Gratemys geographica*) may be attributable to differences in their physical strengths (Pluto and Bellis 1986). Juvenile *G. geographica* had slower swim rates and therefore were restricted to shallower portions of the habitat where water currents were slower. Analogously, smaller *Gopherus* may be physically incapable of excavating some soils used by adults. Thus, differences in microclimate, substrate composition or compactness, and protection associated with different plant species may determine where tortoises of different sizes (ages) establish burrows.

The use of *Opuntia* as a primary burrow site by *G. flavomarginatus* hatchlings may be related to microclimate. Chelonians may seek microenvironments that help regulate physiological processes such as body temperature and water loss. Light intensity apparently is one of the most important physical factors determining the body temperatures of basking slider turtles (*Trachemys, Pseudemys*; Boyer 1965).

Vegetation acts as insulation for tortoises and therefore moderates fluctuations in microclimate (Judd and Rose 1977). Shade provided by plants may enable inactive *G. berlandieri* and *G. flavomarginatus* to maintain body temperatures significantly lower than temperatures of exposed substrate when ambient temperatures are high (Judd and Rose 1977; Aguirre et al. 1979). Similarly, the distribution of burrows of *G. agassizii* correlates more highly with the shading properties of shrub species than with the availability or density of shrubs on a site (Burge 1978). I also found a significantly greater than expected number of burrows of *G. flavomarginatus* hatchlings under cacti (*Opuntia* sp.), suggesting that *Opuntia* may provide a more favorable microclimate for hatchlings than other plant species.

Tortoise hatchlings may construct burrows because of the equitable microclimatic conditions that burrows provide. In general, a thermal gradient exists along the length of the burrow, and temperatures are more stable farther into the burrow; the profile of the gradient in winter is reversed in summer (Woodbury and Hardy 1948; Morafka 1982). Burrows provide the coolest temperatures during the day and the warmest temperatures at night (McGinnis and Voigt 1971; Douglass and Layne 1978).

Besides microclimatic and physiological considerations, *G. flavomarginatus* hatchlings may excavate burrows under *Opuntia* because cacti protect hatchlings from predators better than other vegetation types. *Opuntia* may conceal hatchlings and their burrows more effectively than shrubs because some of the cactus pads grow near to the substrate and form semienclosed compartments. The cactus spines also may thwart or hinder potential predators from approaching the burrows. Furthermore, *G. flavomarginatus* hatchlings seem to prefer burrows over pallets because burrows were occupied longer than pallets. Burrows may offer greater protection from predators because burrows, by definition, completely cover the length of a tortoise. In Texas, disturbed *G. berlandieri* move into brush and *Opuntia* patches instead of pallets (Rose and Judd 1982).

Young *G. flavomarginatus* may be difficult to locate in the field because the recruitment of hatchlings into the population is low. Reproduction of *G. flavomarginatus* is reduced by the low proportion of reproducing adult females in any year, high nest predation, nonviable eggs (Adest et al.1989a), and high hatchling mortality (Janulaw 1978). High nest predation and high hatchling mortality also were reported of other chelonians (Swingland and Coe 1979; Christiansen and Gallaway 1984; Stubbs and Swingland 1985; Ernst 1986; Christens and Bider 1987; Congdon et al. 1987; Diemer and Moore 1994).

In this study, only 4 of the 10 *G. flavomarginatus* hatchlings were still alive at the end of 11 months; 4 dead tortoises were found, and another 2 were presumed dead based on indirect evidence of predation (the burrow of 1 tortoise had been destroyed and the transmitter of the other was recovered). An eleventh tortoise that was not included in the data analysis was severely injured by a predator on the third day after its release and later died in the laboratory.

The small size and cryptic coloration of young *Gopherus* and their shelters also make them difficult to see in the field. Even when a tortoise was radio-tracked to a specific area, I sometimes had difficulty seeing the tortoise when it or its burrow or pallet were under vegetation. Several times I did not see a radio-tracked tortoise in an open area until after it moved because it cryptically matched the soil surface.

Like young *Gopherus polyphemus* (Douglas 1978; Diemer and Moore 1994), *G. flavomarginatus* hatchlings can sometimes occupy preexisting burrows constructed by other species. Thus, besides probable low survivorship of young, *G. flavomarginatus* hatchlings (and their burrows) may be difficult to locate in the field because they stay mostly under vegetation and are small and cryptically colored.

Acknowledgments

Special thanks are extended to G. Adest, G. Aguirre, D. Morafka, and the Instituto de Ecologia, Mexico City, Mexico, for the resources and financial support that made this project possible. I am grateful to M. Recht for instruction in radiotelemetric technique. Others who provided assistance include W. Alley, A. Muchlinski, D. Soltz, and V. Vance. I also thank R. Gonzalez, J. Herrera, A. Rojas, and the other biologists I met at the Laboratorio del Desierto, Durango, Mexico, for their friendship and support.

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Home Range, Activity, and Use of Burrows of Juvenile Gopher Tortoises in Central Florida

by

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Abstract. Juvenile *Gopherus polyphemus* (1–4 years old) were tested for seasonal differences in their activities, moves, home range sizes, and uses of burrows in an upland sandhill community. Tracking with radiotelemetry revealed the tortoises were inactive for 90% of their time. Most activity was in spring. Tortoises spent more time basking on burrow mounds in winter than in other seasons. Daily activity patterns varied among seasons. In fall and winter, tortoises were more active early in the day, and in spring and summer they were more active late in the day. The numbers of moves of juvenile tortoises were greater in summer than in fall, winter, or spring, but the moved distances did not differ among seasons. Home range sizes were smaller than those of adult gopher tortoises and significantly larger in summer than in any other season. Juvenile tortoises used several burrows during the year but spent most of their time in one burrow. Most of the observed behaviors may be responses of juvenile tortoises to either high predation pressure or to high temperatures.

Key words: Activity patterns, burrow use, Florida, *Gopherus polyphemus*, juvenile ecology, movements, tortoise.

Gopher tortoises (*Gopherus polyphemus*) are large, herbivorous reptiles indigenous to the southeastern coastal plain from South Carolina to Louisiana (Auffenberg and Franz 1982). Many populations inhabit xeric environments with well drained sandy soils and herbaceous ground cover. Most previous studies of activities, patterns of moves, home range sizes, and uses of burrows concentrated on adult tortoises (Douglass 1976; McRae et al. 1981a, 1981b; Wright 1982), but Diemer (1992) includes new information on home range sizes of juveniles. Juvenile tortoises (1–4 years old) resemble adults in general morphology; however, the shells of juveniles are soft (Allen and Neill 1953), which makes them vulnerable to a wide range of predators (Diemer 1986; Diemer and Moore 1994; Morafka 1994).

A major portion of a gopher tortoise's life is spent underground. Large, shovellike forelimbs enable this reptile to excavate deep burrows that provide refuge from predators and temperature extremes (Ernst and Barbour 1972). High humidity in a burrow may offer protection from desiccation (Auffenberg and Weaver 1969; Means 1982). During their lifetimes, most gopher tortoises use several burrows (Auffenberg and Franz 1982), which serve as focal points of their daily activities (McRae et al. 1981b). Burrows of juvenile tortoises are similar in appearance to those of adults but smaller. Studies of the use of burrows by juvenile tortoises are few (McRae et al. 1981b; Diemer 1992), and the use of burrows has not been quantified in the extreme southern parts of the range of the gopher tortoise.

Terrestrial turtles, including tortoises, generally have well defined areas of activity (home ranges; Cagle 1944; Woodbury and Hardy 1948; Stickle 1950; Legler 1960). Size estimates of home ranges of adults of all species of North American tortoises are available (Rose and Judd 1975; Douglass 1976; Burge 1977; Auffenberg and Iverson 1979; McRae et al. 1981b; Wright 1982; Judd and Rose 1983; Aguirre et al. 1984; Berry 1986).

The sizes of home ranges of adult gopher tortoises vary seasonally as a function of social interactions among adults (McRae et al. 1981b). Auffenberg and Iverson (1979) distinguish two kinds of home ranges of a gopher tortoise: a feeding home range—an area in which a tortoise feeds; and an annual home range—an area that includes both social and feeding components.

Most estimates of home range sizes of juvenile gopher tortoises were obtained by captures of individuals along roads and by casual observations in the field (McRae et al. 1981b). The first studies of radio-tagged juveniles were of gopher tortoises in northern Florida (Diemer 1992) and of Bolson tortoises in north-central Mexico (Tom 1994).

In general, the activities of terrestrial turtles in temperate areas peak in spring and dwindle in summer and have a minor peak in fall (Auffenberg and Iverson 1979). In adult gopher tortoises in Florida, this pattern coincides with reproduction activities such as mate searching and territorial behavior. Yearly activity patterns of the gopher tortoise in northern parts of its range are affected by periods of dormancy influenced by temperature fluctuations (Auffenberg and Iverson 1979). In Florida, gopher tortoises may be active all year, but activities vary among seasons and age classes (Douglass and Layne 1978; Diemer and Moore 1994).

Diel activity patterns of tortoises are affected by temperature and moisture conditions in a season (Auffenberg and Iverson 1979). Auffenberg and Iverson (1979) report that many species of tortoises show a unimodal distribution of activity in cooler months (the mode during the hottest part of day) and a bimodal distribution in hotter months (the modes before and after the hottest part of the day). McRae et al. (1981b) observed this pattern of activity in a Georgia population of gopher tortoises. They found daily activity peaked during the hottest part of the day, except in late summer when daily activity was bimodal. During an 8-year period in southern Florida, however, daily activities of gopher tortoises along roads and fire lanes were unimodal throughout the year (Douglass and Layne 1978). These activity patterns are mostly of adult gopher tortoises.

Few observations of activity patterns of juvenile tortoises are available because juveniles are not likely to be noticed by casual observation. Juvenile gopher tortoises are small and secretive and do not tend to wander far from their burrows (Diemer 1992). Few captures and difficulties in locating small burrows have limited studies of juvenile gopher tortoises. However, unlike a mark–recapture study, radiotelemetry allows location of more individuals at specific times of day.

Our goal was to record the activities, patterns of moves, home range sizes, and uses of burrows of juvenile gopher tortoises in central Florida by monitoring radio-tagged individuals for 1 year. Such information may guide conservation measures and provide information on the vulnerability of juveniles of this threatened species. Specifically, we addressed seasonal differences in activities, patterns of moves, home range sizes, and uses of burrows by juvenile gopher tortoises.

Materials and Methods

Study Site

We studied juvenile tortoises from October 1988 through September 1989 on the 200-ha Ecological Research Area of the University of South Florida in Hillsborough County, west-central Florida (28° 05′ N, 82° 20′ W). We monitored tortoises in an 11-ha section of xeric upland, consisting of well-drained, yellowish sands (Lakeland series) on a limestone base (Laessle 1958). The ground vegetation was composed of grasses (*Aristida stricta* and *Andropogon* spp.) and a variety of herbs (e.g., *Pityopsis graminifolia*, *Liatris gracilis*, and *Baptisia lecontei*). Saw palmetto (*Serenoa repens*) was the predominant shrub. The canopy vegetation was dominated by longleaf pine (*Pinus palustris*), slash pine (*P. elliottii*), turkey oak (*Quercus laevis*), and sand live oak (*Q. geminata*). Detailed descriptions of the area are in

Williamson and Black (1981) and Mushinsky (1985).

Age and Size Classes

One- to 8-year-old gopher tortoises often are classified as juveniles (McRae et al. 1981b). We classified 1- to 4-year-old tortoises as juveniles because the carapace and plastron are soft from hatching to approximately 4 years of age but begin to harden at 5 to 6 years of age (Landers et al. 1982; Diemer and Moore 1994). In our study, juvenile tortoises ranged from 64 to 130 mm in carapace length and from 49 to 400 g in total body weight.

Radiotelemetry

Juvenile gopher tortoises are difficult to locate because of their small size and secretive nature. Thus, we used radiotelemetry to locate all tortoises for all observations. We constructed lightweight (0.8–1.5 g), crystal-controlled radio transmitters powered with either a 1.35-V mercuric oxide (Hg675, 2.5 g) or a 1.5-V lithium (Li8O3, 1.2 g) battery. The transmitters operated at selected frequencies within a range of 150.0–152.0 MHz. Each antenna was about 10 cm long and provided a tracking range of 30–50 m. Longer antennas would have increased the tracking range, but the carapace of a juvenile tortoise provides inadequate space for attachment. We dipped the transmitters in a waterproof coating of Polystyrene Q-dope, coated the batteries with paraffin to facilitate easy replacement, and sealed the assembled unit in dental acrylic. The total transmitter package weighed from 2.5 to 4.0 g, depending on the size of the battery. We monitored transmitter signals with a Pro32 programmable hand-held scanner (Radio Shack, Ft. Worth, Texas) and a maxrad yagi antenna (Tessco Inc., Hunt Valley, Maryland).

We located small active burrows on the study site and trapped their occupants in plastic containers buried at the burrow entrances. The captured tortoises were taken to the laboratory, weighed, measured, and marked by marginal scute notching (McRae et al. 1981a). The transmitters were adjusted by battery size to weigh 5% or less of the total body mass. We used dental acrylic to attach the transmitters to the posterior margins of the carapaces and the antennas in a straight line from the rear to the front margin of the carapace. The day after it was captured, each tortoise was released into the burrow from which it was captured. We followed 18–20 individuals at one time. Individuals lost to predators or to unknown causes were replaced throughout the study.

Daily and Seasonal Activity

We considered a tortoise active whenever it was observed outside the mouth of its burrow. Two types of activity were distinguished: activity such as foraging, walking, or remaining stationary away from the burrow mound; and basking on the burrow mound.

We selected in advance the hottest time of day (T2 = midafternoon) and the midpoints between this time and the two coolest times of day (T1 = midmorning and T3 = late afternoon) as daily observation times. These times were estimated from data gathered during 3 consecutive years (1984–86) in Tampa, Florida, by the National Oceanic and Atmospheric Administration. To determine daily activity patterns, we located each tortoise three times daily (T1–T3; Table 1) and classified its behavior as active (basking or away from mound) or inactive (below ground).

We determined seasonal activity by combining the number of observed daily activities of all monitored tortoises throughout each season. We divided the year into three thermal periods by average monthly temperature variations obtained from the National Oceanic and Atmospheric Administration: June through September (summer), December through March (winter), and either April through May (spring) or October through November (fall). Although spring and fall had approximately the same thermal profiles, they were separated in time. Thus, we collected data for 15 days each in spring and fall and analyzed these data separately. We monitored tortoises arbitrarily 2 days each week or approximately 30 days/thermal period.

We used contingency tables with Pearson chi-square statistics to determine whether activity

Table 1. Estimated times of three daily observations of daily activities by juvenile gopher tortoises (*Gopherus polyphemus*) in central Florida, 1988–1989.

Observation time[a]	Summer (Jun–Sep)	Spring/fall (Apr–May/Oct–Nov)	Winter (Dec–Mar)
Tl	1000 h	1100 h	1100 h
T2	1300 h	1430 h	1500 h
T3	1600 h	1700 h	1700 h[b]

[a] See Materials and Methods for description of times.

[b] Estimated time was 1900 h, but this time was close to sunset and gopher tortoises have been reported as strictly diurnal.

was independent of time of day and of season. To determine whether tortoises were nocturnal, we placed small sticks vertically in the sand at the mouth of each burrow at dusk and checked for signs of disturbance early the next morning. If it was active at night, a tortoise would have knocked over the sticks on exiting its burrow.

Use of Burrows

We used flags to mark all burrows each tortoise occupied and measured the distances between these burrows. We calculated how many consecutive observation days each tortoise used a particular burrow and how often it changed burrows. We defined three categories of use of burrows by a tortoise. The primary burrow was the burrow in which the tortoise spent the greatest percent of its time. Secondary and tertiary burrows were respectively used second and third most often. We used contingency tables to determine differences in the use of primary burrows among seasons.

We analyzed the use of primary burrows separately from moves between burrows because percent use by a tortoise of its primary burrow may or may not be related to the number of moves between burrows. For example, the percent use of a primary burrow was usually lower by a tortoise that moved frequently between several burrows than by a tortoise that moved infrequently between several burrows. If a tortoise used only two burrows, however, it may have moved between these two burrows frequently and still had a high percent use of its primary burrow because the time spent inside a burrow is only divided between two instead of several burrows. The average seasonal use of burrows was estimated from the observed locations of the tortoises in each season.

Moves From and Between Burrows

We recorded each tortoise's number of moves and the distance a tortoise moved from its resident burrow and its number of moves and moved distance between its resident burrow and an alternate burrow. We defined *resident burrow* as the burrow a tortoise occupied at the time of a particular observation; other burrows a tortoise used but in which it was not located at the time of observation were called *alternate burrows*. For example, if during the first observation a tortoise was inside burrow A, this burrow was its resident burrow. If during the second observation the tortoise was inside burrow B, then burrow B was the resident burrow and burrow A was an alternate burrow. Three daily observations (Table 1) of each tortoise were used to calculate the mean distance moved from resident burrows. To determine the number of moves between burrows, we added two additional observation times: an early morning observation (0800–0900 h) to ascertain in which burrow the tortoise had spent the night and an early evening observation (1800–1900 h) after the tortoise had ceased its daily activity to ascertain in which burrow the tortoise would probably spend the night. These two observations allowed us to detect potential moves between burrows before time Tl and after time T3. We used contingency tables and Pearson chi-square statistics to determine whether the number of moves was independent of season. The Kruskal–Wallis pooled rank test was used to determine whether the moved distance was independent of season.

Home Range

We used the locations of tortoises at each observation to determine the sizes of home ranges by season. At each observation, we plotted the position of each tortoise and connected the outermost location points to form minimum convex polygons (Jennrich and Turner 1969) by season. We calculated the areas in the polygons with a digitizing tablet and Sigma Scan software (Jandel Scientific) on a personal computer. To calculate the average size of seasonal home ranges, we used only tortoises that were known to have moved from at least one resident burrow or to have moved between a resident and an alternate burrow. Zero values (no moves from or between burrows) were not included in home-range computations because the Wilcoxon two-sample test revealed no difference in the calculated sizes of the home ranges between seasons whether or not zero values were included. Some tortoises were observed moving only between two burrows, which resulted in a linear home range. To include these data, we converted straight line distances to areas by multiplying the maximum moved distance by 1 m.

During our study, a few tortoises made long-distance moves usually after some type of disturbance of their resident burrows. The mean distance moved by all juvenile tortoises ($\bar{x}$ = 15.2 m) and two standard deviations (SD = 22.8) was equal to 61 m. Because greater than 61-m moves were rare (3% of total moves), we considered them moves into a new home range and did not include the area in between as part of the home-range estimate. We calculated and compared home ranges of all tracked tortoises in each season. We used Wilcoxon two-sample tests to determine whether sizes of seasonal home ranges were of populations with the same distribution.

Statistical Techniques

We used the described standard nonparametric tests to analyze all data (Sokal and Rohlf 1981). Systat software for personal computers (version 4.0; Wilkinson 1988) was used to perform the tests. The level of significance was set at 0.05 for all tests. Tortoises for which we had accrued data for less than 1 month were excluded from all statistical analyses. Although sample size was maintained between 18 and 20 individuals, only 9 tortoises were observed during the entire study. We used these nine tortoises to calculate the average size of home ranges and use of burrows, which facilitated comparing our results with those of other studies.

Results

Daily and Seasonal Activity

Juvenile tortoises were active during 414 of 3,957 observations (10%). The tortoises were active during every month of the year, but activities varied among seasons (Fig. 1). Tortoises were active significantly more often in spring than in all other seasons (Pearson χ^2 = 13.46 [fall]; 27.03 [winter]; 8.51 [summer]; df = 1 for all tests) and more active in summer than in winter (Pearson χ^2 = 6.34, df = 1). Relative to other activity away from the burrow, the tortoises basked on the mound significantly less in summer (65% of activity) than in all other seasons (Pearson χ^2 = 4.84 [fall, 80%]; 12.03 [winter, 85%]; 5.14 [spring, 79%]; df = 1 for all tests). The recorded average maximum and minimum temperatures during the year of

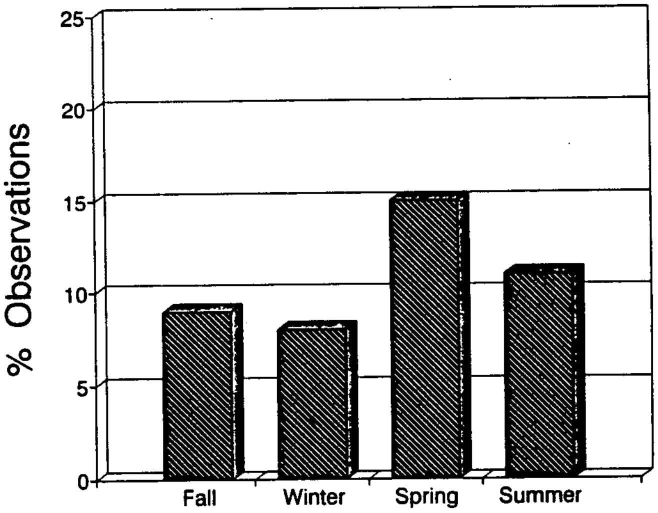

Fig. 1. Percent of seasonal observations during which juvenile gopher tortoises (*Gopherus polyphemus*) were active in central Florida, 1988–89.

our study were similar to the average seasonal temperatures obtained from the National Oceanic and Atmospheric Administration during the previous 3 years (Table 2).

The number and percentage of observations at which tortoises were active at each of the three daily observations varied by season (Table 3). During fall and winter, tortoises were active more in midmorning (T1) and in midafternoon (T2) than in late afternoon (T3; Table 3). During spring, the tortoises were active more during midafternoon than during either morning or during late afternoon, and in summer tortoises were active more during midafternoon and during late afternoon than during midmorning (Table 3). We found no evidence of nocturnal activity.

Use of Burrows

The juvenile tortoises usually occupied burrows they had excavated themselves but occasionally used abandoned burrows of adults or burrowed under litter. The tortoises used an average of 2.0 ± 1.4 burrows during fall, 1.7 ± 0.8 during winter, 2.2 ± 1.1 during spring, and 3.6 ± 1.4 during summer. The average annual number of burrows

Table 2. Comparison of mean maximum and minimum temperatures[a] in each thermal season in 1984–1986 and in the study year (1988–1989).

	1984–86[b]		Present study	
Season	Maximum	Minimum	Maximum	Minimum
Fall	28.6 ± 1.9	18.6 ± 2.4	28.6 ± 2.3	13.2 ± 3.3
Winter	22.9 ± 3.1	11.6 ± 3.5	25.0 ± 4.7	11.3 ± 3.5
Spring	29.3 ± 2.6	18.1 ± 2.7	31.6 ± 4.1	15.5 ± 1.7
Summer	32.2 ± 1.0	23.3 ± 1.0	34.0 ± 2.2	20.8 ± 1.0

[a] Degrees C ± SD.
[b] Averages from National Oceanographic and Atmospheric Administration.

Table 3. Number and percent of daily observations during which juvenile gopher tortoises (*Gopherus polyphemus*) were active in each season in central Florida, 1988–1989.

	Observations		Pearson χ^2 test statistics
Seasons	Total	Number active (%)	
Fall			
T1	221	28(13)	T1:T2— 0.06
T2	237	31(13)	T1:T3—18.41[a]
T3	187	06(01)	T2:T3—16.90[a]
Winter			
T1	514	51(10)	T1:T2— 0.12
T2	453	48(11)	T1:T3—19.27[a]
T3	432	12(03)	T2:T3—21.39[a]
Spring			
T1	233	34(16)	T1:T2— 4.18[a]
T2	218	48(24)	T1:T3— 2.64
T3	219	21(10)	T2:T3—12.69[a]
Summer			
T1	455	25(05)	T1:T2—23.41[a]
T2	414	64(15)	T1:T3—11.31[a]
T3	384	46(12)	T2:T3— 2.03
Total	3,967	414(10)	

[a] Significant differences between daily observation times in each season.

(n = 9 tortoises) used in 1 year was 4.4 ± 2.4 with a range of 1–8 burrows.

The percent use of primary burrows by juvenile tortoises varied among seasons (Fig. 2). The relative number of occurrences in the primary burrows was significantly greater in winter than in all other seasons (Pearson χ^2 = 25.32 [fall]; 26.49 [spring]; 171.80 [summer]) and less in summer than in all other seasons (Pearson χ^2 = 32.65 [fall]; 31.65 [spring]). The percent use of the primary burrows did not differ between spring and fall (Pearson χ^2 = 0.008). Of the total time spent in burrows during the entire year, the juvenile tortoises used their primary burrows an average of 75% of the time, secondary burrows 20% of the time, and tertiary burrows 4% of the time.

Moves From Burrows

Active tortoises moved from their burrows during 24% (98 of 414) of the observations and basked at the mouths of their burrows during 76% of the observations. The number and percentage of the moves from burrows varied among seasons (Table 4). The number of moves from burrows did not differ between fall and spring but was significantly greater in summer than in fall or winter and greater in spring than in winter (Table 4).

Most distances of moves from burrows were between 0.5 and 10.0 m, regardless of season (Fig. 3). The distance a tortoise moved from its burrow did not vary seasonally (Kruskal–Wallis H = 1.13). The annual mean distance moved from burrows by all tortoises combined was 7.97 ± 8.56 m.

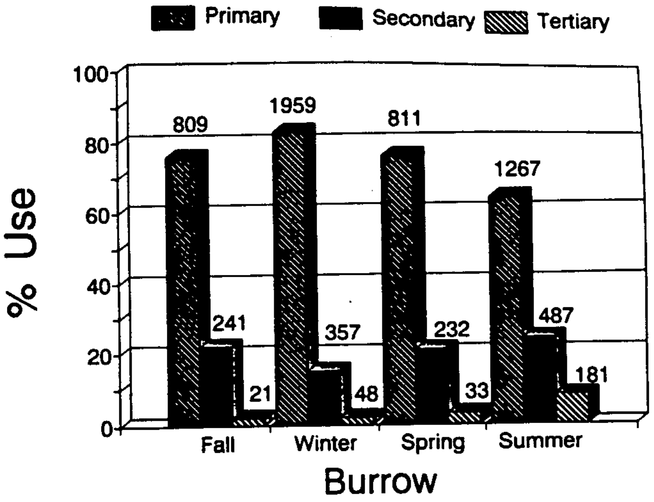

Fig. 2. Seasonal use of primary, secondary, and tertiary burrows by juvenile gopher tortoises (*Gopherus polyphemus*) in central Florida, 1988–89. *Numbers* above bars are occurrences of tortoises in each of the three categories of burrows.

Moves Between Burrows

Burrows that an individual tortoise used were usually in close proximity to each other. The juvenile tortoises made more moves between burrows during summer than during other seasons and fewer during winter than during other seasons (Table 5). The number of moves between burrows did not differ between fall and spring (Table 5).

Distances moved between burrows did not differ among seasons (Kruskal–Wallis H = 3.17; Fig. 4). The annual mean distance moved between burrows

Table 4. Number and percent of total moves by juvenile gopher tortoises (*Gopherus polyphemus*) from burrows in central Florida, 1988–1989.

Season	n[a]	Moves (%)	Pearson χ^2 statistics
Fall	645	12 (2)	F:W— 2.08
Winter	1,399	17 (1)	F:Sp— 1.91
Spring	670	22 (3)	F:S — 3.98[b]
Summer	1,253	47 (4)	W:Sp—10.48[b]
			W:S—18.05[b]
Total	3,967	98 (2)	S:Sp— 0.28

[a] Total daily observations for times T1, T2, and T3 for each season.

[b] Significant differences between numbers of moves between seasons: F = fall, W = winter, Sp = spring, S = summer.

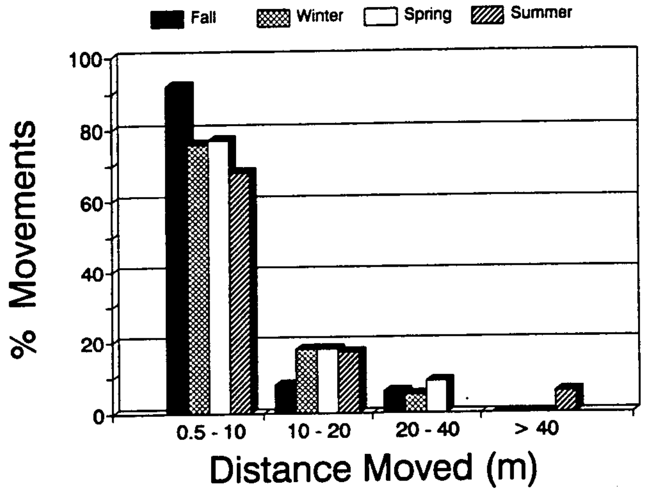

Fig. 3. Distribution of moves from burrows by juvenile gopher tortoise (*Gopherus polyphemus*) by season in central Florida, 1988–89.

was 14.27 ± 10.57 m by all tortoises. All tortoises made a total of 295 moves from and between burrows. Three percent (9 moves) of all moves were long-distance moves (>61.0 m). Eight of the nine long-distance moves were made during summer.

Home Range

The sizes of the home ranges varied greatly among individuals but did not differ among fall, winter, and spring (Table 6). Sizes of home ranges in summer, however, were significantly larger than sizes of home ranges in all other seasons (Table 6). The sizes of annual home ranges of juvenile tortoises in our study (n = 9; Table 6) and those of juvenile gopher tortoises in a northern Florida population (n = 7; Diemer 1992) did not differ (Wilcoxon two-sample U = 40).

Discussion

Annual, Seasonal, and Daily Activities

Juvenile gopher tortoises were underground in burrows during 90% of our observations. Comparable estimates of annual activities of adult *Gopherus polyphemus* are limited to observations of a single male for 13 months (Auffenberg and Iverson 1979). With a device that automatically recorded activity, the investigators calculated that this tortoise was active 9.2% of its time. Adult congeners in western North America also are known to spend limited time aboveground. The estimated time spent aboveground by the Bolson tortoise (*G. flavomarginatus*) is only 1% (Adest et al. 1989). In two separate studies, adult *G. agassizii* were inactive an estimated 98.3% (Nagy and Medica 1986) and 94.9% (Marlow 1979) of the time.

In Georgia, adult tortoises were observed on roads during two winters, and occasionally basking adult tortoises were observed at the mouths of their burrows (McRae et al. 1981b). Activities of juvenile tortoises on roads in Georgia peaked in spring and late summer (McRae et al. 1981b). In northern Florida, most tortoises came to the mouths of their burrows at least once during winter, and juveniles emerged from their burrows more often than adults (Diemer 1992). In a southern Florida population, more juvenile gopher tortoises were seen in April, July, and August than in other months, and activity

Table 5. Number and percent of total moves by juvenile gopher tortoises (*Gopherus polyphemus*) between burrows in central Florida, 1988–1989.

Season	n[a]	Moves between (%)	Pearson χ^2 statistics
Fall	1,095	34 (3)	F:W —16.70[b]
Winter	2,368	27 (1)	F:Sp — 0.20
Spring	1,114	31 (3)	F:S — 6.56[b]
Summer	2,073	105 (5)	W:Sp—12.48[b]
			W:S —59.04
Total	6,650	197 (3)	S:Sp — 9.24

[a] Total daily observations for times T1, T2, and T3 and the early morning and late afternoon observations.

[b] Significant differences in the numbers of moves between seasons: F = fall, W=winter, Sp=spring, S=summer.

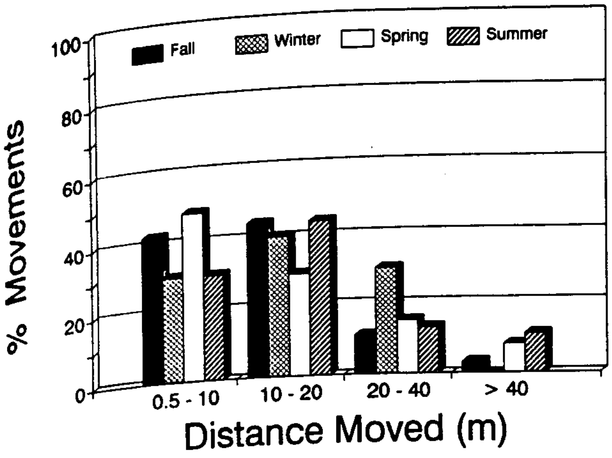

Fig. 4. Distribution of moves by juvenile gopher tortoises (*Gopherus polyphemus*) between burrows by season in central Florida, 1988–89.

in winter was limited to a few warm days (Douglass and Layne 1978). In our study, we found active juvenile tortoises during every month of the year. In summer, approximately one-third of the activity was away from the burrow and the remaining two-thirds was basking on the burrow mound. The summer activity pattern differed significantly from those of fall, spring, and winter when more than 80% of the activity consisted of basking on the burrow mound. Juvenile gopher tortoises were seen away from their burrows on only four occasions from December through February. In March, the tortoises made more moves from their burrows, and the number of moves increased as the days got warmer; most moves were made in May and July. Thus, the activities of juveniles—like those of adults—away from their burrows are limited in the winter months and increase as seasonal temperatures increase. In winter, juvenile tortoises in our study limited their moves from the burrow mounds (14 observations) and basked more often (97 observations) on their burrow mounds than in other seasons. Comparable information on basking behavior of juvenile tortoises is not available from other studies because observations of this secretive animal are difficult without the use of radiotelemetry.

Adult tortoises in Georgia exhibited one activity peak in late afternoon at 1600–1800 h during spring and two daily activity peaks in summer at 1000–1200 and 1600–1800 h (McRae et al. 1981b). The investigators suggested that adult tortoises may be active in late morning and in late afternoon in summer to avoid the hottest part of the day. In southern Florida, juvenile tortoises were more active in the midafternoon at 1300–1600 h and, in contrast to adult tortoises in Georgia, exhibited no evidence of bimodal daily activity in summer (Douglass and Layne 1978).

In western congeners, the activity patterns of adults are bimodal in summer with peaks in the morning and late afternoon (Auffenberg and Weaver 1969; Gourley 1972; Marlow 1979; Luckenbach 1982; Bury and Smith 1986). In our study, we also found seasonal variation in the daily activities of juvenile gopher tortoises. In fall and winter, tortoises were more active during the morning and midafternoon hours than during late afternoon, but in spring they were more active during the midafternoon hours than during the morning and late afternoon. In summer, tortoises were more active during the middle and late afternoon than during the earlier observation time of 1100 h. Thus, like Douglass and Layne (1978), we found no evidence

Table 6. Mean sizes (m^2) of seasonal and yearly home ranges of juvenile gopher tortoises (*Gopherus polyphemus*) in central Florida, 1988–1989.

Season	*n*	Mean	SD	Range	Wilcoxon two-sample *U* statistic[a]
Fall	13	75	132	5–48	F:W — 99.5
Winter	12	32	50	1–168	F:Sp — 104.5
Spring	18	50	86	2–347	F:S — 174.0[b]
Summer	17	358	835	10–3,534	W:Sp — 133.5
					W:S — 181.5[b]
Yearly	9	718	1,139	95–3,576	S:Sp — 241.0[b]

[a] F = fall; W = winter; Sp = spring; S = summer.

[b] Significant differences in sizes of home ranges between seasons.

of bimodal daily activity as summer temperatures increased. Juvenile tortoises in our study tended to be more active later in the day and to bask less on the burrow mound as seasonal temperatures increased. We also found no evidence of nocturnal activity by tortoises in our study, a finding that corroborates results of previous studies of adult gopher tortoises (Douglass and Layne 1978; McRae et al. 1981b).

Use of Burrows

We found that juvenile tortoises usually dug their own burrows but occasionally used abandoned burrows of adults. Once, we observed a juvenile tortoise in an adult burrow that showed signs of recent occupancy by the adult. After its primary burrow had been disturbed, this juvenile tortoise moved 116 m down a firelane to the burrow of the adult. This juvenile used the adult burrow for only one afternoon and then dug a new burrow nearby.

The average number of burrows per activity season used by juvenile gopher tortoises in a population in southern Georgia was 1.1 by 0–1-year-olds, 2.2 by 2-year-olds, and 1.7 by 4–5-year-olds (McRae et al. 1981b). Juvenile tortoises used an average of 2.6 ± 1.3 burrows in 2 years (1985–87) in a northern Florida population (Diemer 1992). The average annual use of burrows was greater by juvenile tortoises in our study (4.4 ± 2.4 burrows) than by individuals in either of these studies. Differences in the uses of burrows between the populations may be the result of one or a combination of several factors: (1) differences in habitat (ground cover) between study sites (a tortoise may need more burrows as refugia from predators in open habitats); (2) differences in soil composition (a tortoise may find it easier to dig burrows in some soil types than in others); (3) differences in temperature extremes at different latitudes (a tortoise may need more burrows in more southern climates to provide refugia from hot temperatures); or (4) differences in number of disturbances to burrows in different habitats (potential predators or agricultural) that may result in tortoises digging new burrows.

Although juvenile gopher tortoises use several burrows, they spend most of their time in a primary burrow. In winter, the juveniles spent 83% of their time belowground (inactive) in the primary burrow, whereas in summer, they spent only 65% of their time belowground in the primary burrow. The use of primary burrows in all seasons combined was 75% of the use of all burrows.

The use of primary burrows by Bolson tortoises during the active season was 79% of the total use by juveniles and 73–75% of the total use by adults (Aguirre et al. 1984). The data for estimated use of primary burrow by adult *G. polyphemus* are not available.

Moves From and Between Burrows

The size of the activity range (home range) of a gopher tortoise increased with the size of the individual, and the average number of monthly moves of juvenile tortoises was greater in summer and lower in winter than in other seasons (Auffenberg and Iverson 1979). We found that the combined moves from resident burrows and between burrows were fewest in winter (2% of winter observations) and most numerous in summer (7% of summer observations). With results from radiotelemetry in northern Florida, Diemer (1992) calculated a mean moved distance from and between burrows of 16.0 ± 17.0 m by juvenile gopher tortoises, 37.0 ± 37.0 m by adult female tortoises, and 79.0 ± 69.0 m by adult male tortoises. We found that the average moved distance was 15.2 ± 22.8 m. Excluding moves between burrows, we found the mean distance tortoises moved from their resident burrow was 7.97 ± 8.56 m. Most tortoises that we observed away from their burrows were foraging and, thus, this mean moved distance could be considered a feeding radius. McRae et al. (1981b) reported a mean feeding radius of 7.8 ± 4.4 m by juvenile gopher tortoises and of 13.0 ± 8.6 m by adult tortoises. Accordingly, juveniles seem to move relatively shorter distances from and between burrows than adult gopher tortoises.

Only 3% of all moves were long-distance moves by juvenile tortoises in our study. Most long-distance moves were made in summer. At least four reasons have been proposed for long-distance moves in turtles (Gibbons 1986): (1) excursions of females to suitable nesting sites, (2) seasonal migrations to and from overwintering sites, (3) departures from unsuitable habitat, and (4) moves by males in search of mating opportunities. Departure from an unsuitable habitat included emigration of turtles in response to adverse environmental conditions such as extreme dry or wet conditions (Gibbons 1986). Physical disturbance of burrows, however, also may render a particular location unsuitable for a gopher tortoise. Gopher tortoises may relocate more frequently in disturbed areas (Douglass 1976), and long-range moves of gopher tortoises may follow destruction of burrows by cattle (Diemer 1992). Most (66%) long-distance moves in our study were made after some type of disturbance to the resident burrow, which included digging at the mouth of the burrow by mammals, mostly by raccoons (*Procyon lotor*) and armadillos (*Dasypus novemcinctus*). One disturbance was by a deer trampling the burrow entrance.

Home Range

In our study area, the average annual home range of juvenile gopher tortoises was 0.072 ± 0.114 ha. In a northern Florida population, the average annual home range of juvenile gopher tortoises was 0.049 ± 0.089 ha (Diemer 1992). Estimated sizes of home ranges of adult female gopher tortoises range from 0.08 ha (McRae et al. 1981b) to 0.56 ha (Doonan 1986) and of adult males from 0.45 ha (McRae et al. 1981b) to 1.27 ha (Diemer 1992). Hence, the sizes of the home ranges of juvenile tortoises in our study and in northern Florida are smaller than the sizes of home ranges of adults.

The sizes of home ranges of gopher tortoises decrease with an increase in the amount of herbaceous ground cover (Auffenberg and Iverson 1979). Our study site was a vegetational mosaic, which results from controlled burning of various plots at different time intervals (1, 2, 5, or 7 years). This prescribed burning of our study site maintains an open habitat, which supports a lush cover of grasses and herbs (Macdonald and Mushinsky 1988). Thus, juvenile tortoises in our population did not have to travel far to find ample food. The sizes of home ranges were small (0.0095–0.3576 ha), and tortoises with the larger of those home ranges generally had burrows that were disturbed and had subsequently moved to another area of the study site.

Possible Explanations of Observed Patterns

Predation Pressure

We found that juvenile gopher tortoises have smaller home ranges than adult gopher tortoises, spend limited time aboveground, and use several burrows. These findings and those about tortoises studied in northern Florida are similar (Diemer 1992) and may be a result of one factor or a combination of factors. One possible cause is predation. Juvenile gopher tortoises are small and have soft shells that make them vulnerable to mammalian, avian, and ophidian predators (Douglass and Winegarner 1977; Fitzpatrick and Woolfenden 1978; Landers 1980; Wright 1982). During the year of our study, 11 of 32 radio-tagged tortoises were dead when found (Wilson 1991). Four additional tortoises could not be located because of lost telemetry signals. Three of the dead tortoises showed evidence of predation by raptors (G. E. Woolfenden, University of South Florida, Tampa, personal communication); one transmitter was found about 4.5 m up a palm tree. The other eight dead tortoises seemed to have been eaten by mammals, possibly by raccoons or opossums (*Didelphis marsupialis*), because their shells were torn apart in a manner indicative of mammalian predation. Most dead tortoises were found within 50 m of the burrow in which they were last observed.

When juvenile tortoises were located, they were usually foraging near one of their burrows. When we located tortoises foraging or walking away from their burrow mounds, we noticed they made quick, hurried movements. During 3,937 observations, we found juvenile gopher tortoises away from their burrow mounds only 98 times. Foraging adult tortoises in this population frequently were seen on sandy fire lanes. When encountered, the adults stopped foraging and pulled their extremities into their shells. If left alone, they usually resumed foraging within a few minutes. In contrast, when a juvenile was encountered and became aware of our presence, it moved quickly to its nearest burrow (usually within 10 m) and retreated inside. Limited aboveground activity of juvenile gopher tortoises may be influenced by a high risk of predation. The availability of several burrows may provide a tortoise with numerous alternatives for quick escape from predators.

The risk of predation may also influence basking behavior of young tortoises. We observed basking juvenile gopher tortoises on the burrow mounds more often in the cooler months than in the hotter months. They also were away from the burrow mound more often in the hot hours of the afternoon in spring and summer. In cooler months, juvenile tortoises first basked on the burrow mound and then moved from the mound to forage. Basking may allow a tortoise the opportunity to elevate its body temperature before leaving the proximity of its burrow, which may be necessary to render a tortoise more capable of quick moves and to aid its escape from potential predators. In the hotter months of spring and summer, a juvenile tortoise could shorten (or eliminate) basking by emerging from the burrow mostly in the hot afternoon hours. By reducing or eliminating basking, a juvenile tortoise shortens the time it spends aboveground and consequently its exposure to predators. The relative importance of these factors needs further investigation. More information is needed about the risk of predation on juvenile gopher tortoises, which we suspect is intense.

Thermoregulatory Behavior

Another possible cause for the limited time juvenile tortoises spend aboveground, their small home ranges, and their use of multiple burrows may be a response to high temperatures (Douglass and Layne 1978; Tom 1994). Because they are smaller, juvenile tortoises heat more rapidly than adults (McDonald 1976; Rose and Judd 1982) and consequently cannot withstand prolonged exposure to the sun. Temperatures inside burrows are generally lower than outside air temperatures during the day in summer (McGinnis and Voigt 1971; Douglass and Layne 1978). In our study, the percent use of primary burrows was less and moves between burrows were more numerous in summer. Juvenile tortoises may use several burrows during summer so that they can forage without straying too far from a burrow. When they become overheated, they can quickly retreat into their burrow, which is a thermal refuge. Furthermore, some tortoises in late afternoon in the hotter months lie buried under leaf litter, which may allow a tortoise that has strayed too far from a burrow to avoid excessive heating. This behavior reinforces the importance of high temperatures in influencing moves and the uses of burrows by juvenile tortoises. Heating and cooling rates of young tortoises should be investigated. These rates could be obtained by coupling thermistors to radio transmitters.

Acknowledgments

We thank Impala Electronics Inc., Motorola University Support Group, and Eveready Battery Co., Inc., for donations of parts that enabled us to build the transmitters. We also thank D. Banaszek, J. Diemer, and P. Wiley for technical advice for the construction of the transmitters. J. Camp administered grants. This research was supported by grants from Sigma Delta Epsilon GWIS, SSAR-Grants-in-Herpetology, The Gopher Tortoise Council, and the Society of Sigma Xi.

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Gopher tortoise (*Gopherus polyphemus*) in native habitat, Florida. *Photo by H. F. Mushinsky.*

Neonates: Missing Links in the Life Histories of North American Tortoises

by

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Abstract. Eggs and neonates (<1 year old) are the most vulnerable life stages of the North American tortoises (*Gopherus*). Neonates have residual yolk stores and higher metabolic rates, protein demands, and evaporative losses than adult conspecifics. Small tortoises differ by other features (e.g., larger and more robust body, shell kinesis, digging, and herbivory) from the neonates of their sister family (the emydids). Neonatal and juvenile shell kinesis may be retained by the adults (heterochrony—i.e., deviation from the typical embryological sequence of formation of organs and parts as a factor in evolution) of small-sized species of tortoises, and diagnostic features may be most manifest in the young. Life history models of tortoises are based on few years of observation of mostly adults, which are inadequate to characterize these species with protracted immature stages and long life spans of adults. A model is proposed to help explain the chaotic nature of precipitation and recruitment in tortoise populations. According to a bet-hedging model, the reproductive efforts of tortoises (*Gopherus*) and emydid turtles (*Pseudemys*) of similar size seem to be similar, but the characteristics of the eggs and neonates of these chelonians are apportioned differently. Tortoises have fewer eggs, but each is 350% of the mass of eggs of many emydid turtle species. Neonatal tortoises are about twice the weight of aquatic emydids. The larger mass of a tortoise and its eggs may be a response to the relatively harsh, variable environments of terrestrial life.

Key words: Bet hedging, chaos model, environmental effects, *Gopherus*, hatchling tortoises, reproductive effort.

Eggs and neonates (<1 year of age) are the least-well-documented stages in the lives of North American tortoises. These missing links compromise efforts to characterize life histories for modeling and managing tortoises. Many field studies revealed a scarcity of eggs, neonates, and juveniles (Burge 1978; Douglass 1978; Judd and McQueen 1980; Shields 1980; Berry and Turner 1986; Diemer 1986; Adest et al. 1989a; Tom 1994; Wilson et al. 1994). Tortoises do not have concentrated nest sites or synchronous emergences of hatchlings that facilitate studies of nesting in sea turtles (Hendrickson 1982; Mortimer 1982). Freshwater emydid turtles are between these two extremes; their terrestrial nest sites are usually not far from shore (<100 m) and often in recognizable substrata of beaches and sand bars (Ernst and Barbour 1972; Congdon et al. 1983; Wilbur and Morin

1988). Explanations for the dearth of information about eggs and neonates include an array of contributing factors: the cryptic appearance of young chelonians, low survivorship of the clutches and early age classes, seasonality and rapid growth of very small juveniles, earlier diel emergence and retreat of young, and the obscurity or ambiguous appearance of small burrow openings (frequently misdiagnosed as rodent burrows).

Losses of chelonian eggs to predation are high, and rates even from different sites and species seem consistent at about 60–90% (Congdon and Gibbons 1990; Diemer and Moore 1994). Furthermore, gopher tortoises (*G. polyphemus*) have first-year mortality rates between 70% (Wright 1982) and 94% (Alford 1980). High mortality rates of juvenile gopher tortoises—some with significant seasonal variation—have also been reported (Wilson 1991; Wilson et al. 1994). Although a composite of losses is mostly guesses (Figure), eggs, neonates, and juveniles seem to be the most vulnerable stages in the lives of tortoises. Some regions are without significant precipitation (e.g., the western Mojave Desert) for one or more years, whereas others (e.g., the Sinaloan thornscrub) may receive precipitation in 2 seasons/year. The effects of different weather on tortoise recruitment is currently unknown.

Most tortoise studies were short (1–3 years), focused on adults that are found more often than juveniles, were conducted on sites with only regional weather histories, and often included only a single growing season. A concern about global declines of tortoises, however, has increased attention to long-term studies (Swingland and Klemmens 1989). Although relative age–size classes are used for demographic categorization of tortoises in the Mojave Desert (Berry 1976, 1981), the aging of desert tortoises by scute annuli defined the growth and longevity of some tortoise populations (Germano 1988, 1992, 1994).

To address many of these questions, this paper presents (1) a review of recent studies of young tortoises (especially during their first year); (2) a comparison of young tortoises with conspecific adults and with the young of other chelonians; (3) an examination of the reproductive investment of tortoises and aquatic turtles with a bet-hedging model; and (4) a model of the recruitment of neonates by the chaotic nature of seasonal and local weather patterns. The model may provide a testable explanation of the patchy and somewhat unpredictable distribution of local tortoise populations in North American deserts.

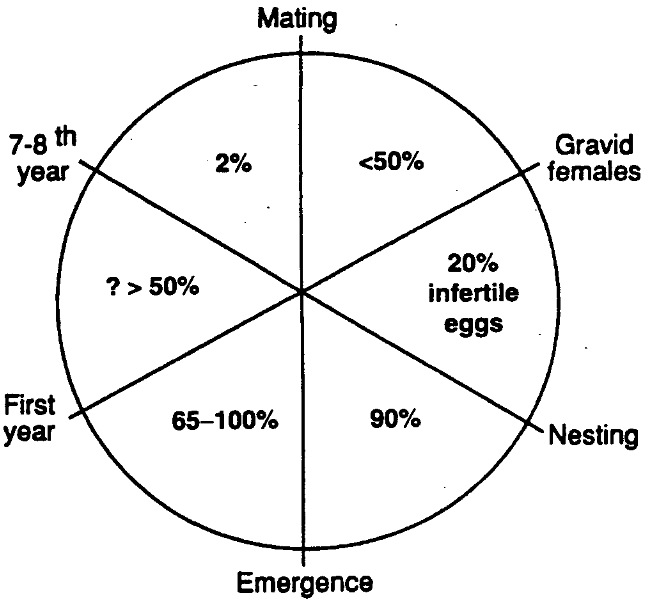

Figure. Speculative losses at each tortoise (*Gopherus* spp.) life stage (e.g., mortality may be 65–100% from emergence to the end of the first year of life).

Terminology

Specific definitions are needed to designate cohorts whose classes are estimated by (1) size based on carapace length (CL), shell wear, or other measures; (2) estimated age (e.g., from the number of scute annuli); and (3) known age (e.g., determined by mark-and-recapture studies).

Because tortoises are hatched rather than born, there is a legitimate semantic question of whether first-year tortoises should be called neonates, given that natal refers to birth (Webster's New Universal Unabridged Dictionary, Second Edition 1983). However, the term *natality* has been used to refer to birth rates, even in species with progenies hatched from eggs. Lincoln et al. (1982) define neonatal as a newborn or recently hatched. Also, neonate has been used for recently born individuals in live-bearing snakes (e.g., rattlesnakes; Macartney et al. 1990) and for first-year young of oviparous species such as the Galapagos land iguana, *Conolophus subcristatus* (Snell and Tracy 1986).

I suggest we refer to individual tortoises that are known to be less than 1 year old as neonates and 1–2-year-olds as 1-year-olds, much as we designate human age. This first year (neonate) corresponds to the class *hatchling* in desert tortoises (Berry 1981) and includes individuals with less than 60-mm CL and no apparent growth rings. Theoretically, however, neonates may undergo two growth bouts in the first year (after fall emergence and during the following spring). Also, neonates may grow more than 60-mm CL (as some captives do) and then qualify as "juveniles #1" based on one system (Berry 1981).

Importance of Neonates to Tortoise Biology

Uniqueness

The neonate has unique features of bioenergetics, ethology, and ecology. Neonates are a distinct component in the lives of tortoises, especially compared with conspecific adults (Table 1) and other chelonian neonates. Distinctive neonatal traits absent in adults are often shared (synpleisomorphic) with young organisms generally (Prosser and Brown 1965): small size with concomitant high surface-to-volume ratio, increased metabolic rate, and high demands for protein and macronutrients. When the functional morphology of a neonate tortoise is compared with its parent's, I suggest that the contrasts would exceed many differences between adult vertebrates of different families or orders.

Interspecific comparisons with chelonians of equivalent ontogenetic classes reveal unique and peculiar aspects of young tortoises. The kinesis (flexion) of the posterior marginal shell in young tortoises is not shared with most emydids. Likewise, fossorial activities and greater body mass of neonate tortoises separate them from aquatic turtles of equal age (e.g., the cooter *Pseudemys concinna*; Table 2).

Several traits characterize the neonate tortoise. It is a small chelonian with a thin, soft, and kinetic shell. Its high metabolic rate (Naegle and Bradley 1974) may stimulate a maintenance of extended surface activity to obtain high-caloric protein and macronutrient-rich forage for growth (Adest et al. 1989b). Energy recruitment may get a head start by the retention of more than 50% of the lipid content of the egg yolk in newly hatched individuals of the gopher tortoises (*G. polyphemus*; Linley and Mushinsky 1994) and in painted turtles (*Chrysemys picta*; Congdon and Tinkle 1982). In the 2 days between piping and emergence, a massive and vulnerable yolk sac is mostly absorbed. The yolk mass and the piping tortoise are gradually drained of egg white, and 12% of this liquid consists of an iron binding protein (conalbumin) that prevents access

Table 1. Characteristics of neonatal tortoises (*Gopherus* spp.).

High protein in diet	16% in juveniles vs. 8% in adults (Adest et al. 1989a)
High oxygen consumption	Aerobic metabolism of a 50-g neonate is 300% greater than of a 100-g individual (Naegle and Bradley 1974)
High surface volume ratio	Evaporation rates are higher in neonatal *G. agassizii* than in larger tortoises (M. Joyner, California State University, Dominguez Hills, Carson, personal communication)
Residual yolk lipid	At least 67% of the egg lipid mass is conserved in the hatchling, which itself is 21% lipid (in painted turtle, *Chrysemys picta*; Congdon and Tinkle 1982)
Shell	For the first 7 years, shells are flexible and capable of carapace kinesis that reduces the anal aperture (D. Morafka, unpublished data)
Diel activity	Early morning peak in surface activity often along home paths, which are peripheral to vegetation and an average of about 20 m long (Berry and Turner 1986; Tom 1994)
Tortoise burrows	80% in vegetation; 67% selfexcavated; low burrow fidelity as neonates move as often as six times in the first year

Table 2. Comparison of reproduction characteristics of cooters (*Pseudemys* spp.) and North American tortoises (*Gopherus* spp.). Data largely from Congdon and Gibbons (1985, 1987, 1990) and Germano (1994).

Characteristics	*Pseudemys*	*Gopherus*
Plastron length (mm)	280	280
Female weight (g)	3,000	3,000
Egg width (mm)	24	43
Egg weight (g)	12	41
Average clutch size	20	5–7
Annual clutch frequency	1 or 2	1(2?)
Clutch/body weight (%)	76	—
Shell/egg weight (%)	19.3	40.8
Shell type	parchment	brittle
Hatchling CL (mm)	28	40
Hatchling weight (g)	20	30
Incubation (days)	50–65	70–90
Overwintering incubation	rare-facultative?	
High growth years	7	20
Maximum annual growth (mm)	30	10–15
1st reproduction (years)	8	13–16
Minimum estimate of life span (years)	30	— 50
Reproductive life span (years)	22	35

of bacteria and fungi to the yolk mass (Weinberg 1984).

When the absorption of the yolk mass is completed, the emergent tortoise (about 40 mm long) extended its length by about 20% from fetal dimensions in the egg shell (D. Morafka, unpublished data). Nuclear magnetic imagery indicates that even several months after hatching the yolk mass remains recognizable internally (M. A. Joyner, California State University, Dominguez Hills, Carson, personal communication). Residual yolk lipid could provide a wide range of options for the timing (seasonality) of emergence (Gibbons and Nelson 1978).

Evidence of overwintering by embryos or neonates of desert tortoises (*Gopherus agassizii*) in North America is limited (Grant 1936; Luckenbach 1982). Similarly, neonates of the leopard tortoise (*Geochelone pardalis*), a large tortoise of temperate southern Africa, may spend 472 days between egg deposition and the emergence from the nest (Jacques 1969). In most cases, the long interval is explained by a long diapause in embryogenesis in winter. But, in a few cases, there may be a second and significant interval between piping of the egg shell and actual emergence from the nest (Gibbons and Nelson 1978). This phenomenon has also been noted in the loggerhead sea turtle (*Caretta caretta*; Christens 1990).

Another unique characteristic of young neonates may be the neutral pH of their stomachs that fosters fermenting of ingested anaerobes as in hatchling *Iguana iguana* (Troyer 1984a). Ingestion of soil or feces seems to occur in neonatal desert tortoises that emerge in the fall in the Mojave Desert (M. Joyner, California State University, Dominguez Hills, Carson, personal communication).

Juvenile Bolson tortoises (*G. flavomarginatus*) created foraging trails at the openings of short burrows under dense shrub canopies (especially *Opuntia* cactus) into open spaces, generally skirting the periphery of edible vegetation (Tom 1994). Some of these trails may expose the young tortoise to predation, microclimatic stress, or high rates of pulmocutaneous water loss. However, their high surface-to-volume ratio may allow neonates to efficiently thermoregulate in cool environments. Neonates possibly emerge earlier within the calendar year and within a single day than their adult counterparts (Turner et al. 1986). The early emergence is supported by observations of Egyptian tortoises (*Testudo kleinmanni*)—a small-sized species that exhibits early seasonal behavior and much winter activity—from Israel's Negev Desert (Geffen and Mendelssohn 1988).

Functional and Comparative Morphology

The size, shape, and kinetics of the neonatal shell help address issues such as minimal viable egg size and paedomorphosis in small-sized adults. The development of maximum egg width in chelonians is limited by the constraints of the female pelvis (Congdon and Gibbons 1985, 1987). A regression of egg width to body size (after Congdon and Gibbons 1985) projects an egg width of 15 mm for the smallest North American emydid, *Clemmys muhlenbergii*, which is a freshwater turtle about 90 mm CL (Carr 1952; Ernst and Bury 1977). The actual egg width of *C. muhlenbergii* is 14–16 mm (Ernst and Barbour 1972). The pelvis in tortoises may have evolved structural proportions to achieve a gait that elevates the shell for overland moves. I found no analysis that identified the lower limits of the egg width in tortoises. In the speckled Cape tortoise (*Homopus signatus*) of Africa, the mean egg width is 20.5 mm (Boycott and Bourguin 1988), which is larger than the width of eggs in other testudinids of about the same size (95 mm CL). The egg width is about 1.3 times larger in *H. signatus* than in *C. muhlenbergii*. The large eggs seem to be possible because the posterior lobe of the female plastrons in *Homopus* are kinetic and abducted for oviposition. Similar passive abduction of the xiphiplastron has been reported of the smallest of the North American tortoises, *Gopherus berlandieri* (Rose and Judd 1991). A plasticity of the egg has also been found in *Homopus* (Rose 1962; Eglis 1963), and the pliability of the parchment egg shell may be unique in testudinids (Ewert 1985).

The greater width of the tortoise eggs may be a response to selection for a larger neonatal tortoise in terrestrial environments. For example, there are positive relations between increased survivorship and larger-sized eggs and larger-sized hatchlings in chelonians (Swingland and Coe 1979; Ewert 1985; Wilbur and Morin 1988) and iguanid lizards (Fergurson and Bohlan 1978; Sinervo and Huey 1990). Selection may also favor a greater yolk reserve with which newborn tortoises can meet uncertain foraging conditions.

Digging by many neonatal tortoises begins soon after emergence from the nest (Tom 1994) and compounds the need for limb strength. Larger young are probably also subjected to fewer losses from small predators (rodents, some reptiles, birds) and have a lower surface-to-volume ratio, which reduces the rate of water loss.

However, terrestrial life alone seems inadequate to explain the adaptations of larger eggs and hatchlings. Box turtles (genus *Terrapene*) are a terrestrial group of emydids but have small eggs (flexible) and neonates (mass about 7 g) like other emydid turtles (Congdon and Gibbons 1985, 1987; Doroff and Keith 1990), their closest relatives. Herbivory, increased aridity of habitat, and fossorial behavior may demand more from *Gopherus* neonates, which have greater mass (about 30 g) than neonates of aquatic turtles.

Increased size apparently contributes to the fitness of an herbivore in environments with scarce low-fiber forage (Demment and Van Soest 1985). For example, diet analyses indicated that desert iguanas (*Dipsosaurus dorsalis*) are herbivorous throughout life (Mautz and Nagy 1987). Neonatal lizards seem to select small plant species that are low in fiber content and may facilitate mechanical ingestion and chemical assimilation of foods. Some neonatal aquatic emydids (such as the 20-mm-long neonates of *Pseudemys concinna*) are also herbivores (Buhlmann and Vaughan 1991). The necessary mechanical effort for eating the highly fibrous content of most terrestrial plants rather than herbivory itself favors a larger size of tortoise neonates.

Larger eggs and neonates of testudinids may be also character states that are fixed by selection operating on the common ancestor of the tortoises. Osteological and morphological characters suggest that testudinids are derived from the batigurid family of turtles, possibly ancestors of the Asian box turtle (genus *Cuora*; Gaffney and Meylan 1988). Relatively large and brittle shelled eggs are a universal characteristic of testudinids and their batagurid ancestors (E. Moll, Eastern Illinois University, Urbana, personal communication). Phylogenetically, large eggs and neonates are synpleisomorphic to tortoises and may be viewed as fixed traits.

The phenomenon of heterochrony in reptiles has also been largely neglected. A differential ontogeny of body parts occurs in small-sized lizards, including microteiids (Presch 1980) and scincids (Griffth 1991). Carapace and plastron kineses are common in small-sized species of chelonians (Richmond 1964), and some of these states may be paedomorphic (e.g., kinesis may be a fundamental characteristic of young tortoises).

I have not found a reduction in the anal aperture of neonatal slider turtles (*Trachemys scripta elegans*), similar to a voluntary response in juvenile tortoises (*G. flavomarginatus* and *G. agassizii*) that reduces the anal gap between posterior margins of the carapace and plastron. A downward adduction of the posterior carapace seems to be most responsible for the kinesis. I observed that the contraction reduces the aperture gap by as much as 50% in *G. flavomarginatus* and occurs through the seventh year of life. However, the anatomical mechanism for the contraction is unknown, partly because the developmental osteology of tortoises has been largely descriptive rather than biomechanical and confined to the European *Testudo* (Ewert 1985).

Most small tortoises also exhibit shell kinesis, especially in the posterior plastron (Pritchard 1979). Not all of these reported kineses are necessarily or entirely paedomorphic. The onset of carapace kinesis late in the ontogeny of African hinge-backed tortoises (genus *Kinixys*) and the progressive flexibility and flattening of the African pancake tortoise (*Malacochersus tornieri*) are not parsimonious with simple paedomorphic explanations (Obst 1988). Perhaps the ontogeny of kinesis in these taxa provides little or no evidence of heterochrony.

Similarly, hinges in some emydid turtles (*Terrapene* and *Cuora*) and in mud turtles (kinosternids) have not been attributed to juvenile antecedents. Softshell turtles (trionychids) represent a special reduction of shell ossification that lead to plastral flaps that may be paedomorphic characters. Some shell flexibility may be a secondary (pleiotropic) consequence of small size. In juveniles and small species, anal gap contractions may reduce the damage from pecking and gnawing attacks by small birds, rodents, and insectivores. The retention of xiphiplastron kinesis may permit oviposition of large eggs in adult females of small species (Rose and Judd 1991).

Systematics

Regional variants and cryptic species of North American emydids and trionychids are usually distinguished more easily from juveniles than from adults. Defining characteristics are often variable or obscure in adults of closely related aquatic turtles, but the colors and patterns of juvenile turtles facilitate identification (Conant 1975). For example, the Cuatro Cienegas softshell turtle (*Apalone spinifera ater*) was described largely from diagnostic characters that were only reliable in juveniles (Webb 1960; Morafka 1977).

The identification of diagnostic character states of young tortoises has been constrained because (1) neonates are poorly known and rarely observed in the field or preserved in collections; (2) the four species of *Gopherus* are allopatric (reducing the need for rigorous diagnostic keys); and (3) no subspecies of any North American tortoise have been described, except in one attempt of classifying all *Gopherus* as subspecies of *G. polyphemus* (Wermuth and Mertens 1961). Studies of molecular genetics (Lamb et al. 1989) and shell morphometrics (Germano 1993) indicate that well-differentiated populations of *G. agassizii* exist. Northern and southern populations of *G. flavomarginatus*, especially juveniles, differ in carapace color (Morafka 1982). Similarly, juvenile desert tortoises in the Mojave Desert generally have greater ratios of shell depth to length, more vivid and contrasting carapace coloration, and more angular or even dentate marginal edges of the carapace than juveniles in the Sonoran Desert (M. A. Joyner, California State University, Dominguez Hills, Carson, and D. Morafka, unpublished data). Like the spiny turtle (*Heoemys spinosa*), a batagurid from Southeast Asia, tortoises in the Mojave Desert tend to have their angular marginals reduced early in ontogeny (Obst 1988). Thus, it may be desirable to develop a diagnosis of gopher tortoises (*Gopherus*) based on variation and differences in juvenile characteristics.

Population Ecology

The recruitment of neonates is a key to understanding the local distributions of tortoises, long-term trends of tortoise densities, and casual factors that limit the colonies. However, there are few data on recruitment of North American tortoises (Germano 1994). Age or size classes are needed to reconstruct past rates and episodes of recruitment. Unfortunately, the success rates of emergence (relative to total deposited eggs) and survivorship of neonates and juveniles may require decades of observations or innovative breakthroughs in data gathering.

As many as 10 years of reproductive effort may be required for successful population recruitment in *Gopherus polyphemus* (Auffenberg and Iverson 1979; Landers et al. 1980) even in environments with relatively stable climates and high vegetative productivity because some individuals and populations of this species may skip reproduction for one or more years. Two species of tortoises (*G. agassizii* and *G. flavomarginatus*) occur in North American deserts, where successful recruitment is probably infrequent because of unpredictable weather in arid environments (Morafka 1977, 1982; Germano

1994). A rare set of environmental conditions may be necessary for the recruitment of tortoises. The absence or rarity of juveniles in populations for 1–2 decades may not indicate recruitment failure in arid environments.

The longevity of researchers, time constraints of studies by graduate students, and inconsistent funding of research combine to make long-term ecological studies rare. Comparative life histories of all four *Gopherus* species may require 20–30 years before precise models for recruitment can be validated with current technology and approaches.

Neonates have as many as 3 times the resting metabolic rates of even 3-year-old juveniles (Naegle and Bradley 1974), and the dietary needs of neonates are twice that of adult tortoises (16% versus 8% protein content; Adest et al. 1989b) and emydids (*Trachemys*; Parmenter and Avery 1990). Neonates presumably have high demands for water and nutrients such as calcium (Esque and Peters 1994).

Neonatal dietary demands may be qualitatively unique as well. For example, neonatal *Iguana iguana* (Troyer 1984a, 1984b) have to acquire appropriate soil microflora and ingest adult feces for efficient fermentation of cellulose in the hind gut of the neonates. There also seems to be a significant role for such fermenting anaerobes in *Gopherus polyphemus* (Bjorndal 1987). The basal metabolic rates are at least one order of magnitude lower in tortoises than in mammals of similar mass (Prosser and Brown 1965). The surface activity of adult tortoises may be only 1–2% of their yearly activity (Nagy and Medica 1986; Adest et al. 1989a).

Tortoises may also have large reserves of bladder water (Nagy and Medica 1986) and stored calories in tissue (liver), which may be physiological factors that buffer environmental stressors. These stores may provide a latent period of several years between unsuitable periods and demographic responses in tortoises. Perhaps scute growth rings can be used to document whether tortoises in stress periods (e.g., droughts) are merely surviving (no growth) or growing slightly based partly on reserves (Germano 1988, 1994).

Recruitment may also be the key to determining whether a population is within the carrying capacity of its environment. When demographic data rely heavily on records of the adult age or size classes, there is little basis to estimate dynamic characteristics, especially recruitment. Criteria of physiology, reproduction, and cohorts (age) may also be useful indicators of the minimum carrying capacity. Although these estimators are more complex than simple numbers (e.g., estimated density), they may be accurate and informative measures of trends. Some indicators may be instructive: (1) blood panels can define the state of health (Morafka et al. 1986); (2) annual increments of shell scutes can indicate the growth of juveniles (Germano 1992); (3) the presence or relative abundance of juvenile classes may be evidence of recruitment (Adest et al. 1989a); (4) the presence of hatchlings may be evidence of successful reproduction; and (5) available protein, calcium, macronutrients, and microhabitats (e.g., friable substrates) indicate resources for neonatal and juvenile tortoises.

A Model of Recruitment in Chaotic Environments

Natural environments may have chaotic processes that do not fit a linear or invariable course of events and thus have unpredictable outcomes. These chaos models have already been useful for simulating dispersal and population densities of arthropods (Hassell et al. 1991). Recently, Lieberman and Morafka (1988) found that physical factors (steep slope, absence of an alluvial substrate, playa borders) limited the occurrence and densities of *G. flavomarginatus* but found no consistent predictors of other habitat variables. The patchy distribution of Bolson tortoises in a desert environment more closely resembles chaos models than simple linear gradients.

To explain the patchy distribution of tortoises, I developed a chaos model for recruitment, much like the sweepstakes dispersal model (Brown and Gibson 1983) that substitutes local weather patterns for the spatial scattering of passive propagules of sweepstakes dispersal. Rather than scatter vagile new reproductive units, the weather patterns themselves scatter unpredictably across a landscape of tortoise demes that are relatively stable in position and reproduction. In the model, the local environment is occupied by clusters of tortoises (colonies or demes) that usually produce small clutches of large eggs ($n = 5–8$) every year, even when nutritional resources are scant (Turner et al. 1986).

The location of significant amounts of seasonal rains (e.g., enough precipitation to trigger the growth of annual and perennial forage plants) represent a call of numbers for each reproductive season. Tortoise clusters that receive sufficient precipitation for one or several years are the winners of a spin of the numbers (chaotic rather than random distribution of precipitation). When local weather produces an unbroken series of years with precipitation and plant blooms, tortoise survivorship increases and robust juveniles eventually replace the aging adults. Or, a few years with relatively high rainfall in every decade may provide enough recruits, some of which survive later droughts.

The minimum reproductive life of tortoises may span 20 years, but some tortoises may survive for shorter (Germano 1992) or longer (Woodbury and Hardy 1948) periods. Each deposition of clutches (cohorts) constitutes the placing of bets for a particular game, and adult female tortoises may participate in 40 or more betting events (20 years × 2 clutches/year) during their reproductive lives. The wagered amount is based on the average clutch size, which is about 5–8 eggs (or 7–10% adult female body weight) per year (Turner et al. 1986; Germano 1994). Whether replacement or population growth is achieved by one successful bet (e.g., one clutch) or by the partial survival of several different cohorts is problematic.

Moderate-to-high precipitation over a large area in winter (Mojave Desert) or summer (Sonoran Desert; Sinaloan thornscrub) leads to vigorous growth of forage for desert tortoises (*G. agassizii*). Tortoise populations in favorable locations (e.g., sites with high local precipitation for 2–3 years) may increase and have individuals or demes expand into adjacent habitats. A dispersion to new areas would probably be by immature tortoises, which seems to occur in *G. flavomarginatus* (Aguirre et al. 1984) and *G. polyphemus* (Auffenberg and Iverson 1979; Diemer 1992).

Precipitation in North American deserts is naturally low in amount, seasonal, often localized, and highly variable from one year to the next (Brown 1982; MacMahon 1988). A few erratic thunderstorms or low amounts of precipitation in a year call only few numbers for a game, resulting in recruitment of few or perhaps no tortoises. Eventually, local extirpations may result in suitable habitats with none or few tortoises. This pattern may be reflected in the disjunct distribution reported of Bolson tortoises (Lieberman and Morafka 1988, but they did not examine this scenario).

Traditional approaches rely on simple linear or multivariate correlations to match tortoise densities with large-scale climatic gradients (e.g., averaged regional precipitation). If the chaos model of recruitment is more representative of local weather patterns (with stochastic events) than regional climates, then chaos process models may better simulate patterns of recruitment and dispersion of tortoise populations. These chaos models may be most applicable to tortoise populations (*G. agassizii* and *G. flavomarginatus*) that occupy arid lands (Table 3).

Reliable and extensive summer rains in habitats of *G. berlandieri* and *G. polyphemus* reduce the chaotic ordination of local populations, and there is considerable mobility of both individuals and populations of these two species (Auffenberg and Iverson 1979). The Berlandier's tortoise (*G. berlandieri*) tends to have recruitment because of the favorable local weather and its mostly continuous habitat (Tamaulipan plain). These tortoises are expected to saturate habitat throughout most of their range, which seems to be the case in the wild (at least before human settlement and farming). Similarly, the relatively stable and abundant rainfall in the southeastern United States is also conducive for the distribution and abundance of *G. polyphemus*. Still, a sequential pattern of fire occurs on sandy hummocks during dry seasons, leading to open stands of longleaf-pine and turkey-oak forest that *G. polyphemus* favors (Auffenberg and Iverson 1979; Diemer 1986).

Life History Models

Growth of all North American tortoises correlated with climatic pattern (Germano 1992, 1994), but there are few models of the life history of tortoises. Here, I attempt to employ the bet-hedging model (Stearns 1976; Congdon and Tinkle 1982), which was first applied to tortoises by Germano (1989). However, I also contrast assessments of total reproduction to that of each reproductive unit (egg or neonate).

Table 3. Demographic characteristics of tortoise (*Gopherus* spp.) populations in different weather patterns as predicted by a Chaos Model of Recruitment.

Characteristic	Reliability and frequency of precipitation: Low	Reliability and frequency of precipitation: High
Neonate survivorship	low and uneven	high and even
Recruitment frequency	low	high
Subadult age classes	absent, rare, or uneven	common or uniform
Local deme densities	low and uneven	high and more even
Deme distribution	unpredictable (chaotic)	highly predictable
Clustered individuals	an effect of weather	social interactions
Individual vagility	low	high

Bet hedging is a life-history strategy of a physically substantial and long-lived parent that makes a limited reproductive investment annually, thereby hedging its energetic bet against a variable environment in which the survivorship of its offspring is doubtful. Couching this model in terms of a predecessor, the "r" versus "K" selection paradigm (MacArthur and Wilson 1967; Pianka 1972; Congdon and Gibbons 1990), the bet hedger has a relatively limited but persistent annual reproduction (K-selected organism) to cope with uncertainties of the environment (r-selecting).

Aquatic sliders (*Pseudemys* and *Trachemys*) represent an aquatic extreme (a stable environment) in contrast to terrestrial *Gopherus* (in a more unpredictable climate). Based on individuals of similar body size, *G. polyphemus* is strikingly different from the cooter turtle *(Pseudemys concinna*; Table 2). Consistent with the model for a bet hedger, the tortoise has a longer life span, later maturity, longer reproductive life, and fewer eggs than the cooter. However, the two seem to make similar investments (annual reproductive effort) relative to body weight (6% in *Gopherus* versus 7% in *Pseudemys*), which does not support the bet-hedging hypothesis.

Ewert (1985) identified several turtles with a high ratio (5–7%) of investment, representing species from a wide range of habitats and life histories. For his comparisons he assumed, perhaps incorrectly, that all taxa produce clutches at the same annual frequency. Even if the assumption is correct, a similar percentage of reproduction is not reflected in the number of the produced eggs. Cooters (*Pseudemys*) have clutches of 20 or more eggs (Table 2) or 400% more than tortoises (*Gopherus*). However, each egg of *Gopherus* is 350% greater in mass (shell accounts for twice the amount of egg) than an egg of *Pseudemys*.

The average mass is 50% greater and the internal lipid content is also relatively greater in neonatal *Gopherus* than in neonatal *Pseudemys*. These features of the neonate tortoise may convey critical advantages for life on land including greater strength, more nutritional reserves, and improved physiological stability from a more favorable surface-to-volume ratio of the body. Combined with mechanical and behavioral flexibilities (Table 1), these attributes may permit the neonate tortoise to better survive and physiologically regulate in a harsh and variable terrestrial environment.

In summary, unlike *Pseudemys,* the reproductive effort (% investment per clutch) of *Gopherus* is not that of a bet hedger. However, for material (especially eggshell calcification) and caloric investment per egg and per neonate, *Gopherus* differentially conserves more resources than aquatic turtles as a hedge against uncertainty. Also, the use of resources may be by a different strategy in the neonates than in adults. The investment per egg or per neonate may be as important as the total reproductive efforts, which is suggested in alligators (Fischer et al. 1991). Thus, the sizes of viable eggs and neonates contribute to optimal clutch size and life history strategies of chelonians.

Neonates as Subjects of Study

Studies of neonatal tortoises afford several opportunities to resolve long-standing debates in chelonian biology. Although currently scarce in nature, neonates sometimes can be obtained from tortoise breeders, many of whom provide the placement of excess neonates in captivity. Also, most North American tortoises are easily bred in captivity, especially in outdoor pens.

Studies of captive neonates and juveniles also offer important practical advantages. For example, 25 neonates comprise about 1 kg of biomass to house, feed, and water, whereas the same sample size of adults would require care of 50 kg of individuals. Young tortoises have some unique features but nevertheless reduce the size and cost of an experiment.

In the field, gravid female turtles may be diagnosed by either radiography (Gibbons and Greene 1979) or with less certainty by manual palpation (Adest et al. 1989b). Oviposition of fully calcified shelled eggs may be induced in the field after intramuscular injection of oxytocin (Ewert and Legler 1978; Adest et al. 1989b). Eggs induced by oxytocin hatch at a rate similar to those naturally deposited, and artificial incubation is equally successful (Adest et al. 1989b). For all captive and field experiments, permits may be required and are mandatory for listed species.

Recent advances in the miniaturization of radio transmitters allow better tracking of free-ranging juvenile tortoises. For example, one company now manufactures a transmitter package that weighs no more than 10% of the neonate body and has a battery life of >150 days. Small transmitters are beginning to reveal important data on young tortoises in the wild (Tom 1994; Wilson et al. 1994).

Acknowledgments

I thank the Southern California Edison Company, especially J. Palmer of Environmental Affairs, and the U.S. Army Corps of Engineers, Fort Irwin, California, for support. Much of the literature for this review was in an annotated bibliography of juvenile desert tortoises by M. Joyner, who also pointed out to me the faults in the current estimation of carrying capacities. I thank D. Germano for information and fruitful discussions, G. Aguirre for valuable field data, E. Buckrucker and T. Clark for valuable analytical suggestions, and G. Adest for comments on the manuscript. Much of this review, especially the comparison of emydids and testudinids, reflects the influence of L. Vitt and the graduate students in his fall 1989 herpetology seminar, University of California, Los Angeles, especially H. Avery, B. Henan, and C. Peterson. I thank J. Hernandez, S. Papadakos, and H. Peck and for technical improvement of the manuscript. All responsibility for the presented errors and opinions rests entirely with me.

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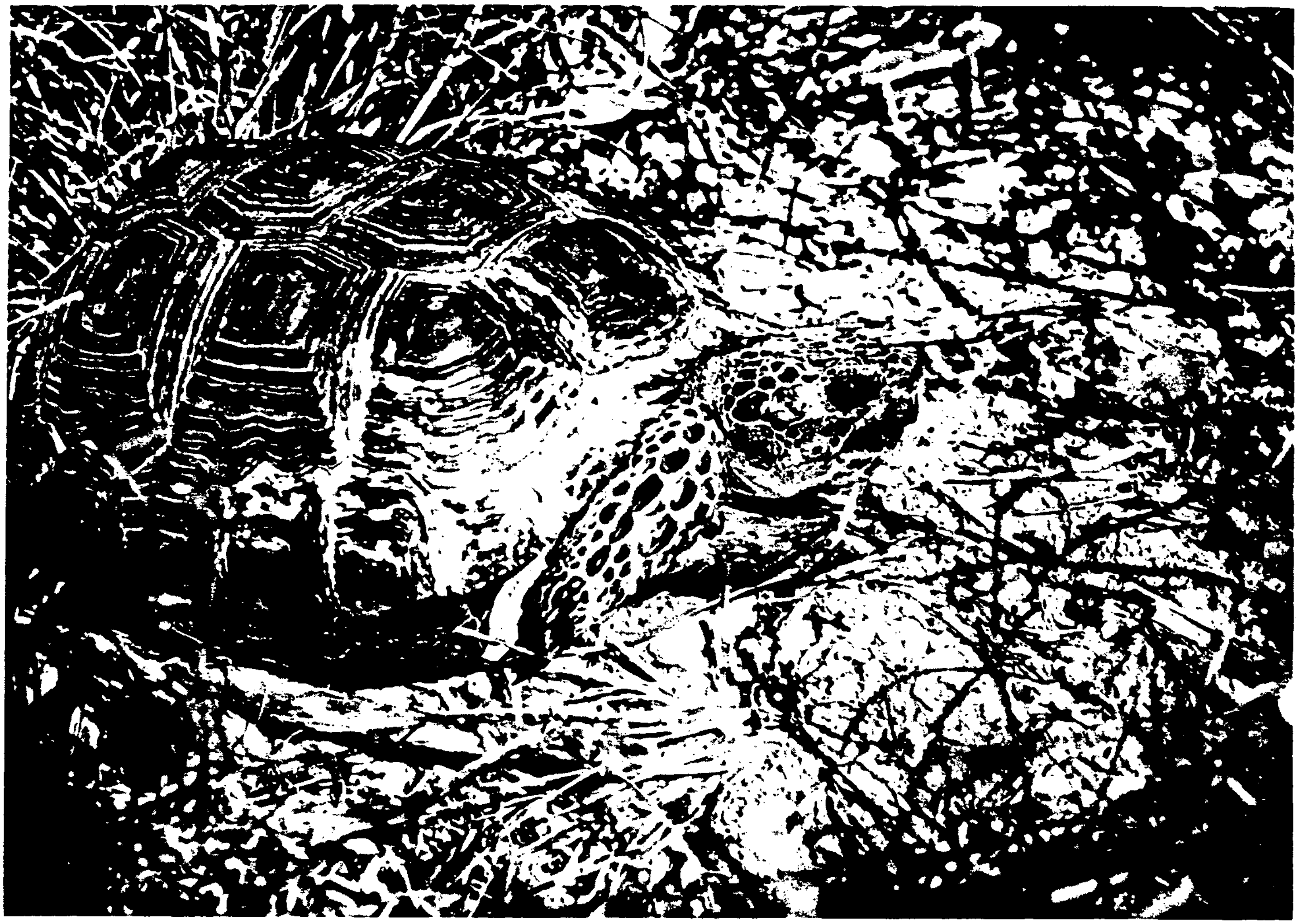

Adult Berlandier's (Texas) tortoise (*Gopherus berlandieri*) from Texas. This is the smallest of the North American tortoises. *Photo by D. J. Germano.*

Comparative Life Histories of North American Tortoises

by

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Abstract. Since 1978, many studies of the four extant species of North American tortoises (*Gopherus* spp.) were conducted. However, few studies on life-history traits have been made, and data are incomplete or not easily compared across species. The best available data are on gopher tortoises (*G. polyphemus*), but information about the life histories of the Berlandier's tortoise (*G. berlandieri*) and the Bolson tortoise (*G. flavomarginatus*) is incomplete. Only two studies on reproduction of desert tortoises (*G. agassizii*)—both in the Mojave Desert—were published; data about the Sonoran or Sinaloan populations are not available. In North American tortoises, the maximum longevity seems to be 50–70 years; the minimum size at first reproduction for females varies from 140-mm carapace length (CL) in *G. berlandieri* to 285-mm CL in *G. flavomarginatus*; the minimum age at first reproduction varies from 13 years in *G. berlandieri* and *G. agassizii* from the western Mojave Desert to 16–21 years in *G. polyphemus* from the northern part of their range. The mean number of eggs per clutch is 1.4–4.3 in *G. berlandieri* to as many as 8.9 in one population of *G. polyphemus*; the number of clutches per year varies from 0 to 3 (all species); and yearly survivorship of eggs and hatchlings is low but that of adults of all species is high (as high as 100%).

Key words: Age at maturity, clutch frequency, clutch size, *Gopherus*, longevity, reproduction, size at maturity, survivorship.

Four extant species of tortoises (*Gopherus* spp.) occur in North America. All are similar in morphology and phylogeny (Auffenberg 1969; Bramble 1982; Germano 1993; Crumly 1994). They are large reptilian herbivores, and at least two species are important to their communities because their burrows provide shelter for other species (Auffenberg 1969). The North American tortoises differ considerably in length; the smallest (*G. berlandieri*) is about 200 mm in carapace length (CL) and the largest (*G. flavomarginatus*) about 350 mm CL (Morafka 1982; Rose and Judd 1982; Germano 1993). *Gopherus agassizii* and *G. polyphemus* are intermediate in size, and some *G. polyphemus* are slightly larger than some *G. agassizii* (Germano 1989; 1993).

Although all four species of North American tortoises are closely related, two species groups are distinguished by minor skeletal differences and differences in ecology (Auffenberg 1976; Bramble 1982; Crumly 1994). The two largest species, *G. flavomarginatus* and *G. polyphemus*, are more closely related to each other than to either *G. agassizii* or *G. berlandieri* (Auffenberg

1976; Bramble 1982; Lamb et al. 1989), although *G. agassizii* and *G. berlandieri* are not sister species (Crumly 1994).

Gopherus flavomarginatus and *G. polyphemus* construct long burrows in sandy soils, whereas *G. agassizii* and *G. berlandieri* construct much shallower burrows or, in some parts of both species' range, may not construct burrows (Auffenberg 1969; Germano et al. 1994). The distributions of *G. flavomarginatus* and *G. polyphemus*—but not usually the distributions of populations of *G. agassizii* and *G. berlandieri*—are clumped (Auffenberg 1969; Morafka 1982). Most of the range of *G. polyphemus*, the coastal range of *G. berlandieri*, and the southern part of the range of *G. agassizii* can be considered subtropical (Auffenberg 1969; Germano 1989). In contrast, the entire range of *G. flavomarginatus* is in the Chihuahuan Desert, much of the range of *G. agassizii* is in the Mojave and Sonoran deserts, and the inland portion of the range of *G. berlandieri* is in semiarid scrubland (Auffenberg 1969; Germano 1989).

Sexual dimorphism is greatest in the smallest species, *G. berlandieri*; males have distinct secondary sexual characteristics. The largest species, *G. flavomarginatus*, is least sexually dimorphic. Among the four species, sexual dimorphism inversely correlates with size (Germano 1993). The range of behavioral differences among these species is unknown.

Morphological and ecological differences among *Gopherus* species may significantly affect life history traits. Data on longevity, birth rate, age at first reproduction, survivorship, sex ratio, and age distribution are vital to a complete understanding of these species and to their proper conservation. The Endangered Species Act of 1973 lists all populations of *G. flavomarginatus* as endangered and *G. agassizii* and *G. polyphemus* as threatened in portions of their range. Data on life history traits can be used to simulate population dynamics and to predict the viability of a population. Without these data, little progress in the conservation of these species can be expected.

This paper presents a review of the known life history traits of North American tortoises and includes a comparison of the completeness and accuracy of these data and recommended techniques for further comparisons between species.

Life History Traits

Longevity

Species of *Gopherus* seem to be long-lived, but the actual average and maximum longevities of these species are not known (Table 1). Although some individuals may live 50 to 60 years and possibly longer, many adults may not live that long. No estimates of the maximum age of *G. flavomarginatus* exist. The only estimates of the longevity of *G. berlandieri* are of captive animals and indicate that individuals can live more than 60 years (Judd and McQueen 1982; Judd and Rose 1989). However, longevity is often greater of captive than of wild animals (Gibbons 1987). The estimated longevity of *G. polyphemus* (Landers 1980) is not supported by data on known ages of tortoises in the wild. The estimated longevities of *G. agassizii* (Table 1) are based on tortoises in the wild but are minimum values because of the uncertainty of the accuracy of the estimates (Germano 1992). These estimates also reflect ages of only the oldest individuals, not average longevity. For example, although the oldest adult (≥16 years) *G. agassizii* from the eastern Mojave Desert died when it was about 50 years old, only 17% of the adults lived longer than 25 years (Germano 1992).

The few estimates of the longevity of any chelonians in the wild indicate that *Testudo hermanni* may live about 40 years (Meek 1985), *Geochelone gigantea* 55–70 years (Bourne and Coe 1978), *Che-*

Table 1. Estimated maximum longevity of individuals in the four species of North American tortoises (*Gopherus* spp.).

Species	Age (years)	Source
G. berlandieri	60+[a]	Judd and Rose (1989)
G. agassizii		
Western Mojave Desert	32	Germano (1992)
Eastern Mojave Desert	48–52	Germano (1992)
Sonoran Desert	35	Germano (1992)
Sinaloan habitats	32	Germano (1992)
G. polyphemus	40–60	Landers (1980)
G. flavomarginatus	—	

[a] Captives.

lydra serpentina 60 years (Galbraith and Brooks 1989), *Terrapene carolina* 36–59 years (Schwartz and Schwartz 1991) and 50–80 years (Stickel 1978), and *T. ornata* 32 years (Blair 1976). The estimated longevity of the slider turtle (*Trachemys scripta*) has varied from as many as 75 years (Cagle 1950) to not greater than 30–35 years (Gibbons and Semlitsch 1982; Gibbons 1987). The similarity of the estimated maximum longevity of *Gopherus* species with other chelonians supports the notion that individuals rarely live more than 50–60 years in the wild.

Size at First Reproduction

Data on the size at first reproduction (SFR) of *G. polyphemus* (but not of the other species) are fairly complete (Table 2). Data on male *G. agassizii*, *G. berlandieri*, and *G. flavomarginatus* do not exist. Size at first reproduction of *G. polyphemus* differs in the geographic range of the species and between sexes. The only published data on *G. flavomarginatus* is from a captive female raised in Los Angeles (Morafka 1982), and the relevance of these data to individuals in the wild is unknown. Female *G. berlandieri* first reproduce at 140-mm CL (Judd and Rose 1989), which is the smallest SFR of females in the four species (Table 2).

Techniques for determining SFR may profoundly affect results. The use of radiography is the most effective noninvasive technique for determining the presence of eggs inside a female (Gibbons and Greene 1979) and is becoming widely used. However, the choice of subjects to radiograph in the field may determine or influence the lower limits of size of reproducing females. Until radiography was used in the eastern Mojave Desert, SFR of female *G. agassizii* was considered to be greater than 200-mm CL (Woodbury and Hardy 1948; Burge 1977; Burge and Bradley 1976). However, radiographs of females of less than 200-mm CL showed that some 189–194-mm-CL females reproduced regularly (Turner et al. 1986).

Recent work in the western Mojave Desert revealed smaller SFRs. At a site northeast of Barstow, California, all females and all nonadult tortoises (whose sex could not be determined) were radiographed during spring of 1990, and the second smallest tortoise (176-mm CL) had three eggs (M. A. Griffith, California State University, Carson, personal communication). The sex of *G. agassizii* of less 180-mm CL cannot be determined confidently from shell characteristics. Thus, SFR of *G. agassizii* may be lower than currently reported after smaller individuals will have been examined with radiography.

Techniques for determining SFR of male tortoises have included the examination of secondary sexual characteristics (Landers et al. 1982; Rose and Judd 1982; Diemer and Moore 1994), observation of courtship behavior (Douglass 1976; Landers et al. 1982; Diemer and Moore 1994), and the observation of sperm in seminiferous tubules (Taylor 1982). Data from several sources are available only on *G. polyphemus* and provide the best basis for estimating male SFR (Table 2). Based

Table 2. Minimum size at first reproduction of females and males in the four species of North American tortoises (*Gopherus* spp.).

Species	Carapace length (mm)		Source
	Females	Males	
G. berlandieri	140	—	Judd and Rose (1989)
G. agassizii			
Western Mojave Desert	176	—	M. A. Griffith (unpublished data)
Eastern Mojave Desert	189	—	Turner et al. (1986)
G. polyphemus			
Northern range	250–265	230–240	Landers et al. (1982)
Southern range	226–238	180–230	Auffenberg and Iverson (1979); Iverson (1980); Diemer and Moore (1994); Taylor (1982); Linley (1986)
G. flavomarginatus	285[a]	—	Morafka (1982)

[a] Captive.

only on the appearance of secondary sexual characteristics, male *G. berlandieri* may mature at 110-mm CL (Rose and Judd 1982). Using this criterion, male *G. agassizii* may mature at 180-mm CL (Burge and Bradley 1976), although male characteristics sometimes are evident at 120–140-mm CL (Grant 1936). However, whether the sizes of these three species of *Gopherus* correspond to sexual behavior is not known. Male *G. flavomarginatus* do not have pronounced secondary sexual characteristics (Adest et al. 1989), but sometimes the sex of a male can be confirmed when his carapace length is about 200 mm.

Age at First Reproduction

Based on limited data, female North American tortoises mature at between 13 and 20 years of age (Table 3). Differences in CL do not affect the estimates of age at first reproduction (AFR) because females of the largest (*G. flavomarginatus*) and the smallest (*G. berlandieri*) species mature at approximately the same age. Some females mature when they are only 10 years old (Table 3). The only data on male tortoises pertain to *G. polyphemus* and indicate that males reach maturity at a slightly younger age than females (Table 3).

The most complete data on AFR are of *G. polyphemus*. Data on the other species are based on one study (Germano 1994). In all cases, the age of an individual is determined by counting growth annuli on either the carapace or the plastron. The age at which most females first started to reproduce is usually estimated from a regression of age to SFR (Germano 1994; Diemer and Moore 1994). Therefore, the accuracy of AFR depends on knowing the size at which females first produce eggs. This makes the estimated AFRs of *G. flavomarginatus* and the Sonoran and Sinaloan populations of *G. agassizii* equivocal. The estimated age of *G. flavomarginatus* is based on a single captive individual, and the estimated ages of the Sonoran and Sinaloan populations of *G. agassizii* are based on size to maturity of tortoises from the eastern Mojave. Whether this size is accurate for the Sonoran and Sinaloan populations is not known. Comparable data on AFR will be possible only when SFRs of *G. flavomarginatus* , *G. agassizii*, and *G. berlandieri* are reliably estimated.

Number of Eggs per Clutch

The information about the number of eggs per clutch in *G. flavomarginatus*, *G. agassizii*, and *G. berlandieri* is incomplete (Table 4). On clutch size, ten studies of wild *G. polyphemus*, three studies of wild *G. berlandieri*, two studies of wild *G. agassizii* (one from the eastern Mojave Desert

Table 3. Minimum age at first reproduction (range) of females and males in the four species of North American tortoises (*Gopherus* spp.).

Species	Age (years)		Source
	Females	Males	
G. berlandieri	13.3(11–17)		Germano (1994)
G. agassizii			
Western Mojave Desert	13.0(9–18)		Germano (1994)
Eastern Mojave Desert	15.4(12–19)		Germano (1994)
Sonoran Desert	15.7(11–21)[a]		Germano (1994)
Sinaloan habitats	13.8(12–15)[a]		Germano (1994)
G. polyphemus			
Northern range	16–21	16–18	Landers et al. (1982); Germano (1994)
Southern range	13.6(10–16)	ca. 10	Iverson (1980); Linley (1986); Germano (1994); Diemer and Moore (1994)
G. flavomarginatus	13.9(12–17)[b]		Germano (1994)

[a] Ages based on minimum size-at-first reproduction of eastern Mojave Desert *G. agassizii*.

[b] Captive.

and one from the western Mojave Desert), one study of captive *G. agassizii* (not counting anecdotal reports), and one study of captive *G. flavomarginatus* (Table 4) are available. The largest clutch size is of *G. polyphemus* from the southern part of its range, and the smallest is of *G. berlandieri*. Clutch sizes in the Sonoran and Sinaloan populations of *G. agassizii* and in wild populations of *G. flavomarginatus* have not been published.

Number of Clutches per Year

The number of clutches per year ranges from 0 to 3, and means by species and region range from 1.0 to 1.7 (Table 4). Techniques to determine the number of clutches per year have included examining dead specimens (Auffenberg and Weaver 1969; Iverson 1980; Rose and Judd 1982), using oxytocin to induce egg deposition (Adest et al. 1989), measuring sudden weight changes (Turner et al. 1984), and applying periodic radiography (Turner et al. 1986; Judd and Rose 1989; Diemer and Moore 1994).

Three studies of *G. polyphemus* revealed that females lay 1 clutch/year (Table 4). Earlier, it was believed that *G. berlandieri* deposited as many as 2 or more clutches/year (Auffenberg and Weaver 1969; Rose and Judd 1982). It has been suggested that females lay only one clutch annually (Judd and Rose 1989). No supporting data were given for the estimated average of 1.39 clutches/female by wild *G. flavomarginatus* (Adest et al. 1989), but this estimate indicates that some females lay more than 1 clutch/year. Captive female *G. flavomarginatus* can have as many as 3 clutches/year (Table 4). The fecundity of *G. agassizii* in its range in the western Mojave, Sonoran, or Sinaloan deserts is not known, but two studies in the eastern Mojave Desert revealed common multiple clutching (Turner et al. 1986, 1987). Both studies were based on frequent measurements, and one study (female tortoises radiographed every 10 days) indicated that most females had 2 clutches/year and one female had 3 clutches in 2 of 3 years (Turner et al. 1986).

Double and triple clutching in North American tortoises seem to be limited to *G. agassizii* from the eastern Mojave Desert and perhaps to *G. flavomarginatus* but may be more widespread. One

Table 4. Mean number of eggs per clutch (range, number of clutches) and mean number of clutches per year (range) in the four species of North American tortoises (*Gopherus* spp.).

	Mean		
Species	Eggs per clutch	Clutches per year	Source
G. berlandieri	1.42(1–3,73)	ca. 2	Auffenberg and Weaver (1969)
	4.30(3–7,10)	1–2	Rose and Judd (1982)
	2.65(1–5,29)	1	Judd and Rose (1989)
G. agassizii	6.71(2–14,7)[a]	1–2[a]	Miller (1955)
Western Mojave Desert	(1–7,39)	—	M. A. Griffith (unpublished data)
Eastern Mojave Desert	4.50(1–8,107)	1.73(0–3)	Turner et al. (1986)
		1.60(0–2)	Turner et al. (1984)
G. polyphemus			
Northern range	7.0(4–12,47)	1	Landers et al. (1980)
	3.5(1–6,4)	—	Marshall (1987)
	5.3(1–7,7)	—	Marshall (1987)
Southern range	5.2(1–9,32)	1	Iverson (1980)
	6.7(2–10,24)	1	Taylor (1982); Diemer and Moore (1994)
	7.8(5–10,16)	—	Linley (1986)
	7.6(3–25,32)	—	Godley (1989)
	8.9(5–11,11)	—	Burke (1987)
	5.8(3–10,62)	—	Diemer and Moore (1994)
G. flavomarginatus	6.0(3–9,9)[a]	ca. 2(0–3)[a]	Morafka (1982)
		1.39	Adest et al. (1989)

[a] Captive.

study of the reproduction of *G. polyphemus* was based on dissections of museum specimens and recently killed tortoises (Iverson 1980), and the investigator stated that *G. polyphemus* laid only 1 clutch/year. However, the data are of the duration of the reproductive cycle and not of the number of the deposited clutches. Graphic data (Fig. 1 *in* Iverson 1980) showed enlarged follicles or eggs in females from late March until late June, whereas tabular information indicated the presence of enlarged follicles from October to May and oviductal eggs from April to June. The latter interval is perhaps long enough for the production of more than 1 clutch/year.

Female *G. polyphemus* in the northern portion of their range reportedly lay 1 clutch/year based on periodic examinations of burrow mouths and surrounding areas for signs of nesting (Landers et al. 1980). However, how frequently burrows were examined and whether nesting immediately after an inspection could be detected during a subsequent visit are unclear. Finally, whether any females failed to reproduce in a given year was also not known (Landers et al. 1980). One study with radiography to detect clutches of eggs in female *G. polyphemus* revealed that only one clutch was deposited annually, but females were usually radiographed only once a year (Diemer and Moore 1994).

Similarly, data on *G. berlandieri* suggest only one clutch of eggs annually, but radiographs were taken every 2 weeks and the investigators pointed out that multiple clutches could have been missed in some cases (Judd and Rose 1989). This study further revealed that egg production begins in April, but radiographs were not taken at 2-week intervals until 20 May.

Consistent multiple clutches in wild populations of North American tortoises were found only in *G. agassizii* from the eastern Mojave desert (Turner et al. 1984, 1986), where tortoises were evaluated at intervals shorter than 2-weeks. Female tortoises were radiographed every 10 days between late April and early to mid-July (Turner et al. 1986). The short intervals between radiographing may have been the reason for the discovery of multiple clutches. Until these studies, no data indicated that wild *G. agassizii* laid more than 1 clutch/year. Although female *G. polyphemus* and *G. berlandieri* may only lay 1 clutch/year, the data are equivocal.

Survivorship

From Egg to Emergence From the Nest

Survivorship of any age class of *G. berlandieri* (Judd and Rose 1989) or of *G. agassizii* from Sonoran or Sinaloan habitats have not been estimated (Table 5). The only estimated clutch survivorship in *G. berlandieri* is an estimate of egg fertility.

Clutch survivorship in *G. agassizii* in the eastern Mojave Desert, which was estimated from nest destruction, was 24–28% in 1983 (Turner et al. 1987) and 70% in 1984 (Roberson et al. 1989; F. B. Turner and K. H. Berry, unpublished report to Southern California Edison Company, 85-RD-63). The estimated fertility was 88%, but the estimated hatching rate was only 46% in nests protected from predation. This low hatching rate may have been due to the effects of human disturbance when eggs were moved.

In contrast, the hatching rate in tortoises from a western Mojave Desert study site was high (Table 5). In this study (M. A. Griffith, California State University, Carson, personal communication), gravid females were placed in a large enclosure in native habitat close to where they were captured. The females deposited eggs in nest sites they constructed, and the eggs were incubated in an undisturbed nest free from predation. I used this fertility rate with the estimates of nest destruction to estimate clutch survivorship in tortoises from the eastern Mojave Desert (Table 5).

In southwestern Georgia, 34 of 38 nests of *G. polyphemus* were destroyed (11% survivorship), although 154 of 179 protected eggs hatched at an 88% fertility rate (Table 5). The estimated clutch survivorship of *G. flavomarginatus* (Adest et al. 1989) is not supported by data and may not be accurate.

The survivorship of clutches should be interpreted with caution. Predation seems to be a major cause of clutch failure, but exact estimates of clutch survival are not easily produced. Tinkle et al. (1981) pointed out that, when Cagle (1950) reported counting 500 destroyed nests of *Chrysemys picta* and only one intact nest, this could not be interpreted as only 1 surviving clutch of 500 clutches because the actual total number of nests in the area was unknown. Investigators may find nests that have been disturbed by predators more easily than intact nests.

From Hatching to Year One

The survival rate (51%) of *G. agassizii* hatchlings (Table 5) was estimated from smaller-than-80-mm-CL tortoises (F. B. Turner and K. H. Berry, unpublished report to Southern California Edison Company, 85-RD-63), which probably included 2–3-year-old individuals. The low survivorship of *G. polyphemus* (Table 5) is the estimated survivorship from egg to age 1, which integrates two sets of survivorship estimates. Furthermore, this low estimate is based solely on counts of burrows and may partially represent a failure to locate small burrows. The estimated survivorship of *G. flavomarginatus* (Table 5) was based on a group of 11 hatchlings that was followed for 1 year. Five died in 11 months (54.5% survivorship), only three were found a year later (27.2% survivorship), and the fates of another three individuals were not known (Tom 1988).

From Year One to Maturity

The yearly survivorship of *G. agassizii* (Table 5) was estimated by the skeletal remains on two plots in the eastern Mojave Desert and was 71% of ≤180-mm CL tortoises during 1977–80 and 89% of 81- to 160-mm CL tortoises during 1983–84 (F. B. Turner and K. H. Berry, unpublished report to Southern California Edison Company, 85-RD-63). I used the sizes of these tortoises to estimate the survivorship to maturity, but these estimates only roughly correspond to correct ages. Furthermore, these estimates are only crude approximations and may not accurately reflect survivorship (F. B. Turner, University of California, Los Angeles, personal communication); I included them because they are the only available estimates.

Similarly, the estimated survivorship to maturity of *G. polyphemus* (Table 5) is only approximate. One estimate was made with a Jolly–Seber model and pertains to less than 100-mm CL and 100–199 mm CL tortoises (J. E. Diemer, unpublished report to Florida Game and Fresh Water Fish Commission, Study 7536). Many assumptions

Table 5. Estimates of survivorship in the four species of North American tortoises (*Gopherus* spp.) at four life stages.

Species	Eggs laid to hatching (%)	Hatching to year one (%)	Year one to maturity (%)	Adult (%)
G. berlandieri	60[a,b]	—	—	—
G. agassizii				
Western Mojave Desert	93[a,c]	—	—	83.7–100[d]
Eastern Mojave Desert	46–67[e]	51[e]	71–89[g,e]	75–98[e]
G. polyphemus				
Northern range	11–86[a,f]	—	—	—
Southern range	—	5.8[h]	53–66[g,j]	44–95[j]
			12.5–79[i]	—
G. flavomarginatus	12.5–65[a,k]	27.2–54.5[l]	60–96[k]	—

[a] Fertility.
[b] Rose and Judd (1982).
[c] M. A. Griffith (personal communication).
[d] Berry (1986).
[e] Turner and Berry (unpublished report).
[f] Landers et al. (1980).
[g] Tortoises 1–4 years old followed for 1 year.
[h] Alford (1980).
[i] Diemer (unpublished report).
[j] Wilson (1991).
[k] Adest et al.(1989).
[l] Tom (1988).

for this model were not met. The other estimated survivorship is of 1–4-year-old tortoises that were followed for 1 year (Wilson 1991). Of 32 tortoises that were fitted with radio transmitters, 11 were dead and 4 were missing after 1 year (Wilson 1991).

The survivorship of *G. flavomarginatus* (Table 5) was estimated from 27 tortoises marked as juveniles (117–198-mm CL) between 1980 and 1985 (Adest et al. 1989). Only 2 of these tortoises were later found alive in the colony—5 dead were found, and the disposition of the remaining 20 was unknown (Adest et al. 1989). If the remaining 20 tortoises were alive but not found, the mean yearly survivorship of this group was about 96%; if only the 2 tortoises found in the colony after 5 years survived, the yearly rate was about 60%.

Adults

The only estimated adult survivorship was of *G. agassizii* from the Mojave Desert and of one population of *G. polyphemus* (Table 5). This may have been due in part to the ease of finding skeletal remains of tortoises in the Mojave Desert, from which death rates of adults are computed. Vegetation in most other parts of the range of the North American tortoises is considerably more dense and may impede finding remains. Although the habitat is fairly open, few adult *G. flavomarginatus* are ever found (Bury et al. 1986). Alternatively, adult *G. flavomarginatus* may die in their burrows, which may be as long as 10 m.

The estimated adult survivorship of *G. agassizii* from the Californian portion of its range is high (Berry 1986). These estimates were obtained during 3–9 year studies at 14 sites and indicate that mortality was low in the eastern Mojave Desert and moderate to high in the western Mojave Desert (Berry 1986; Corn 1994). The usual survivorship of adult *G. agassizii* seems to be high, but occasionally adult mortality is high in some years (Turner et al. 1987; Germano and Joyner 1989).

The population dynamics of tortoises in North America are not well known (Auffenberg and Iverson 1979). Survivorship of different age classes and their interrelations will be difficult to determine but must be determined for an understanding of the responses of North American tortoises to their environment and to perturbations.

Conclusion and Recommendations

More data on the life histories of North American tortoises are needed. The fecundity, longevity, and survivorship of all species—especially of Sonoran and Sinaloan populations of *G. agassizii* and inland and Mexican populations of *G. berlandieri*—have to be determined. Studies of fecundity should be patterned after the study of *G. agassizii* in the eastern Mojave Desert (Turner et al. 1986). At least 30 reproductive female tortoises should be studied and fitted with radio transmitters, so that they can more easily be found during the breeding season. Each female should be X-rayed every 10 days from the onset to the end of the breeding season. Radiographing should continue until the investigator is certain no more eggs are being produced. However, the possibility of detrimental effects on females or eggs from periodic exposure to X-rays should be evaluated first.

In addition to studies of clutch size in adult tortoises, the smallest size at which females and males can reproduce should be determined. Radiography should be used for the detection of eggs in larger-than-90-mm-CL *G. berlandieri*, in larger-than-150-mm-CL *G. agassizii* and *G. polyphemus*, and in larger-than-200-mm-CL *G. flavomarginatus* to determine the lower limits of female reproductive maturity. Injections of the cloacae with water should be used for the detection of sperm in known males and in smaller individuals whose sex is not ascertained and in which eggs are not found. The same males should be monitored to determine the age at which males begin to exhibit sexual behavior.

The ages of all individuals must be determined. The age of many tortoises can be determined by the counting of scute rings by a technician who has learned to distinguish annuli from false rings (Germano 1988; Germano and Joyner 1989). A thin section of scute of older tortoises can be taken for later age determination or, at least, the individual can be assigned an age group (e.g., >25 years old). Counts of growth rings of North American tortoises as old as 20–25 years are reasonably accurate (Landers et al. 1982; Germano 1988, 1992). Easily seen scute rings in individuals that are older than 25 years are no longer useful, but sections of thin scute may be used to determine the age of older individuals (Germano 1992). Other nondestructive techniques of aging living tortoises have yet to be developed. Counts of scute rings should be made in a random sample of tortoises that are studied in the field.

Data on small individuals are important missing information of the demography of tortoises. Locating small tortoises can be aided by using dogs, which have been successful in finding box turtles (Schwartz et al. 1984). Dogs have shown some promise for locating desert tortoises in California (K. H. Berry, Bureau of Land Management, Riverside, California, personal communication) and Arizona (personal observation), but there has been no consistent testing. Recent work with radio-tagging hatchling tortoises and following them for extended periods will help determine survivorship rates, but many studies and large sample sizes will be needed to accurately determine rates and patterns of hatchling and juvenile survivorship.

Determination of survivorship is perhaps most difficult but efforts should continue because tortoises lend themselves to long-term studies of demography. With recent advances of aging tortoises, the age of any young and subadult individual can be determined. This allows the building of static life tables. Combining the ability to age individuals with effective mark–recapture–study areas will provide information about the survivorship of the age groups.

Acknowledgments

I thank G. A. Adest, R. B. Bury, J. E. Diemer, M. A. Joyner, F. L. Rose, and F. B. Turner for critically reviewing earlier drafts of this paper.

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Bolson tortoise (*Gopherus flavomarginatus*), Mapimi Field Station, Mexico, 1988. *Photo by D. J. Germano.*

Research on North American Tortoises: A Critique With Suggestions for the Future

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Abstract. Research and conservation of North American tortoises (genus *Gopherus*) increased greatly in the past 20 years, but the quantity and quality of the studies of each of the four species vary widely. Only work on the gopher tortoise (*G. polyphemus*) was sufficiently broad in geographic scope and in coverage of topics to begin answering basic biological questions. More rigorous studies of the biology of all four species are needed for comprehensive information, including better definitions or evaluations of distribution, range limits, use of habitats, life histories, juvenile ecology, and physiology. An obstacle to past and current research is the preponderance of unpublished literature and lack of scientific hypotheses, especially of studies on desert tortoises (*G. agassizii*). Important management decisions have been made without adequate knowledge about the biology of the affected species. We suggest that future studies of all four species should be comparable (e.g., analyze growth rates between species), test hypotheses, and be designed for publication in peer-reviewed outlets. These efforts will improve the research and conservation of North American tortoises.

Key words: Bibliography, *Gopherus*, gray literature, habitat evaluations, methodology, reproduction studies.

Surveys and studies of tortoises, particularly of the desert tortoise (*Gopherus agassizii*) and the gopher tortoise (*G. polyphemus*), increased profoundly in the 1970's and 1980's. However, the work did not lead to an equal increment in the understanding of the biology of North American tortoises for reasons we address here. Specifically, this paper provides a review of published literature on North American tortoises, a critique of current studies and research on tortoises, and suggestions to

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[1] Now with National Biological Survey, same address.

improve the study and conservation of North American tortoises.

Adequacy of the Research

Summaries of Publications

Bibliographies on North American tortoises (Douglass 1975, 1977; Hohman et al. 1980; Diemer 1981; Beaman et al. 1989) list hundreds of papers, most of which were not reviewed by peers or are difficult to obtain. This paper partially fills the need for tabulated recent literature (Tables 1–4), but we selected only major publications (judged as seminal works), key historic references, and advancements in the study of each species.

Published Literature

The quantity and quality of research on each species of the North American tortoises differ markedly. Although the geographic scope of work on the Berlandier's tortoise (*G. berlandieri*) is limited, studies of this species have been exceptional because of the diversity of topics and intensive methodology (Table 1) and because almost all studies were published in journals or books. The findings on the Bolson tortoise (*G. flavomarginatus*) are remarkable because the animal was only recently discovered (Legler 1959) and ecological studies of the species have been under way for only about 10 years. To the credit of the investigators, most papers on the Bolson tortoise are available in outlets for peer-reviewed publications (Table 2).

Numerous studies of the gopher tortoise (Table 3) and desert tortoise have been conducted (Table 4). Based on the number of the studies, expanse of the studies over the species' range, diversity of the topics, and publication of results in journals, the best-studied North American tortoise is the gopher tortoise. Many graduate students selected this species as the topic of their theses—for example, parts of two theses are in this volume (Linley and Mushinsky 1994; Wilson et al. 1994). Many topics have been studied in detail (Table 3). Several comprehensive studies of the ecology and other topics on the desert tortoise have been completed (Table 4). The extent of past research does not preclude more work but points out existing information.

Unpublished Literature

Unlike information on the other species of North American tortoises, much information

Table 1. Selected publications on the biology of *Gopherus berlandieri*.

Ecology	Strecker (1927); Hamilton (1944); Mittleman (1947); Auffenberg (1969); Auffenberg and Weaver (1969); Rose and Judd (1982); Bury and Smith (1986)
Growth	Judd and McQueen (1980); Germano (1994b)
Morphology	True (1882); Smith and Brown (1946); Paxson (1961);Auffenberg (1976); Auffenberg and Franz (1978a); Bramble (1982); Rose and Judd (1991); Crumly (1994); Germano (1993)
Reproduction	Brown (1964); Auffenberg and Weaver (1969); Rose and Judd (1982); Judd and Rose (1989)
Longevity	Judd and McQueen (1982)
Physiological processes	Olson (1976); Voigt and Johnson (1976,1977); Horne and Findeisen (1977); Judd and Rose (1977); Neck (1977); Rose and Judd (1982); Olson (1987); Rose et al. (1988)
Disease and parasites	Bowen (1977); Goff and Judd (1981); Schmidt and Fletcher (1983)
Food Habits	Rose and Judd (1982)
Activity and home range	Rose and Judd (1975)
Behavior	Eglis (1962); Weaver (1970)
Demography	Judd and Rose (1983); Bury and Smith (1986)
Distribution	Gunter (1945); Brown (1950); Auffenberg and Franz (1978c); Rose and Judd (1982)

Table 2. Selected publications on the biology of *Gopherus flavomarginatus*.

Ecology	Auffenberg (1969); Morafka et al. (1981); Morafka (1982); Appleton (1986); Bury et al. (1988); Morafka and McCoy (1988); Lieberman and Morafka (1988); Adest et al. (1989a); Morafka (1994); Tom (1994); Germano (1994b)
Morphology	Legler (1959); Legler and Webb (1961); Auffenberg (1976); Auffenberg and Franz (1978a); Bramble (1982); Morafka (1982); Crumly (1994); Germano (1993)
Reproduction	Morafka (1982); Adest et al. (1989a)
Physiological processes	Aguirre et al. (1979); Rose (1983)
Husbandry	Appleton (1980); Adest et al. (1989b)
Food habits	Aguirre et al. (1979)
Activity and home range	Aguirre et al. (1979, 1984); Lindquist and Appleton (1985); Adest et al. (1988); Tom (1994)
Demography	Aguirre et al. (1979); Bury et al. (1988)
Biogeography	Morafka (1988)
Distribution	Auffenberg and Franz (1978d); Morafka (1982); Bury et al. (1988)

Table 3. Selected publications on the biology of *Gopherus polyphemus*.

Ecology	Hubbard (1893); Hallinan (1923); Hansen (1963); Auffenberg (1969); Douglass and Winegarner (1977); Douglass (1978); Dietlein and Franz (1979); Landers (1980); Lohoefner and Lohmeier (1981); Auffenberg and Franz (1982); Lohoefner (1982); Means (1982); Kushlan and Mazzotti (1984); Diemer (1986); Kaczor and Hartnett (1990); Breininger et al. (1991); Wilson (1991); Wilson et al. (1991)
Growth	Goin and Goff (1941); Landers et al. (1982); Germano (1990, 1994b)
Morphology	True (1882); Allen and Neill (1953); Neill and Allen (1957); Spearman (1969); Auffenberg (1976); Auffenberg and Franz (1978a); McRae et al. (1981a); Bramble (1982); McEwan (1982); Palmer and Guillette (1988); Palmer (1989); Crumly (1994); Germano (1993)
Reproduction	Hubbard (1893); De Sola and Abrams (1933); Kenefick (1954); Arata (1958); Auffenberg and Iverson (1979); Iverson (1980); Landers et al. (1980); Linley (1986); Martin (1989); Diemer and Moore (1994); Germano (1994a); Linley and Mushinsky (1994)
Courtship and mating	Auffenberg (1966); Douglass (1976, 1990)
Physiological processes	Jackson et al. (1974); Minnich and Ziegler (1977); Ross (1977); Douglass and Layne (1978); Minnich (1979); Taylor and Jacobson (1982); Bjorndal (1987); Ultsch and Anderson (1986); Linley and Mushinsky (1994)
Burrow commensals	Young and Goff (1939); Brode (1959); Speake (1981); Woodruff (1982); Franz (1986); Jackson and Milstrey (1989); Lips (1991)
Food habits	Garner and Landers (1981); MacDonald and Mushinsky (1988)
Behavior and movement patterns	Brode (1959); Gibbons and Smith (1968); Gourley (1972, 1974, 1984); Douglass and Layne (1978); McRae et al. (1981b); Hailman et al. (1991); Diemer (1992b); Wilson et al. (1994)
Relocation	Diemer and Moler (1982); Lohoefner and Lohmeier (1986); Diemer (1987); Burke (1989a, 1989b); Diemer et al. (1989 and papers within)
Demography	Auffenberg and Iverson (1979); Alford (1980); Wester (1983); Linley (1986); Cox (1989); Diemer (1992a); Mushinsky and McCoy (1994)
Distribution	Auffenberg and Franz (1978e); Sanders (1981); Auffenberg and Franz (1982); Mann (1990)

Table 4. Selected publications on the biology of *Gopherus agassizii.*

Ecology	Grant (1936b, 1946); Woodbury and Hardy (1940, 1948); Loomis and Giest (1964); Burge and Bradley (1976); Burge (1978, 1979, 1980); Bury et al. (1978); Hohman and Ohmart (1978); Barrow (1979); Medica et al. (1980); Sheppard (1981); Reyes Osorio and Bury (1982); Luckenbach (1982); Berry and Turner (1987); Turner et al. (1987a, 1987b); Barrett (1990); Fritts and Jennings (1994); Germano et al. (1994)
Growth	Bogert (1937); Miller (1932, 1955); Grant (1960a); Patterson and Brattstrom (1972); Medica et al. (1975); Jackson et al. (1976, 1978); Patterson (1977, 1978); Turner et al. (1987b); Germano (1988, 1990, 1992, 1994b)
Age determination and longevity	Miller (1932); Woodbury and Hardy (1948); Turner et al. (1987b); Germano (1988, 1992, 1994a)
Morphology	True (1882); Grant (1936a, 1937, 1944, 1960a, 1960b); Miller (1932, 1955); Woodbury and Hardy (1948); Nichols (1953); Shaw (1959); Auffenberg (1976); Auffenberg and Franz (1978a); Jackson et al. (1980); Bramble (1982); Good (1987); Crumly (1994); Germano (1993)
Reproduction	Miller (1955); Nichols (1957); Turner et al. (1981, 1986, 1987b); Luckenbach (1982); Germano (1994a)
Physiological processes	Dantzler and Schmidt-Nielsen (1966); Schmidt-Nielsen and Bentley (1966); McGinnis and Voigt (1971); Voigt (1975); Minnich (1977, 1979); Rosskopf (1980); Nagy and Medica (1986)
Disease and parasites	Harbinson (1937); Fowler (1976); Snipes et al. (1980); Rosskopf et al. (1981); Harper et al. (1982); Snipes and Biberstein (1982); Greene (1986)
Food habits	Burge and Bradley (1976); Hansen et al. (1976); Coombs (1979); Luckenbach (1982); Marlow and Tollestrup (1982); Jarchow (1987); Esque and Peters (1994); Oldemeyer (1994)
Behavioral ecology	Patterson (1971a, 1971b, 1971c); Black (1976); Burge (1977); Barrett and Humphrey (1986); Esque and Peters (1994)
Relocation	Cook et al. (1978); Weber et al. (1979); Berry (1986b)
Effects of human-induced disturbance	Berry (1978); Nicholson (1978); Nicholson et al. (1980); Turner et al. (1981); Nicholson and Humphreys (1981); Luckenbach (1982); Medica et al. (1985); Berry (1986c); Burge (1986); Woodman (1986); Oldemeyer (1994)
Demography	Berry (1976); Burge and Bradley (1976); Burge (1978); Turner et al. (1987b); Esque and Duncan (1989); Germano and Joyner (1989); Berry et al. (1990a, 1990b); Corn (1994)
Distribution	Auffenberg and Franz (1978b); Burge (1979, 1980); Hulse and Middendorf (1979); Karl (1980, 1981); Patterson (1982); Luckenbach (1982); Schneider et al. (1985); Walchuk and deVos (1985); Berry et al. (1986); Collins et al. (1986); Bury et al. (1994); Fritts and Jennings (1994); Germano et al. (1994)

about the desert tortoise is in unpublished reports, sometimes called "gray literature," and is exemplified by a review of recent research on desert tortoises in California (Berry 1986a). Of the 28 citations, 15 (54%) are unpublished reports, 7 (25%) are from the proceedings of The Desert Tortoise Council and one other conference (which were not reviewed by peers), 2 (7%) are government publications, and 4 (14%) are from journals with peer-reviewed papers. Thus, about 61% of the citations are unpublished reports and papers.

Similarly, unpublished reports on the desert tortoise occupy about 1.5 m (depth) of our file cabinet and weigh about 65 kg. These files include neither many recent contract reports nor 1,850 pages of the 1976–86 Proceedings of The Desert Tortoise Council and approximately 650 pages of the 1987–92 proceedings (not yet released). This volume of unpublished literature reflects the verbosity and generally low quality of studies of desert tortoises. Unpublished literature is not unique to desert tortoises and has been criticized in other disciplines, especially in the fisheries science (Collette 1990; Wilbur 1990).

Although several substantial papers appeared in the proceedings of the Desert Tortoise and Gopher Tortoise councils, the overall quality is uneven, and until recently most papers were not subject to reviews by anonymous peers. Also, time to publication is long (often over 5 years), and the date of publication is unclear—for example, the Proceedings of the Desert Tortoise Council from 1982 to the present have a copyright date that is the year of publication and not the years of the symposia.

Although both proceedings are suitable outlets for progress reports and discussions of conservation, we urge that original research be published in established journals and other outlets that solicit reviews of anonymous peers. Recently, The Gopher Tortoise Council decided to publish only a quarterly newsletter, including abstracts from its annual meeting. This is an effective means for disseminating information and discontinuing contributions to the gray literature.

The proliferation of unpublished reports is a disservice to the scientific and wildlife-management communities for several reasons. The trivialization of the literature results in reports that are unobtainable or difficult to secure, which in turn affects timely decisions in management and conservation. Federal and state governments list species as threatened or endangered based on the best available biological information that implies objective research and credible science. However, the gray literature is dominated by economic–political needs, advocacy viewpoints, or immediate cures of issues that can compromise effective long-term conservation of tortoises.

Geographic Coverage

Although important for long-term studies (Rose and Judd 1982; Judd and Rose 1989), most research on the Berlandier's tortoise has been limited to coastal areas of south Texas (Table 1). Parallel research is needed in other parts of the range of the Berlandier's tortoise at inland sites in Texas and Mexico. The distribution of the Berlandier's tortoise in Mexico is unsurveyed, although this area includes over half of the range. This area is important because recent changes in land-use patterns from pastoral to agricultural fields in Mexico may have already eliminated part of the tortoise's range (F. W. Judd, University of Texas-Pan American, Edinburg, Texas, personal communication).

Research on desert tortoises deserves similar criticism because most studies were on populations in creosotebush (*Larrea tridentata*)-scrub habitats of the Mojave Desert (Woodbury and Hardy 1948; Luckenbach 1982; Berry 1986a, 1986b; Berry et al. 1990a). However, this species exists in a wide variety of habitats locally and over its large range (Lowe 1990; Bury et al. 1994; Fritts and Jennings 1994; Germano et al. 1994). Little research has been conducted on populations in the Sonoran Desert, and almost no ecological studies have been done on the desert tortoise in the Sinaloan thornscrub and Sinaloan deciduous woodland in Mexico. As an example of our lack of knowledge, the range of the desert tortoise in Sonora and Sinaloa was recently described in almost 50% more sites than were previously known (Fritts and Jennings 1994).

Information on distributions of the North American tortoises is incomplete. In particular, we recommend thorough surveys of the ranges of the desert tortoise and the Berlandier's tortoise in the Mexican portion. The southernmost range of the desert tortoise in Sinaloa is not known (Patterson 1982; Fritts and Jennings 1994; Germano et al. 1994).

Suggested Research: Approaches and Questions

Estimates of Occurrence and Density

Although much information about the occurrence and relative abundance of tortoises is available (Auffenberg and Franz 1982; Luckenbach 1982; Berry 1986a), the current techniques of estimating population density need a better statistical design and efficient implementation. One of our major concerns is that walking transects is routinely used to estimate densities of desert tortoises (Nicholson 1978; Burge 1979, 1980; Karl 1981; Schneider et al. 1985; Collins et al. 1986), but these techniques yield only relative-abundance data. The results of sampling with linear transects have not been rigorously compared with known populations in varied habitats (e.g., valley, midslope, and rocky hills) or with results of other line–transect methods (Buckland et al. 1993).

Small populations of tortoises may be remnants of formerly larger populations or recent invaders of an area. Furthermore, tortoises may have a small population size or occupy marginal habitat today but not in future years or decades if weather or rainfall patterns change. We need to ask why certain areas have high, moderate, or low densities of tortoises and what determines population size.

Quantifications of habitats, vegetation, and soils that tortoises use are lacking. For example, most studies of population trends in desert tortoises are based on intensive sampling in small plots of about 2.6 km^2 (Berry 1986a, 1990a, 1990b). Because desert tortoises have large home ranges (Luckenbach 1982; Berry 1986a), we suggest that sampling in larger habitats (e.g., 10–20 km^2) and in all habitats (e.g., a valley and adjacent hillsides) with the same level of effort provides greater insight into the biology of the animals. This change may provide larger sample sizes and sufficient young individuals to estimate population sizes and may let investigators meet the assumptions of mark–recapture methods (White et al. 1982; Corn 1994).

Geographic Variation

We need a better understanding of the biology of each species from the major habitat or geographic portions of their ranges. For comparative studies, a minimum of three study sites determines the range and mean of variables. Representative areas can be selected to serve as intensive ecological research foci with an emphasis on year-to-year variation in population features, and animals on these sites need to be followed for 5-year periods or longer to detect environmental variability.

Many study sites for the desert tortoise exist in the Mojave Desert but are revisited at intervals of only 5 or more years (Berry 1990a, 1990b). To complement these sites, we suggest a set of permanent sites in the western Mojave Desert, eastern Mojave Desert, Sonoran Desert, and Sinaloan thornscrub for yearly sampling in representative habitats. Because precipitation patterns are unpredictable in most of these arid habitats, studies of populations must be continuous to assess responses of resident tortoises to environmental fluctuations.

More studies of the gopher tortoise are needed on islands off Florida and in Florida, Alabama, and Georgia and of peripheral populations in Mississippi and South Carolina. Established study sites exist in many of these areas (Douglass and Layne 1978; Lohoefner and Lohmeir 1981; Auffenberg and Franz 1982; Landers et al. 1982; Diemer 1992b; Mushinsky and McCoy 1994), and coordination among researchers and adequate funding are the key for the collection of comparative data and long-term studies.

For sampling the Berlandier's tortoise, sites need to be established in inland Texas and in Mexico. Study sites for the Bolson tortoise exist only in the southern portion of its range, but efforts are under way to expand work into other areas (Morafka and McCoy 1988; Adest et al. 1989a).

Studies of Habitats

Habitat quality and quantified habitat use are basic information for effective management of tortoises and their habitats. Moreover, this information is critical for defining the habitat requirements of the species in the next few decades because of rapid human exploitation in arid habitats.

Most surveys of the desert tortoise in the Mojave Desert were on bajadas (alluvial fans) and valley floors (Woodbury and Hardy 1948; Berry 1986a; Berry et al. 1990b) but not on the mountain slopes where tortoises also occur (Luckenbach 1982; Bury et al. 1994). Desert tortoises favor hills and mountain slopes in the Sonoran Desert (Burge 1980; Lowe 1990; Germano et al. 1994) and in Sinaloan thornscrub (Fritts and Jennings 1994). However, a lack of surveys in hills and on mountains in the Mojave Desert probably has biased our understanding of where tortoises live and how they use their habitats. Thus, we should be cautious in believing that desert tortoises prefer only flats or bajadas in some regions.

We suggest random surveys in all potential habitats, along elevational gradients, and across habitat types to determine how tortoises use resources in different plant communities and ecotones. Equal effort and quantitative information will best answer the question of habitat selectivity by tortoises. Then, in each habitat, the roles of soil and cover types that tortoises need have to be identified.

Life History Traits

Information is needed on the fecundity, longevity, and survivorship of all species, especially of southern populations (Sonoran and Sinaloa) of desert tortoises and inland populations of the Berlandier's tortoise (Texas, Nuevo Leon, and Tamaulipas). Much of the life history of the Bolson tortoise remains unknown. For comparisons across species, research methods must be standardized.

Studies of the fecundity of all species may be patterned after two models: desert tortoises (Turner et al. 1986) and freshwater turtles (Congdon and Gibbons 1990; Gibbons and Greene 1990; Vogt 1990). For the most convincing results, about 30 mature female tortoises have to be equipped with radio transmitters for relocation about every 10 days during the breeding season. Eggs in females can be detected with radiography (Turner et al. 1986; Rose and Judd 1989; Diemer and Moore 1994) or perhaps with sonograms (Kuchling 1989). Radiographing may have to be done for 2–3 months until no more eggs are observed. Besides radiographing mature females, smaller individuals must be radiographed to determine the size and age at which females can first produce eggs. This basic information has not been quantified for any species of tortoise. Sexual maturity has to be better quantified by sizes and ages of males that engage in sexual behavior or by the detection of sperm. Cloacae can be injected with water to flush sperm into vials for later examination in the laboratory.

The ages and longevity of individuals are important for determining population viability. Counts of growth rings are reasonably accurate for aging North American tortoises as old as 20–25 years (Landers et al. 1982; Germano 1988; Zug 1991). Thin scute sections may be useful for aging older individuals (Germano 1992), but this technique and other nondestructive methods of aging living tortoises have not been finalized. Scute rings of most tortoises less than 20 years old can be counted in the field and compared with those of individuals whose ages are known from mark–recapture studies.

Survivorship in wild animal populations is difficult to determine. Large sample sizes are needed to accurately determine rates and patterns of hatchling and juvenile survivorship, but young tortoises are difficult to find in the wild (Luckenbach 1982; Judd and Rose 1983; Berry and Turner 1987; Adest et al. 1989a). Information from prior reports (Berry and Turner 1987) and from reports in this collection (Morafka 1994; Tom 1994; Wilson et al. 1994) indicates that the ecology of hatchlings and small juveniles is markedly different from the ecology of adults—for example, small tortoises are secretive and rarely active away from cover. The absence of reliable techniques to locate juveniles also precludes assessment of age structure and trends in numbers of tortoises in populations.

Several new techniques may increase the captures of young tortoises. Dogs have been used successfully to locate box turtles (*Terrapene carolina*; Schwartz et al. 1984) and may be able to locate young desert tortoises. Intensive surveys at relatively small study sites (4.0–10.8 ha) revealed that juveniles comprised 38–60% of gopher tortoise populations (Diemer and Moore 1994). Furthermore, after young tortoises are located, they can be followed with radiotelemetry for extended periods (Wilson 1991; Tom 1994; Wilson et al. 1994) to obtain much information on their biology.

Analyses of the age and size classes of all captured individuals in an area can identify the population structure (Aguirre et al. 1979; Auffenbreg and Iverson 1979; Judd and Rose 1983; Germano and Joyner 1989; Berry et al. 1990a, 1990b; Diemer 1992a; Germano 1992; Mushinksy and McCoy 1994). Many populations of desert tortoises seem to consist of mostly adults and only few or no juveniles. This structure is sometimes assumed to represent populations with little or no recruitment (Berry 1976, 1986a, 1986b). However, there are alternative explanations for skewed adult-age or size structure in tortoise populations.

A disproportionate number of adults may be due to a subjective division of desert tortoises into general categories (Berry et al. 1990b): juvenile 1, 2; immature 1, 2; subadult; and adult 1, 2. Juvenile and immature categories are transitory and short stages, including only 1 or few years of life. The adult group is large (60–75% of most samples) but also more permanent and has many age or size classes of tortoises (Figure). The adult category spans 20–30 or more years of life because tortoises are long-lived (Woodbury and Hardy 1948; Bury 1982; Gibbons 1990), although adult desert tortoises in some populations may not live as long as earlier thought (Germano 1992, 1994a).

There is a tendency to be concerned about few juveniles and immatures in populations (Berry and Turner 1987; Adest et al. 1989a; Berry et al. 1990b), mostly because they are compared with adults. However, we need to recognize that adult survivorship may be equally or more important for the continuity of a population over the long term. Also, skewed distribution frequencies do not always equal declining populations. In chelonians, mortality is high in hatchlings, moderate to high in juveniles, and low in adults (Bury 1979; Frazer et al. 1990). Adult chelonians often live a long life, and population structures are skewed toward adults (Gibbons 1990).We suspect that recruitment in tortoises may be naturally low and only 3–5% of the total population per year. More likely, we suggest that recruitment is low or nonexistent until there is a combination of favorable factors every few years or perhaps decades. Juvenile cohorts probably occur when for 2 or more years conditions are optimal (e.g., normal to high precipitation), a condition that is probably needed for the survival of eggs, hatchlings, and young. Thus, uneven numbers of cohorts enter the population and in time compensate for adult losses. Such a pattern of survivorship is expected in environments such as deserts where weather is unpredictable and precipitation is spotty and low.

Use of Plants

Although the diets of most species of tortoises (Tables 1–4) have been studied and most consist of annual plants, few investigators examined geographic variation in diet and food selection. Concurrent with food studies of tortoises, we recommend studies of yearly changes in the life histories of tortoises that are related to the production of plants that tortoises eat (Oldemeyer 1994) and the evaluation of nutritional values of food plants (Esque and Peters 1994).

Employment of the Scientific Method

Many studies purport to be—but are not—scientific inquiries because they are unpublished and lack rigor. For example, advocacy groups want

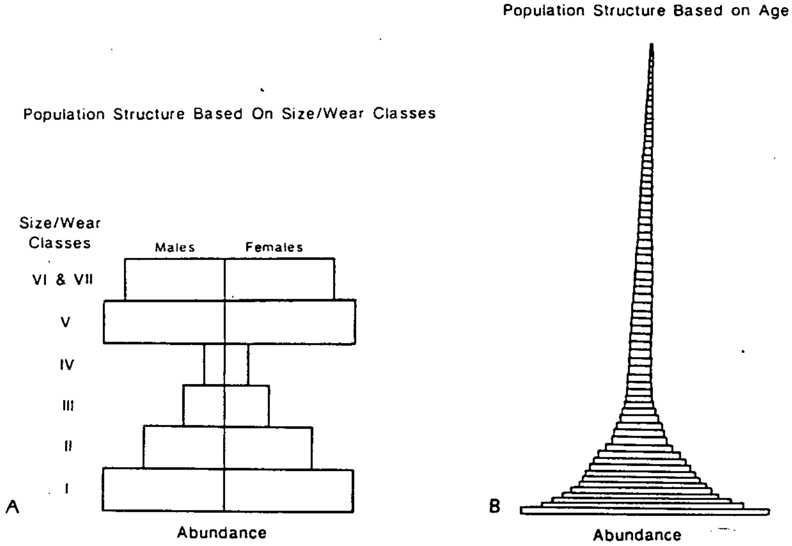

Figure. Comparison of two methods to estimate age and size structure in tortoises: (A) Classes based on shell size and wear categories (I–VII), which tend to emphasize a high proportion of adults in populations; (B) Classes from age (based on count of years on scute annuli), which indicate many increments and greater equability (e.g., the pattern is that of a tall pyramid).

results that support their stance or predetermined ideas. In such cases, we believe that there is no need to pretend that biological studies are being performed. The scientific method is based on rigorous statistical testing of hypotheses, which cannot predict the results of studies (i.e., their outcome is unknown).

The necessity for the application of the scientific method to studies of tortoises seems obvious but needs constant reinforcement. In particular, the desert tortoise is now listed as a threatened species in the Mojave Desert, and many quarters are campaigning for conservation and economic and political interests. Although these pressures are intense, there remains a need for scientific inquiry that is exemplified by objectivity in the study design and by high productivity of peer-reviewed publications. Surveys are important but probably are best performed by contract funding (e.g., consulting firms). Scientific research is better performed by independent investigators (e.g., university professors, research scientists) who test hypotheses.

We found that resource managers generally abhor duplication of effort as a waste of money. Too often, studies are funded for only one area or for one sampling period. However, the replication of studies is a crucial part of the scientific method. For example, three or more study sites are a minimum sample for statistical analyses (i.e., to calculate a range and mean value). The scientific study of animals is an analysis of variation because complex biological systems change over time and space.

Lastly, the employment of the scientific method for management must be addressed. Conservation is wise management of natural resources, and conservation depends on sound biological information. However, the mixing of advocacy with scientific goals may cloud each endeavor. Unlike science that is based on the objective collection and testing of data, ideas, and hypotheses, advocacy is usually biased with emotions and social or economic convictions.

When we recognize them from the outset and clearly state what we do, advocacy roles and objectivity (science) can be compatible human traits or endeavors. Better, separation of these disciplines may be essential for clarity of purpose, sound interpretations, and improved biology and conservation of tortoises and habitats.

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1. Life History and Status of the Endangered Cui-ui of Pyramid Lake, Nevada, by G. Gary Scoppettone, Mark Coleman, and Gary A. Wedemeyer. 1986. 23 pp.
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